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Learning and feedback processing: Contextual influences and clinical implications for obsessive-compulsive disorder

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SUMMARY

Motivational biases describe a tendency in learning and decision-making to perform an action to obtain a reward and to withhold an action to avoid punishment. These biases have been linked to striatal mechanisms and are generally considered robust across task contexts, although alterations have been reported in several mental disorders. Although generally thought to reflect anticipatory Pavlovian response biasing of action selection, recent accounts suggest that they also involve biased instrumental learning of response-outcome associations. This raises the possibility that motivational biases may already emerge during feedback evaluation and processing, possibly reflected in the feedback-related negativity/reward positivity (FRN/RewP) of the event-related potential. Across four consecutive studies, this dissertation investigated motivational biases across different learning contexts and the role of feedback processing in these biases, while also exploring their clinical relevance in obsessive-compulsive disorder (OCD), alongside broader alterations in instrumental learning and feedback processing.

Despite previous evidence highlighting their robustness, Study I demonstrated that motivational biases were attenuated when learning from emotional compared to neutral facial cues. Study II found that motivational biases emerged independently of feedback timing, despite learning from delayed feedback being associated with reduced striatal engagement. It also provided only limited support for a substantial role of biased instrumental learning to motivational biases while motivational biases were not reflected in altered feedback processing.

Study III explored instrumental learning and feedback processing in OCD, showing impaired learning, across active and observational task contexts, increased indecisiveness and altered reward processing in the FRN/RewP. Finally, Study IV investigated motivational biases in OCD but found no evidence for alterations in OCD, although they were generally attenuated for observational compared to active learning. Consistent with Study II, motivational biases were not reflected in altered feedback processing. Interestingly, however, OCD patients showed altered self-other distinction in the FRN/RewP for self- versus other-related outcomes.

Taken together, while partially sensitive to the learning context, motivational biases persisted across contexts, highlighting them as a particularly robust

hallmark of learning and decision-making, that may most substantially reflect a Pavlovian response bias on action selection. Findings from OCD patients suggest that, although associated with alterations in learning and decision-making, these alterations are not general but rather context-dependent, converging with the notion of cognitive inflexibility in OCD.

LIST OF ABBREVIATIONS

CON	emotional-congruent
CR	conditioned response
CS	conditioned stimulus
CSTC	cortico-striato-thalamo-cortical
DA	dopamine
EEG	electroencephalography
ERN	error-related negativity
ERP	event-related potential
fMRI	functional magnetic resonance imaging
FRN/RewP	feedback-related negativity/reward positivity
GA	grand average
GAL	go to avoid-losing
(G)LMM	(generalized) linear mixed-effects model
GPi	globus pallidus interna
GW	go to win
HC	healthy control
INC	emotional-incongruent
MCC	midcingulate cortex
MWT-B	Mehrfachwahl- Wortschatz-Test B
NEU	neutral
NGAL	nogo to avoid-losing
NGW	nogo to win
OCD	obsessive-compulsive disorder
OFC	orbitofrontal cortex
PE	prediction error
PIT	Pavlovian-to-instrumental transfer
PRO	predicted response outcome
RL	reinforcement learning
SAD	social anxiety disorder
SNr	substantia nigra pars reticulata
S-S/S-R-O	stimulus-stimulus/stimulus-response-outcome
UCR	unconditioned response
US	unconditioned stimulus
vmPFC	ventromedial prefrontal cortex

CONTENTS

1 INTRODUCTION _____ **1**

Principles of learning and decision-making _____ 1

Neural signatures of goal-directed behavior _____ 11

Modulators of learning and feedback processing _____ 21

Clinical implications: Obsessive-compulsive disorder _____ 24

Research gap, aim & objectives _____ 28

2 STUDY SUMMARIES _____ **31**

General procedures _____ 31

Study I: Emotional cues reduce Pavlovian interference in feedback- based go and nogo learning _____ 35

Study II: Motivational biases in go and nogo learning from immediate versus delayed feedback _____ 40

Study III: Altered reward processing in obsessive-compulsive disorder: Insights from active and observational learning _____ 48

Study IV: Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder _ 55

3 GENERAL DISCUSSION _____ **61**

Insights into the nature of motivational biases _____ 61

Alterations in learning and feedback processing in OCD _____ 68

Insights into the functional significance of the FRN/RewP _____ 73

Limitations _____ 76

Conclusion _____ 78

BIBLIOGRAPHY _____ **79**

AFFIDAVIT _____ **113**

DECLARATION OF AI USE _____ **114**

ACKNOWLEDGEMENTS _____ **115**

APPENDIX _____ **116**

1 INTRODUCTION

Principles of learning and decision-making

Behavioral learning mechanisms

From motor development and language acquisition to the formation of knowledge and advanced skills, all these capacities are substantially shaped by learning. Although there is no universally accepted definition, most influential learning theories agree that learning refers to changes in behavior or its underlying mechanisms that result from experience and interactions with the environment (e.g., de Houwer et al., 2013; Domjan, 2014; Hilgard & Bower, 1975; Lachman, 1997; for an overview see Schneider, 2024).

In particular, associative learning, i.e., predicting which stimuli likely co-occur or which consequences follow which behaviors, helps us navigate our environment and interact with it more efficiently. Yet, albeit learning carries an overall positive association, it can also contribute to the development and maintenance of self-defeating behaviors (e.g., Krypotos et al., 2015; Maier & Seligman, 2016; Shechner et al., 2014). A major distinction in behavioral learning mechanisms can be drawn between Pavlovian and instrumental learning, which, although primarily derived from animal research, are also considered to extend to humans.

Pavlovian learning

Pavlovian learning is rooted in classical conditioning, discovered around the 20th century by Russian physiologist Ivan P. Pavlov.[1] In his pioneering work, Pavlov (1927) demonstrated that repeatedly pairing an *unconditioned stimulus* (US; e.g., food), which inherently elicits an *unconditioned response* (UR; e.g., salivation), with a neutral *conditioned stimulus* (CS; e.g., tone), eventually causes the CS alone to elicit the innate response, thereby becoming a *conditioned response* (CR). Originally described in simple reflexes, Pavlovian learning has been shown to apply to a wide range of innate and evolutionarily inherited CRs, including emotional responses (e.g., Maren, 2001) but also prepotent approach to reward-predictive and withdrawal from punishment-predictive

[1] Note, however, that an instance of classical conditioning was independently discovered by American psychologist Edwin B. Twitmyer around the same time as Pavlov (see Twitmyer, 1974).

cues (Rangel et al., 2008). Pavlovian responses directed toward the CS have been referred to as *sign-tracking* (or sometimes *autoshaping*; Brown & Jenkins, 1968; Hearst & Jenkins, 1974), with the CS acquiring incentive motivational value (Berridge, 2000; Flagel et al., 2009). Yet, Pavlovian responses can also be directed toward the US, then referred to as *goal-tracking*, with evidence from animal research indicating that the susceptibility for sign- versus goal-tracking may vary across individuals (Flagel et al., 2009; Nasser et al., 2015).

In an attempt to formalize how CS-US associations are learned, Rescorla and Wagner (1972) famously proposed that learning is driven not by the US itself but by the *prediction error* (PE), i.e., the difference between the actual US and the predicted US based on the association strength of the CS towards the US (also see Wagner & Rescorla, 1972). Importantly, this framework suggests that Pavlovian learning relies on stimulus-stimulus (S-S) learning, in which the Pavlovian response is elicited *indirectly* via the US-predictive CS. This is different from stimulus-response (S-R) learning, which presumes Pavlovian responses to be *directly* elicited by the CS. Indeed, the notion that Pavlovian learning involves S-S rather than S-R learning is supported by evidence showing that Pavlovian responses to the CS decreased when the US was devalued by satiation (e.g., Holland & Rescorla, 1975).

Instrumental learning

While Pavlovian learning can explain behavior that is elicited by predictive relationships between *stimuli*, over which we have no direct control, it fails to explain more deliberate behaviors. Filling this gap, instrumental learning emphasizes how behavior is shaped by its outcomes, enabling us to control our environment in accordance with our needs and desires (see Dickinson, 1994). As stated by the *law of effect*, proposed by American psychologist Edward L. Thorndike, behaviors followed by satisfying consequences become more likely to be repeated, while those followed by unsatisfying consequences are less likely to recur in a similar context (Thorndike, 1927). Appetitive consequences that increase the likelihood of behavior are typically referred to as *reinforcement*, whereas those with aversive consequences that decrease the likelihood of behavior are referred to as *punishment*. Depending on whether reinforcement or punishment involves the presentation or removal of a stimulus, it can be further classified as positive or negative reinforcement or punishment, respectively (see e.g., McConnell, 1990).

While Thorndike conceived instrumental learning as S-R learning, where outcomes are merely *modulatory* and not itself part of the learned association, instrumental learning may also involve response-outcome (R-O) or even stimulus-response-outcome (S-R-O) representations (Domjan, 2014). With these extensions, instrumental learning can support adaptive and goal-directed decision-making by flexibly selecting those behaviors that likely yield appetitive, and avoid those that likely yield aversive consequences.

However, for outcomes to effectively shape behavior, they must carry motivational value, i.e., individuals must perceive them as appetitive or aversive. The value of such outcomes can either be innate as for unconditioned (or primary) reinforcers (e.g., food; for a detailed overview see Table 1 in Rolls, 2023), or must be learned via association with an unconditioned reinforcer, rendering them a conditioned (or secondary) reinforcer (e.g., smell of food). When associated with an increasing number of (unconditioned) reinforcers, conditioned reinforcers can eventually become *generalized* (e.g., money), making them even more powerful due to their reinforcing properties across different contexts (Daniel & Pollmann, 2014; Skinner, 1953).

Behavioral control systems

Given the variety of learned associations, what eventually *determines* behavior in a certain environmental context is not always straightforward. Within the cognitive sciences, dual-system theories have gained immense popularity, broadly converging on the idea of two antagonistic systems: one rapid, autonomous and another slow but controlled (Evans, 2008; Evans & Stanovich, 2013; Frankish, 2010). Drawing on the learning mechanisms introduced above, a related distinction has been made between a Pavlovian and instrumental control system (Miller & Konorski, 1969; Mowrer, 1947; Rescorla & Solomon, 1967; see also Daw & O'Doherty, 2014). Within this conceptualization, the Pavlovian system reflects fast, reflexive and evolutionary-sophisticated responses, whereas the instrumental system is considered slower but more flexible, enabling adaptive and goal-directed behavior.

Importantly, note that an alternative distinction has been made between *stimulus-driven* (or *habitual*) and *goal-directed* control of behavior, given that the instrumental system involves both stimulus-driven S-R *and* goal-directed (S-)R-O associations (Balleine & O'Doherty, 2010; Dickinson, 1985; O'Doherty et al., 2017). Accordingly, instrumental behavior is considered goal-directed only if it

encodes a causal R-O association, such that a behavior is performed with the *intention* of obtaining or avoiding a particular outcome in accordance with the current goals (de Wit, 2017; see also Heyes & Dickinson, 1990). Most archetypically, such goals refer to maximizing cumulative reward (Dayan & Daw, 2008). Conversely, with S-R associations, instrumental behavior does not involve goal (or outcome) representations, making them more habitual and inflexible to changes in outcome contingencies (O'Doherty et al., 2017).

Importantly, stimulus-driven control is particularly characteristic of Pavlovian learning, where Pavlovian cues evoke automatic Pavlovian responses, such as approach for reward-predictive and avoidance for punishment-predictive cues (Rangel et al., 2008). Moreover, although less flexible than the instrumental system, also the Pavlovian system may involve at least goal-*oriented* behaviors, as suggested by goal-tracking (cf. Flagel et al., 2009).

Taken together, while instrumental and Pavlovian learning are more readily associated with goal-directed and stimulus-driven control of behavior, respectively, both forms of learning contribute to either mode of behavioral control.

Pavlovian-instrumental interactions

Behavioral control systems do not operate in isolation, but dynamically interact and compete for control (Daw et al., 2005; Dayan et al., 2006; Dorfman & Gershman, 2019; O'Doherty et al., 2017). These interactions can often be synergistic, and hence facilitate adaptive decision-making (e.g., Estes, 1948; Lovibond, 1983; also see Mahlberg et al., 2021). For instance, this would be the case if both the instrumentally required response, and the automatic Pavlovian response promote the same (or complementary) behavior, such as when encountering a snake prompts instant Pavlovian withdrawal, thereby preventing possible harm.

In certain situations, however, interactions between behavioral control systems may conflict, and hence become maladaptive (Breland & Breland, 1961; O'Doherty et al., 2017). This has been famously illustrated by Hershberger's *"room through the looking-glass"* experiment, in which food-deprived cockerel chicks aimed to access a food source, that moved toward the same direction as the chicks, but twice as far. Crucially, the chicks failed to learn that they had to move away from the food source in order to gain access to it, but instead "chased" the food source away (Hershberger, 1986). Accordingly, Pavlovian

approach to the reward-predictive food source interfered with the instrumentally required response ("moving away"), hence involving a Pavlovian-instrumental conflict, exemplifying that the Pavlovian system can sometimes *bias* decision-making of the instrumental system. Although there may also exist interactions among other control systems (e.g., goal-directed versus stimulus-driven), this dissertation will primarily focus on more basal Pavlovian-instrumental interactions.

Pavlovian-to-instrumental transfer

Cooperative Pavlovian-instrumental interactions have been typically studied using the (appetitive) Pavlovian-to-instrumental transfer (PIT) paradigm (for an overview see Cartoni et al., 2016). At the core, the PIT paradigm involves three distinct phases. First, there is a *Pavlovian learning phase,* in which participants learn to associate a Pavlovian CS with a reward. Second, in an *instrumental learning phase*, which may either precede or succeed the Pavlovian learning phase, participants learn to associate an instrumental response with the same reward, without the CS being present. Finally, a *PIT test phase* aims to examine the influence of the Pavlovian CS on instrumental responding, while participants are free to perform the instrumental response during occasional presentations of the CS. What is typically observed in this paradigm is that the presentation of the CS *increases the likelihood* of engaging in the instrumental response, even though the CS and the instrumental response were never directly paired during learning (e.g., Bray et al., 2008; Nadler et al., 2011; Paredes-Olay et al., 2002; Talmi et al., 2008; Watson et al., 2014).

Pavlovian-instrumental conflicts

The PIT paradigm has several shortcomings in unveiling the full spectrum of Pavlovian-instrumental interactions. As stated above, it typically focuses on cooperative Pavlovian-instrumental interactions (see Cartoni et al., 2016), thereby often neglecting Pavlovian-instrumental conflicts that may interfere with goal-directed behavior. Although there is also an aversive counterpart that technically allows examining such Pavlovian-instrumental conflicts, appetitive and aversive PIT are only rarely studied in combination (but see Huys et al., 2011). Most critically, however, the PIT paradigm separates Pavlovian and instrumental learning into distinct experimental phases, and therefore does not involve *incidental* Pavlovian and instrumental learning. As a consequence, Pavlovian-instrumental interactions can be assessed only *after* but not during

learning through the PIT test phase, which typically omits outcome presentation and may therefore be further influenced by extinction processes (e.g., Bray et al., 2008; Nadler et al., 2011).

In an attempt to overcome these limitations, Guitart-Masip et al. (2011) developed a motivational feedback learning paradigm, the *orthogonalized go/nogo task*, aiming to investigate Pavlovian-instrumental interactions directly during learning. In this paradigm, action (*approach*, *withdrawal*) and valence (*reward*, *punishment*) are orthogonalized into four cued conditions: go to win (GW), go to avoid-losing (GAL), nogo to win (NGW) and nogo to avoid-losing (NGAL), in which participants are correspondingly required to press a button ("go") or withhold a button press ("nogo") to either obtain a reward ("win") or avoid punishment ("avoid-losing").

In GW and NGAL, the innate Pavlovian response *aligns* with the required instrumental response (i.e., reward-predictive approach/punishment-predictive withdrawal), hence typically facilitating learning and decision-making. Conversely, in GAL and NGW, the innate Pavlovian response *interferes* with the required instrumental response, that is why they have been referred to as Pavlovian conflict conditions (e.g., Albrecht et al., 2016; Cavanagh et al., 2013). Using this paradigm, it has been robustly shown that Pavlovian-instrumental interactions manifest in the asymmetric coupling of action and valence, with increased performance in non-conflict relative to conflict conditions, i.e., GW>GAL and NGAL>NGW (e.g., Cavanagh et al., 2013; Guitart-Masip, Duzel, et al., 2014; Guitart-Masip et al., 2011). This phenomenon has been referred to as the *Pavlovian bias*[2], hence suggesting a Pavlovian mechanism during action selection whereby the anticipation of reward or punishment favors action invigoration or suppression, respectively (e.g., Guitart-Masip, Duzel, et al., 2014; Guitart-Masip, Huys, et al., 2012). However, as the underlying mechanisms are not yet fully resolved, the more agnostic term *motivational biases* was established (e.g., Algermissen et al., 2024; Richter et al., 2021; Scholz et al., 2022), which I will adopt for this dissertation.

[2] Notably, while the term *Pavlovian bias* is often used in the singular, some authors have argued that it may be better conceptualized as reflecting separable, valence-specific Pavlovian bias*es*, e.g., reward-based invigoration and punishment-based suppression (Cavanagh et al., 2013) or reward bias and avoid-loss bias (Eisinger et al., 2020).

Reinforcement learning: Computational foundations of learning and decision-making

Thus far, I have reviewed the core learning mechanisms that shape behavior and discussed that interactions among these mechanisms and underlying behavioral control systems can sometimes facilitate or hinder adaptive and goal-directed behavior. While generally striving to maximize expected cumulative reward (Dayan & Daw, 2008), it is inevitable to learn which stimuli and/or actions predict appetitive or aversive consequences. A central challenge is therefore how *value* is assigned to these stimuli and/or actions and how these value representations are updated during learning. Reinforcement learning (RL; Sutton & Barto, 2018) provides a computational framework for addressing this challenge.

Principles

RL is a machine learning approach used in computer science to optimize an agent's decision-making in a dynamic environment via feedback. Because of its conceptual origins in psychology, it has been increasingly adopted to model learning and decision-making in psychological and neuroscientific research (Subramanian et al., 2022). Although there are various RL algorithms (for an overview see AlMahamid & Grolinger, 2021), the most common algorithms used in cognitive neuroscience are based on the Rescorla-Wagner model—specifically, the idea that learning is not driven by reward or punishment itself but by the PE (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972). Originally, developed to formalize the learning of Pavlovian CS-US associations, this model assumes[3]

$$\Delta V = \varphi(\lambda - V)$$

where on a given conditioning trial, V represents the association strength of the CS to the US, and λ denotes the learning asymptote, i.e., the maximal association strength supported by the actual US, while $\varphi \in [0, 1]$, serves as a learning rate. Accordingly, learning is reflected as the change in the association strength (ΔV), which is driven by the PE ($\lambda - V$), i.e., the difference between the actual US (λ) and the expectation of the US, represented by its current association strength (V), scaled by the learning rate (φ). Learning hence

[3] Importantly, the equation provided here captures only the core theoretical idea of the Rescorla-Wagner model. The original model formulation extends this principle to compound CSs and involves separable learning rates for the CS and US.

proceeds as long as $\lambda \neq V$, while the PE monotonically decreases during the course of learning.

In RL, this principle has been adopted as follows:

$$V_{t+1}(s_t) = V_t(s_t) + \alpha\,(r_t - V_t(s_t))$$

where V represents the expected value of state s (e.g., seeing a cue) at time t. State values $V(s)$ are learned and updated via the PE, i.e., the difference between the actually received outcome (r) and the expected value of the current state ($V(s)$), scaled by a learning rate ($\alpha \in [0, 1]$). The learning rate captures the impact of PEs on value-updating and hence the speed of learning (e.g., Zhang et al., 2020). Given outcomes are aversive or appetitive, i.e., $r \in \{-1,1\}$, -PEs (<0) reflect worse-than-expected outcomes, whereas +PEs (>0) reflect better-than-expected outcomes. Aligning with the original Rescorla-Wagner model, this formula refers to learning outcome predictions as in Pavlovian S-S associations—i.e., independent of any decision-making—hence providing a computational framework for how (Pavlovian) *cues* are assigned value based on their outcomes.

The same principle can also be applied in order to formalize how *actions* are assigned value, i.e.:

$$Q_{t+1}(a_t, s_t) = Q_t(a_t, s_t) + \alpha\,(r_t - Q_t(a_t, s_t))$$

where Q denotes the expected value for action a being performed in state s at time t, thereby representing a state-action value, corresponding to learning of instrumental S-R-O associations. Apart from that, Q is computed analogously to V, i.e., updated by the PE and scaled by a learning rate $\alpha \in [0, 1]$. Generally speaking, the PE hence reflects the difference between the actual and predicted action outcome, where +PEs reflect better-than-expected outcomes and -PEs reflect worse-than-expected outcomes.

Notably, the value functions introduced so far correspond to the most rudimentary case of RL, therefore sometimes referred to as simple RL (e.g., Zhang et al., 2020). Building on this basic formulation, more advanced models can be derived by, e.g., implementing additional parameters such as dual learning rates for +/-PEs (e.g., Frank et al., 2007), updating not only chosen but also unchosen options (e.g., Palminteri et al., 2017), or by incorporating expected *future* outcomes as in temporal difference learning (e.g., Alexander & Brown, 2011).

Choice stochasticity

Importantly, however, the action with the highest expected value is not necessarily selected on every occasion. Instead, behavior is often stochastic, and exploring outcomes gained through alternative actions can sometimes be useful, e.g., when it leads to the discovery of even larger rewards. A common way to deal with choice stochasticity in RL is by applying a softmax decision rule (cf. Daw, 2011),

$$p(a_t|\, s_t) = \frac{\exp\big(\beta * Q_t(a_t, s_t)\big)}{\sum_{a'} \exp(\beta * Q_t(a', s_t))}$$

where the probability to perform action a in state s (at time t) depends on an inverse temperature parameter $\beta \in (0, +\infty)$, with lower values corresponding to more exploratory and higher values to more deterministic decision-making, such that β models the exploration-exploitation tradeoff. Again, this is only one possibility (and the method of choice in this dissertation), and there are many alternative ways to model choice stochasticity in RL.

Modeling motivational biases

Beyond choice stochasticity, also motivational biases can prevent engaging in the action that is associated with the highest expected action value. Aiming to unveil the computational mechanisms of motivational biases, Guitart-Masip, Huys, et al. (2012) proposed an extended RL model that successfully captured the behavioral patterns of motivational biases in the orthogonalized go/nogo task.

Crucially, in their update equation,

$$W_t(a_t, s_t) = \begin{matrix} Q_t(a_t, s_t) + b + \pi V_t(s_t) & if\ go \\ Q_t(a_t, s_t) & else \end{matrix}$$

$Q(a, s)$ is transformed into a state-action weight $W(a, s)$. For go (but not nogo) choices, two bias parameters, b and π, are added before W is eventually passed through a (squashed) softmax function.[4] Accordingly, $b \in (-\infty, +\infty)$ denotes a go bias, where more positive values indicate a stronger (but valence-independent) tendency toward action execution ("go") and more negative

[4] The softmax function used to model choice stochasticity differed slightly from that described earlier, as did the calculation of Q- and V-values. To keep the presentation concise, and because motivational biases have also been successfully modeled using the RL algorithms introduced above (see Chapter 2, Study II), I focus here only on the substantial extension most relevant to modeling motivational biases.

values a stronger tendency toward action suppression ("nogo"). Most, importantly, $\pi \in (-\infty, +\infty)$ constitutes a Pavlovian (response) bias parameter, which scales the incidentally learned Pavlovian state value $V(s)$, such that higher values promote action execution in anticipation of reward while concurrently inhibiting action execution in anticipation of punishment. Accordingly, this model conceptualizes motivational biases as biased action selection, arising through (at least) two distinguishable computational processes, i.e., a general go bias as well as a valence-dependent Pavlovian response bias. This or extended variants of this RL model have since successfully applied to model motivational biases (e.g., Algermissen et al., 2024; Swart et al., 2018; Swart et al., 2017).

Enabling goal-directed control through performance monitoring

Although we generally strive to act in an adaptive and goal-directed manner, we are not always successful. For instance, we may occasionally make decisions that turn out to be wrong and lead to unsatisfying consequences, e.g., as a consequence of motivational biases. Detecting and evaluating such goal-deviating states and behaviors as well as properly adjusting future behavior in accordance with our goals and needs therefore constitutes a core capacity for learning and adaptive decision-making.

Within cognitive neuroscience, *performance monitoring* has become established as an umbrella term that subsumes all (neuro-)cognitive, affective and somatic processes that support goal-directed and adaptive behavior (see Peterburs & Desmond, 2016; Ullsperger, 2017; Ullsperger, Danielmeier, et al., 2014; Ullsperger, Fischer, et al., 2014). At its core, performance monitoring involves the detection and evaluation of goal-deviating states and behaviors that signal the necessity, magnitude and type of adaptation required for goal achievement and is therefore closely tied to cognitive control (Ullsperger, 2017; Ullsperger, Danielmeier, et al., 2014). Accordingly, while performance monitoring is a continuous and dynamic process that refers to separable mechanisms supporting goal-directed behavior, it has been most consistently referred to error and feedback monitoring (Ullsperger, Fischer, et al., 2014). Yet, while error monitoring is particularly relevant *after* learning in order to maintain current performance, feedback monitoring is crucial *during* learning as it supports goal-directed behavior by allowing adaptation to new or changing environments. Accordingly, this dissertation focuses on performance monitoring in terms of the detection, evaluation and adaptation to feedback. Because behavioral

measures can only provide indirect inferences about these processes, the next section aims to provide an overview of the neural signatures underlying these processes to enable goal-directed learning and decision-making.

Neural signatures of goal-directed behavior

Dopamine and reinforcement learning

As a key neuromodulator, dopamine (DA) has been widely implicated in learning and decision-making (Wise, 2004). Most densely located in the substantia nigra pars compacta and ventral tegmental area of the mesencephalon, dopaminergic neurons project to various cortical and subcortical areas—most notably to the frontal cortices and the striatum (see e.g., Björklund & Dunnett, 2007a; Glimcher, 2011). While originally linked primarily to motor function and/or motivation (Berke, 2018; Björklund & Dunnett, 2007b; Salamone & Correa, 2012), our current understanding of DA is profoundly shaped by the discoveries concerning its role in reinforcement learning, paved by German-British neuroscientist Wolfram Schultz (Schultz, 1998; Schultz et al., 1993; Schultz et al., 1997).

Among his groundbreaking work, summarized in Schultz et al. (1997), Schultz and colleagues found that when macaques were presented with an appetitive or rewarding stimulus, mesencephalic DA neurons responded with phasic increases in firing activity. After various repetitions, however, in which the rewarding stimulus was preceded by an environmental cue, these phasic increases in DA firing activity no longer occurred at the time of the reward but already at the time of cue onset, resonating with the formation of a CS (cue)-US (reward) association. Notably, when an anticipated reward was omitted, DA neurons exhibited reduced firing activity below baseline. Collectively, these findings indicated that DA did not reflect reward itself, but the *PE*, i.e., a +PE with increased firing following unexpected rewards, and a -PE with decreased firing below baseline for unexpected reward omission (or punishment). The notion of such PEs is central to RL (Sutton & Barto, 2018), thereby qualifying DA as a neural RL signal.

Value representations in the brain

Mesencephalic DA alone does not yet explain how goal-directed behavior is implemented. However, DA projections reach widely distributed (sub)cortical areas, that contribute not only to the computation and representation of value

but also to goal-directed behavior. In the following subsections, I summarize some of the key structures involved in these processes.

Striatum

The striatum constitutes the largest part and primary input structure of the basal ganglia. It is the main projection target of mesencephalic DA neurons, while also receiving input from the cerebral cortex and thalamus (Delgado, 2007; Haber, 2014). Anatomically (and functionally), the striatum can be segregated into a dorsal and ventral component[5]: the dorsal striatum entails the caudate and putamen, whereas the ventral striatum primarily consists of the nucleus accumbens, though also including parts of the putamen and ventral caudate (Delgado, 2007).

Both the dorsal and ventral striatum have been implicated in learning and decision-making (Balleine et al., 2007; Daniel & Pollmann, 2014; Delgado, 2007; Haber, 2011). For instance, evidence from functional magnetic resonance imaging (fMRI) showed differential sensitivity to reward and punishment in both the dorsal and ventral striatum (Delgado et al., 2003; Delgado et al., 2000; Ullsperger & Von Cramon, 2003), while the dorsal striatum additionally encoded (outcome) magnitude (Delgado et al., 2003; see also Delgado et al., 2004). Interestingly, functional differences between the dorsal and ventral striatum appear to depend on agency. In seminal work by Tricomi et al. (2004), it has been shown that activity in the caudate, as part of the dorsal striatum, was not sensitive to reward itself but depended on the *action* that produced the reward. Aligning with that, it has been demonstrated that, whereas the ventral striatum encoded PEs in both Pavlovian S-O and instrumental S-R-O learning, the dorsal striatum reflected PEs only in instrumental S-R-O learning (O'Doherty et al., 2004). This aligns with evidence suggesting a role of the dorsal striatum in mediating action selection and the ventral striatum in learning (Atallah et al., 2007; Hiebert et al., 2014).

Orbitofrontal cortex/ventromedial prefrontal cortex

Both the orbitofrontal cortex (OFC) and ventromedial prefrontal cortex (vmPFC) have been linked to goal-directed behavior (Ullsperger, Danielmeier,

[5] Note, that also other distinctions have been made, e.g., Voorn et al. (2004) suggested a gradient in striatal processing from dorsolateral to ventromedial structures (also see Mattfeld et al., 2011).

et al., 2014). Specifically, the OFC has been shown to encode outcome valence along a mediolateral gradient with the medial OFC being primarily sensitive to reward and the lateral OFC to punishment (O'Doherty et al., 2001; Xie et al., 2021). Moreover, intracerebral recordings have recently demonstrated that the vmPFC more strongly reflected +PEs, whereas the lateral OFC more strongly reflected -PEs (Gueguen et al., 2021). While a valence-based functional segregation may be too simplistic and remains debated (Ullsperger, Danielmeier, et al., 2014), the lateral OFC has been suggested to be particularly involved in contingent learning, whereas the medial OFC/vmPFC may be involved in value comparison and the translation of value into choice (Klein-Flügge et al., 2022; Noonan et al., 2017; Ullsperger, Danielmeier, et al., 2014).

Midcingulate cortex

The midcingulate cortex (MCC)[6] has widespread connections with a distributed network of brain regions, including the dopaminergic midbrain (Wei et al., 2018; Zhang et al., 2017), (dorsal) striatum, parietal and dorsal prefrontal cortex, as well as motor-related areas (Beckmann et al., 2009). Given this extensive connectivity, the MCC has been functionally implicated in a diverse set of psychological processes, spanning time perception and bodily representation to goal-directed behavior and cognitive control (for an overview, see e.g., Clairis & Lopez-Persem, 2023). In the context of learning and decision-making, the MCC has been shown to be sensitive to conflict (Botvinick et al., 1999; Carter et al., 1998; Carter & Van Veen, 2007), errors (Carter et al., 1998; Gilbertson et al., 2021; Shen et al., 2015), reward and punishment (Seo & Lee, 2009), as well as both signed and unsigned PEs (Fouragnan et al., 2018; Hayden et al., 2011; Ide et al., 2013; Jessup et al., 2010; Vassena et al., 2014). Accordingly, several theories have been proposed on its broader functional significance (Clairis & Lopez-Persem, 2023; Vassena et al., 2017).

An early seminal theory, motivated by electrophysiological evidence, suggested that the MCC may reflect a "motor control filter" that guides action selection through dopaminergic signed PE signals (Holroyd & Coles, 2002; Nieuwenhuis et al., 2004). Yet, it has also been theorized that the MCC may be rather involved

[6] Note that there is some inconsistency in the anatomic labelling of the MCC in the literature. Specifically, the region referred to here as the MCC has elsewhere sometimes been labeled as the dorsal anterior cingulate cortex or medial (pre)frontal cortex (see Clairis & Lopez-Persem, 2023). In this dissertation, I adopt the label MCC in accordance with the anatomical nomenclature proposed by Vogt (2016).

in predicting the *likelihood* of committing an error in a given situational context, thereby not only accounting for MCC sensitivity to errors but also conflict (Brown & Braver, 2005). Consistent with evidence suggesting that PE representations in the MCC are primarily driven by general surprise (Fouragnan et al., 2018; Vassena et al., 2020), the *predicted response outcome* (PRO) model (Alexander & Brown, 2011) proposed that the MCC may serve more generally as an S-R-O predictor that generates and updates its predictions based on discrepancies between actual and expected responses or outcomes (i.e., unsigned PEs). Recently it has been further proposed that the MCC may reflect the extent to which allocating additional control is worthwhile, based on integrating costs and benefits into an *expected value of control* (Shenhav et al., 2013; Shenhav et al., 2016), whereas alternatively the MCC may reflect the value of behavioral change by encoding the value to switch and update the current behavioral policy (Kolling et al., 2016).

Importantly, however, all these theories have difficulties in explaining the large variety of signals reflected by the MCC. Consistent with the emerging idea that brain areas may not be limited to a single function (Anderson, 2010), it has been suggested that the MCC may reflect multiple signals and functions (Clairis & Lopez-Persem, 2023). In contrast, Heilbronner and Hayden (2016) theorized that the diversity of MCC sensitivity may be explained through an adaptive coding account. Following this view, the MCC may act highly flexible and context-dependent by tracking signals that are most informative for implementing cognitive control and/or adjusting behavior in a given task.

Taken together, although the functional significance of the MCC remains actively debated, current theories broadly converge on the idea that the MCC supports goal-directed behavior by signaling the need for (or value of) cognitive control and/or behavioral change, thereby qualifying for a central role in performance monitoring (Ullsperger, Danielmeier, et al., 2014).

Cortico-striato-thalamo-cortical circuitry

While value representations are distributed across multiple brain regions, learning and goal-directed behavior are considered to rely on their interaction within closed cortico-striato-thalamo-cortical (CSTC) circuits (Cox & Witten, 2019; Frank, 2011; Peak et al., 2019). It comes as no surprise that they have thus been implicated in performance monitoring and goal-directed behavior (Ullsperger, Danielmeier, et al., 2014).

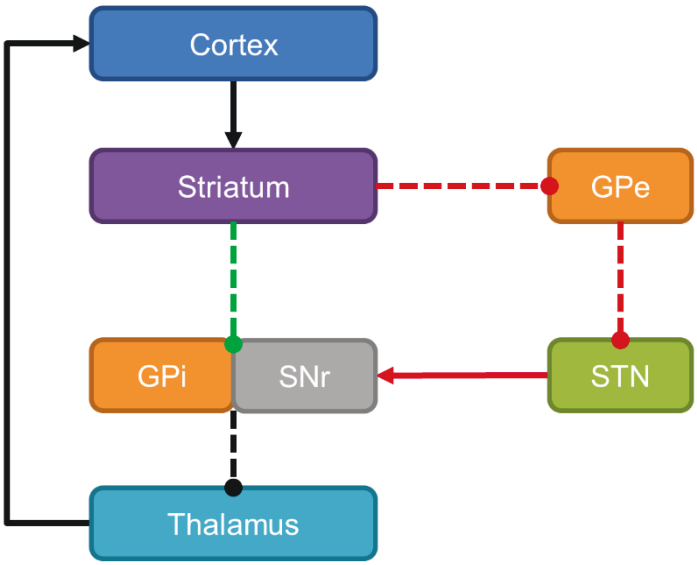


Figure 1. CSTC circuit with the direct pathway in green and the indirect pathway in red. Arrowhead ending indicates excitatory connections, ball ending inhibitory connections. Abbreviations: GPe = globus pallidus externa; GPi = globus pallidus interna; SNr = substantia nigra pars reticulata; STN = subthalamic nucleus

In its generalized form (Alexander & Crutcher, 1990; Alexander et al., 1986; Haber, 2016), such CSTC circuitry involves cortical projections to the striatum, whose output is conveyed via the basal ganglia output nuclei—globus pallidus interna (GPi) and substantia nigra pars reticulata (SNr)—to the thalamus, and eventually back to the cortex (see Figure 1). Crucially, projections from the striatum to the thalamus run along two parallel basal ganglia pathways, which have opposing net effects on the thalamus and thereby differentially modulate cortical excitation/inhibition. The *direct pathway* is net excitatory and originates from striatal D1 receptor-expressing neurons that project directly to and inhibit the GPi/SNr, thereby *disinhibiting* the thalamus (↑cortex). By contrast, the *indirect pathway* is net inhibitory and originates from striatal D2 receptor-expressing neurons that first project to and inhibit the globus pallidus externa, thereby disinhibiting the subthalamic nucleus, which then excites the GPi/SNr and leads to *inhibition* of the thalamus (↓cortex).[7]

[7] Note, however, that besides this dual pathways architecture, contemporary models also distinguish a net-inhibitory *hyperdirect pathway* with direct cortical projections to the subthalamic nucleus, hence surpassing the striatum, which may support rapid stopping of already initiated actions (Chen et al., 2020; Nambu et al., 2002).

Accordingly, action invigoration ("go") would be facilitated through the direct pathway, whereas action suppression ("nogo") would be facilitated through the indirect pathway, which has received corresponding empirical support (Bateup et al., 2010; Freeze et al., 2013; Kravitz et al., 2010). However, subsequent studies found that both the direct and indirect pathway were concurrently activated during action initiation and execution, suggesting complementary roles for action selection (Cui et al., 2013; Tecuapetla et al., 2016). An influential framework has therefore postulated a competitive model (Bariselli et al., 2019; Collins & Frank, 2014; Frank et al., 2004), suggesting the relative dependence on the direct or indirect pathway to determine action selection, with the former facilitating approach and the latter facilitating avoidance of actions (to stimuli).

Importantly, this dual pathway architecture suggests a modulatory role of DA, as DA is considered to facilitate activity and plasticity in striatal D1 receptor-expressing neurons of the direct pathway while having opposing effects on D2 receptor-expressing neurons of the indirect pathway (Collins & Frank, 2014; Frank, 2005). Accordingly, DA increases, e.g., following reward-predictive cues or +PEs, are thought to promote action invigoration/approach via enhanced signaling in the direct pathway (↑D1>↓D2), whereas DA decreases, e.g., following punishment-predictive cues or -PEs, would preferentially promote action suppression/avoidance via enhanced signaling in the indirect pathway (↑D2>↓D1). In line with this hypothesis, it has been shown that patients with Parkinson's disease, characterized by DA depletion, showed a bias toward learning from negative relative to positive feedback and that dopaminergic medication reversed this effect (Frank et al., 2004). Similarly, baseline DA synthesis in healthy participants was shown to be positively associated with reward- versus punishment-based reversal learning (Cools et al., 2009; see Collins & Frank, 2014, for a review of evidence on DA-mediated learning effects).

Neural basis of motivational biases

Although the neural mechanisms underlying motivational biases have not yet been fully resolved, they have generally been assumed to arise through the dopaminergic modulation of the striatum along CSTC loops (Collins & Frank, 2014; Richter et al., 2021; Richter et al., 2014). Specifically, there are currently two prevailing mechanistic hypotheses: one suggesting a Pavlovian response bias on action selection (Guitart-Masip, Huys, et al., 2012) and one suggesting biased instrumental learning (Swart et al., 2017).

Focusing on outcome anticipation in the striatum, a Pavlovian response bias assumes that reward-predictive cues, eliciting an increase in DA, may favor action invigoration ("go"), whereas punishment-predictive cues, eliciting a decrease in DA, may promote action suppression ("nogo"). It would therefore be suggested that the striatum should primarily reflect cue valence in the orthogonalized go/nogo task. By contrast, however, previous studies have instead shown that striatal BOLD signaling is dominated by the required response rather than cue valence (Guitart-Masip, Chowdhury, et al., 2012; Guitart-Masip et al., 2011; Guitart-Masip, Huys, et al., 2012; Moutoussis et al., 2018), thereby challenging the notion that motivational biases arise solely from a valence-anticipatory Pavlovian response bias on action selection in the striatum. However, although the neural source of the Pavlovian response bias is not entirely resolved yet, the presence of such a Pavlovian response bias is largely supported across various computational modeling studies (Algermissen et al., 2024; Guitart-Masip, Huys, et al., 2012; Swart et al., 2017).

Importantly, the CSTC architecture gives rise to another candidate mechanism that may contribute to motivational biases. Besides biasing action selection in *anticipation* of outcomes via a Pavlovian mechanism, motivational biases may also emerge during outcome evaluation and the updating of S-R-O associations, thus reflecting an instrumental learning bias (Swart et al., 2017). Specifically, +PEs, reflecting better-than-expected outcomes and eliciting increases in DA, may promote subsequent action invigoration ("go"), whereas -PEs, reflecting worse-than-expected outcomes and eliciting decreases in DA, may promote subsequent action suppression ("nogo"). As a consequence, this framework predicts *enhanced learning from rewarded action* (relative to rewarded inaction), because rewarded actions are more likely to be repeated, and *impaired learning from punished inaction* (relative to punished action), because punished inactions are less likely to result in behavioral change.

Indeed, results from computational modeling have provided evidence for such biased instrumental learning (Algermissen et al., 2024; de Boer et al., 2019; Swart et al., 2018; Swart et al., 2017), although it remains unclear whether it complements a Pavlovian response bias (Algermissen et al., 2024; Swart et al., 2018; Swart et al., 2017) or is sufficient to explain motivational biases on its own (de Boer et al., 2019). In further support for biased instrumental learning, while de Boer et al. (2019) found that interindividual striatal DA D1 receptor availability predicted the strength of such biased learning, Algermissen et al.

(2024) recently demonstrated that biased PE representations in the MCC preceded those in the striatum, suggesting a cortical role in the emergence of motivational biases.

Indeed, several brain areas have been linked to motivational biases, not limited to the MCC (Algermissen et al., 2024; Koutsoumpari et al., 2026) but also including the vmPFC, amygdala and hippocampus (Queirazza et al., 2023), as well as the anterior insula (Koutsoumpari et al., 2026). Still, it remains unclear whether these areas "merely" provide input to the striatum, as in the study of Algermissen et al. (2024), which may then give rise to motivational biases, or whether they drive these biases themselves.

Importantly, the (pre)frontal cortex, in particular, has additionally been involved in the regulation or overcoming of motivational biases. This was first suggested by Guitart-Masip, Economides, et al. (2014), who demonstrated that the reduction of motivational biases following levodopa administration could not reasonably be accounted for by enhanced striatal DA, but may instead have reflected modulation of frontal DA. A frontal role in overcoming motivational biases has additionally been suggested by Cavanagh et al. (2013) who showed that increased midfrontal theta oscillatory power was associated with a greater ability to overcome motivational biases both inter- and intraindividually. Similarly, Queirazza et al. (2023) suggested that the sensorimotor cortex may contribute to the suppression of motivational biases. In line with a frontal role in overcoming motivational biases, Kim et al. (2023) demonstrated that anodal transcranial direct current stimulation over the dorsolateral prefrontal cortex led to a reduction of motivational biases (in the punishment domain).

Taken together, motivational biases may arise from a Pavlovian response bias and/or biased instrumental learning, for both of which a striatal contribution has been suggested. However, while biased instrumental learning suggests motivational biases may emerge during outcome evaluation, research on feedback processing is surprisingly scarce (but see Albrecht et al., 2016; Csifcsák & Mittner, 2026) and dominated by research focusing on the action selection process (e.g., Cavanagh et al., 2013; Guitart-Masip et al., 2011; Guitart-Masip, Huys, et al., 2012).

Electrophysiology of performance monitoring

Despite neuroimaging techniques such as fMRI provide good spatial resolution, they may not be ideal to investigate the fine-grained temporal dynamics of

performance monitoring. Given its excellent temporal resolution and widespread use in prior research on performance monitoring, electroencephalography (EEG), specifically the event-related potential (ERP) technique, was the neuroscientific method of choice in this dissertation (see also Luck, 2014; Ullsperger, Fischer, et al., 2014). The following subsections provide an overview of the most widely used electrophysiological correlates of performance monitoring. Although the primary focus will be on feedback processing, I will also briefly refer to error processing because of its theoretical implications for feedback processing and its relevance to the rationale and theoretical motivation for one of the conducted studies as part of this dissertation.

Error processing

The error-related negativity (ERN) is a well-established electrophysiological marker of error processing, emerging as a characteristic negative-going ERP deflection that peaks within 100 ms after error commission relative to correct responses and is most pronounced over fronto-central electrodes (e.g., FCz; Falkenstein et al., 1991; Gehring et al., 1993; for a review see Gehring et al., 2012). Converging evidence has identified the MCC as the main neural generator of the ERN (Debener et al., 2005; Dehaene et al., 1994; Fu et al., 2019), while also the pre-supplementary motor area has been suggested as an additional source (Fu et al., 2019; Grützmann et al., 2016).

Most influentially, the *reinforcement learning theory* (RL-theory) suggests that the ERN reflects a -PE signal and emerges when phasic decrease of mesencephalic DA disinhibits the apical dendrites of motor neurons in the MCC (Holroyd & Coles, 2002). In support of this account, ERN amplitudes for incorrect responses have been shown to increase with learning (Bellebaum & Colosio, 2014) and to be predicted by the difference in RL-derived action values between response options (Huvermann, Berlijn, Groiss, et al., 2025; Vahedi et al., 2025).

Feedback processing

Feedback-related negativity/reward positivity

Feedback processing is commonly studied through a characteristic ERP component that emerges 200-350 ms after feedback presentation with more negative amplitudes for aversive compared to appetitive feedback, which is most pronounced over fronto-central electrodes (Faßbender et al., 2023; San Martín, 2012; Walsh & Anderson, 2012). This ERP component has been shown

to originate from the MCC (Hauser et al., 2014; Luu et al., 2003; Oerlemans et al., 2025) and additionally reflect striatal processing (Becker et al., 2014; Carlson et al., 2011; Foti et al., 2011).

Originally labeled the feedback-related negativity (FRN), it has been first thought to be an extension of the ERN, hence specifically linked to be sensitive to punishment feedback and to reflect a -PE (Holroyd & Coles, 2002).[8] Within this view, it has been assumed that the ERN may reflect *predictive* error processing based on internal information, whereas the FRN may reflect *postdictive* error processing based on external information (Holroyd & Coles, 2002; Maurer et al., 2021; Walsh & Anderson, 2012). Accordingly, this framework suggests an inverse relationship between the magnitude of the ERN and FRN during learning, with more reliance on external feedback during early phases of learning and more on internal representations when R-O associations have been consolidated and/or internalized. In support of that, it has indeed been shown that as amplitudes of the ERN increase during learning, the FRN decreases (Bellebaum & Colosio, 2014; Holroyd & Coles, 2002).

More recently, however, it has been suggested that the FRN to punishment feedback may more appropriately be accounted for by an ordinary N2, that is superimposed by a reward positivity (RewP), which ultimately drives the well-established differentiation between reward and punishment feedback (Holroyd et al., 2008; Krigolson, 2018; Proudfit, 2015). Indeed, some studies found the FRN/RewP to primarily reflect +PEs (Berlijn et al., 2025; Kirsch et al., 2022; Weber & Bellebaum, 2024). Yet, other studies found the FRN/RewP to be primarily modulated by -PEs (Chase et al., 2011; Huvermann, Berlijn, Thieme, et al., 2025), therefore challenging the RewP account. By contrast, other studies did not find the FRN/RewP to reflect signed but unsigned PEs (e.g. Hauser et al., 2014; Oliveira et al., 2007; Pfabigan et al., 2015; Sallet et al., 2013; Talmi et al., 2013), aligning with the predictions of the PRO-model, suggesting the MCC to be primarily sensitive to general surprise signals (Alexander & Brown, 2011). Given their spatiotemporal overlap and unclear mechanistic interpretation, I will therefore opt the term *FRN/RewP* for this dissertation.

[8] Note, however, that while originally thought to reflect -PEs only, an early extensions of the RL-ERN model has likewise explained ERN/FRN reductions by positive dopaminergic PE signals inhibiting the apical dendrites of motor neurons in the MCC (Nieuwenhuis et al., 2004).

P3

Feedback processing is additionally often investigated through the P3, which emerges as a positive-going deflection that immediately follows the FRN/RewP within 250-500 ms after feedback presentation (San Martín, 2012; Ullsperger, Fischer, et al., 2014). In contrast to the FRN/RewP, the P3 generally appears less sensitive to outcome valence but rather to motivational significance, as amplitudes have been shown to increase with outcome magnitude (Wu & Zhou, 2009; Yeung et al., 2004) and to reflect unsigned PEs (Kirsch et al., 2022; Philiastides et al., 2010).

The functional significance of the P3 has been primarily discussed within two (complementary) frameworks (Nieuwenhuis, 2011). First, the context-updating hypothesis posits that the P3 reflects contextual or memory updating (Donchin, 1981; Donchin & Coles, 1988). Second, the more recent locus coeruleus-P3 hypothesis assumes the P3 to reflect phasic activity of the locus coeruleus-norepinephrine system, which is thought to mediate neural responsiveness to motivationally significant, salient stimuli (Nieuwenhuis, Aston-Jones, et al., 2005).

However, the neural origin of the P3 is less clear and appears to involve distributed cortical areas (Huang et al., 2015; Ullsperger, 2024). As a consequence, the P3 has sometimes been distinguished into a fronto-central P3a and centro-parietal P3b subcomponent, reflecting attentional orienting and contextual updating, respectively (Polich, 2007; Ullsperger, Fischer, et al., 2014).

Modulators of learning and feedback processing

Emotion

Emotion and cognition are deeply intertwined (Pessoa, 2008; Storbeck & Clore, 2007). Hence, it comes as no surprise that emotion can modulate learning and decision-making (Lerner et al., 2015; Phelps et al., 2014; Tyng et al., 2017). For instance, emotional content is better consolidated than non-emotional content (e.g., Cahill & McGaugh, 1995; Sharot & Phelps, 2004; also see Cowan et al., 2021) and emotion has been shown to facilitate and speed up conflict resolution (Kanske & Kotz, 2010, 2011; Zinchenko et al., 2015), while a recent study found enhanced processing of emotional compared to non-emotional feedback (Braunwarth & Ferdinand, 2025).

Interestingly, emotion has been linked to approach-avoidance motivation (see Elliot et al., 2013), where positive emotional valence may promote approach and negative emotional valence may promote avoidance tendencies (Cacioppo et al., 1999; Lang, 1995). Indeed, several studies have reported faster response times when approaching positive emotional stimuli or avoiding negative emotional stimuli than the reverse (Krieglmeyer et al., 2010; Phaf et al., 2014; Seidel et al., 2010). Using joystick data measuring, it could further be shown that, whereas approach behavior was facilitated in response to happy faces, angry faces were associated with avoidance (Marsh et al., 2005; Seidel et al., 2010). Finally, evidence from an emotional go/nogo task revealed more commission errors to positive emotional than negative emotional faces as well as increased response times to negative compared to positive emotional faces (Hare et al., 2005; Schulz et al., 2007).

Feedback delay

Distinct neural systems have been proposed for learning when feedback immediately follows response selection or when it is delayed by several seconds. In a seminal study, Foerde and Shohamy (2011) found the hippocampus to be selectively involved in the processing of delayed feedback whereas striatal activation was found for immediate feedback. These findings led to suggest a shift in neural activity from the striatum, supporting implicit and non-declarative learning, to the medial temporal lobe including the hippocampus, supporting more explicit and declarative learning, when feedback is delayed (Foerde & Shohamy, 2011; Hinneberg & Hegele, 2022). In support of this notion, Foerde et al. (2013) reported selective learning impairments in patients with Parkinson's disease, characterized by striatal DA depletion, when learning from immediate—but not delayed—feedback. Conversely, they found that learning from delayed—but not immediate—feedback was impaired in amnestic patients with hippocampal damage (Foerde et al., 2013).

Moreover, converging EEG evidence found outcome valence coding in the FRN/RewP to be markedly reduced for delayed relative to immediate feedback (Arbel et al., 2017; Höltje & Mecklinger, 2018, 2020; Weismüller & Bellebaum, 2016), while Peterburs et al. (2016) further demonstrated that FRN/RewP outcome valence coding *gradually* decreased with increasing feedback delay, consistent with a shift-away from implicit striatum-based processing.

However, recent evidence from single-trial EEG revealed that the FRN/RewP reflected +PEs, regardless of feedback timing (Weber & Bellebaum, 2024), contributing to emerging evidence that while neural systems for processing immediate and delayed feedback partly dissociate, they may also share common mechanisms (Hinneberg & Hegele, 2022; Weismüller et al., 2018). In support for such common mechanisms, learning performance was found to be typically unaffected by feedback timing in healthy individuals (see e.g., Weismüller & Bellebaum, 2016).

Observation and agency

Although decision-making is, to a large degree, shaped by our own experiences, it can also be informed by observation. This may not only include simple action imitation but also strategic learning involving inferences about action values via vicarious feedback that can eventually be used for one's own decision-making (Charpentier & O'Doherty, 2018; Dunne & O'Doherty, 2013).

Notably, using feedback-based learning tasks, observational learning is generally found to be similarly effective as active learning (e.g., Bellebaum & Colosio, 2014; Peterburs et al., 2021). It is therefore not surprising that brain regions involved in the processing of own errors and outcomes from self-produced outcomes are similarly engaged also during observation of other's errors or action outcomes (de Bruijn et al., 2009; Mobbs et al., 2009; Newman-Norlund et al., 2009; for an overview see Morelli et al., 2015 and Ninomiya et al., 2018). Accordingly, the FRN/RewP is typically also found for vicarious feedback during observational learning, albeit generally less negative (Bellebaum et al., 2010; Itagaki & Katayama, 2008; Leng & Zhou, 2010) and less differentiated between positive and negative feedback (Bellebaum & Colosio, 2014; Bellebaum et al., 2010), suggesting that, despite similarities, feedback processing is at least partly modulated by the *sense of agency* over behavior. Consistent with evidence from Bellebaum and Colosio (2014), indicating that unlike the active FRN/RewP, the observational FRN/RewP was not modulated by learning, it was shown that PE coding was reflected in the FRN/RewP only for own but not observed outcomes (Burnside et al., 2019). These findings generally align with evidence suggesting that the striatum and DA system are *less strongly* involved in feedback processing for observational relative to active learning (Bellebaum, Jokisch, et al., 2012; Kobza et al., 2012).

Clinical implications: Obsessive-compulsive disorder

Clinical characteristics

Obsessive-compulsive disorder (OCD) is a severe and debilitating mental disorder characterized by recurrent and persistent intrusive thoughts, urges or images (*obsessions*) and/or repetitive, ritualized behaviors or mental acts (*compulsions*), which are time consuming, cause a significant amount of distress or interfere with psychosocial functioning (American Psychiatric Association, 2013). Correspondingly, OCD is a phenotypically heterogeneous disorder with a wide range of clinical manifestations, which can be broadly organized into four major symptom dimensions, i.e., (1) contamination obsessions and washing/cleaning compulsions (2) responsibility for harm and checking/reassurance seeking compulsions, (3) unacceptable thoughts (e.g., violent, sexual or religious obsessions) and mental rituals, and (4) symmetry and completeness and ordering/repeating compulsions (Abramowitz et al., 2010).[9]

OCD is relatively common, with an estimated global lifetime prevalence of 1.3%, being slightly higher for women compared to men (Fawcett et al., 2020), and moderate heritability of up to 50% (Blanco-Vieira et al., 2023; Mataix-Cols et al., 2013). Beyond that, OCD patients exhibit high comorbidity rates, primarily involving comorbid mood and anxiety disorders (Ruscio et al., 2010; Sharma et al., 2021; Torres et al., 2006). Not surprisingly, affected individuals often experience reduced quality-of-life (for an overview see Coluccia et al., 2016) and have been linked to a broad range of health problems including heightened mortality risk (de la Cruz et al., 2022; Meier et al., 2016). Recent evidence further suggests suicide risk to be substantially increased among OCD patients (Fernández de la Cruz et al., 2017; Pellegrini et al., 2020). Nonetheless, OCD often goes unrecognized and may be undertreated (Veldhuis et al., 2012).

Etiology

Cognitive-behavioral determinants of OCD

Building on Mowrer's influential *two-factor theory of fear and avoidance* (Mowrer, 1960), learning models have emphasized the importance of Pavlovian and

[9] Notably, however, Bloch et al. (2008) proposed an alternative four-factor model in which hoarding-related obsessions and compulsions replace responsibility for harm/checking compulsions.

instrumental learning mechanisms in the development and maintenance of OCD (Foa, 2010; Franklin & Foa, 2011; McGuire et al., 2016; Taylor et al., 2007). For instance, consider a person whose stove (CS) led to a harmful kitchen fire (US), such that the stove itself became to elicit fear of harm (CR) via Pavlovian learning. The person may learn that checking the stove results in the (temporary) relief of distress (negative reinforcement), which therefore turns checking compulsive and being performed over and over again. Importantly, obsessional distress may be generalized to other stimuli, such that various, seemingly arbitrary stimuli (e.g., all electrical devices) can likewise trigger obsessions and compulsions (McGuire et al., 2016).

An important implication of this etiological model is that the continuous engagement in compulsive behaviors prevents extinction, i.e., learning that exposure to the CS without engaging in compulsive behaviors does generally not lead to the distressing event, thereby reducing obsessional distress. This basic principle has resulted in the therapeutic method of *exposure and response prevention*, which has been proven highly efficaciously and considered first-line treatment within cognitive-behavioral therapy of OCD (Hezel & Simpson, 2019).

However, the etiology of OCD cannot be explained solely by Pavlovian and instrumental learning experiences, as e.g., not all individuals with a corresponding learning history inevitably develop OCD. This and other limitations (see e.g., Taylor et al., 2007) led to consider cognitive determinants in the etiology of OCD (e.g., Rachman, 1998; Salkovskis, 1985). Accordingly, while intrusive thoughts can be found in everyone, cognitive models of OCD have considered dysfunctional beliefs and appraisals that may drive them pathological (for an overview see Hezel & McNally, 2016). Notably, while compulsions may be negatively reinforced by temporarily relieving obsessional distress, they are assumed to simultaneously prevent OCD patients from learning that their beliefs and appraisals are in fact irrational, and hence dysfunctional (Salkovskis, 1985, 1989).

Relevant cognitive biases in OCD include inflated responsibility beliefs (Salkovskis et al., 2000), overestimation of threat (Moritz & Pohl, 2009), importance of or need to control thoughts (Taylor et al., 2010; also see Sandstrom et al., 2024) as well as perfectionism (Frost et al., 2002) and intolerance of uncertainty (Pinciotti et al., 2021). Moreover, OCD can involve feelings of incompleteness and not-just-right experiences (Coles et al., 2003;

Coles et al., 2005), which may at least partially reflect dysfunctional satiety and goal-attainment, that could account for the persistent reassurance seeking in OCD (Szechtman & Woody, 2004). More recently, OCD has been increasingly linked to an altered sense of agency (Borrelli et al., 2024; Gentsch et al., 2012; Grossmann et al., 2025; Szalai, 2019), which may at least partly underlie some cognitive biases such as inflated responsibility or perceived control.

OCD pathophysiology

Neurobiological models suggest a critical role of the striatum along dysregulated CSTC circuits in the pathophysiology of OCD (Aouizerate et al., 2004; Burguiere et al., 2015; Graybiel & Rauch, 2000; Milad & Rauch, 2012; Saxena et al., 1998). Such dysregulation is widely believed to involve an imbalance between the direct and indirect pathway, where relative overactivity on the net-excitatory direct pathway in OCD may generate a positive feedback loop, hence resulting in CSTC circuit hyperactivation (for current reviews see Goodman et al., 2021; Jalal et al., 2023; Pauls et al., 2014).

Most notably, such hyperactive CSTC circuitry has been reported to particularly involve the OFC and caudate nucleus and theorized to underlie compulsive behaviors (e.g., Saxena et al., 1998). However, more recent refinements have expanded this framework to involve multiple interconnected but functionally distinct neurocircuits in OCD, with abnormalities not limited to uniform hyperactivity (Milad & Rauch, 2012; Shephard et al., 2021; van den Heuvel et al., 2016).

Overall, the notion of dysregulated neurocircuitry in OCD is well supported across various studies (Beucke et al., 2013; de Wit et al., 2014; Harrison et al., 2009; Jung et al., 2013; Liu et al., 2022; Naze et al., 2023), with functional neuroimaging studies suggesting alterations in several brain regions involved in these circuits, including increased activity in the caudate nucleus of the striatum (Menzies et al., 2008; Whiteside et al., 2004) and OFC (Menzies et al., 2008).

Given its extensive connections and involvement across different CSTC circuits, the MCC has attracted particular interest as a potential hub underlying the pathophysiology of OCD (McGovern & Sheth, 2017; van de Veerdonk et al., 2023). This is supported by evidence of hyperactive MCC activation in OCD during symptom provocation (Adler et al., 2000; Breiter & Rauch, 1996), resting-state (Cheng et al., 2013) and various task-based contexts (e.g., Maltby et al.,

2005; Vriend et al., 2013; but see also the next section), as well as evidence of efficacy of cingulotomy in refractory OCD patients (Brown et al., 2016). It has therefore been theorized that increased MCC activation may create an overreliance on threatening stimuli and suboptimal selection of neutralizing behavior, resulting in persistent maladaptive behaviors and impaired goal-directed control (McGovern & Sheth, 2017; van de Veerdonk et al., 2023).

Performance monitoring in OCD

OCD has been linked to widespread deficits in executive functions such as response inhibition (Bannon et al., 2002; Penadés et al., 2007; see also Mar et al., 2022), stopping behaviors (Hinds et al., 2012; Wahl et al., 2008) and cognitive flexibility (Gruner & Pittenger, 2017), as well as deficits in goal-directed behavior (Gillan & Robbins, 2014; Vaghi et al., 2019)—all indicating alterations in performance monitoring.

Most prominently, OCD has been linked to aberrant error monitoring, where activity in various brain regions, most notably the MCC, is abnormally increased in response to error commission (e.g. Fitzgerald et al., 2005; Grützmann et al., 2016; but see Norman et al., 2019). Consistent with that, OCD has been robustly associated with ERN enhancement (Endrass et al., 2008; Ruchsow et al., 2005; for a review see Riesel, 2019), which appears to be unmodulated by OCD symptom-severity (Nawani et al., 2018) or -expression (Riesel et al., 2014), and has even been found independent of the medication status (see Riesel, 2019). Given that ERN enhancement has even been observed in unaffected first-degree relatives of OCD patients, it has been considered that a hyperactive ERN may constitute a candidate endophenotype for OCD (Riesel et al., 2011). Yet, given ERN enhancement has been observed also across various anxiety disorders (Endrass et al., 2014; Riesel et al., 2017; Weinberg et al., 2015), it has been suggested that such an endophenotype may be transdiagnostic rather than OCD-specific (Riesel, 2019).

Crucially, however, while error processing and the ERN have been extensively investigated, research on feedback processing and the FRN/RewP is relatively understudied. Available fMRI evidence is scarce and inconsistent, with some studies reporting altered processing of rewards or avoided losses in OCD (Jung et al., 2011; Koch et al., 2018; Remijnse et al., 2006), whereas others have found no group differences (Figee et al., 2011; McDonald et al., 2024). By contrast, studies examining PE signaling in OCD have reported enhanced PE-related

activity in the OFC (Sen et al., 2025), MCC and putamen (Hauser et al., 2017; Murray et al., 2019).

If the ERN and FRN/RewP rely on similar functional mechanisms (Holroyd & Coles, 2002), it could be predicted that the FRN/RewP response to negative feedback may be likewise more negative in OCD. While some studies indeed found more negative FRN/RewP amplitudes in (sub)clinical OCD (Luo et al., 2020; Zhu et al., 2014), others found the FRN/RewP to negative feedback to be more positive (Endrass et al., 2013) or not differentiating from positive feedback (O'Toole et al., 2012). In other studies, however, no differences were found in the FRN/RewP between OCD patients and healthy controls (Nieuwenhuis, Nielen, et al., 2005; Schüller et al., 2015). While the available FRN/RewP studies are limited, often rely on subclinical samples, and employ inconsistent experimental paradigms, it remains unclear whether and how feedback processing is altered in OCD.

Research gap, aim & objectives

The overarching aim of this dissertation was to advance understanding of how learning and decision-making, along with their neural signatures, are modulated by contextual factors and psychopathology. Particular emphasis was placed on motivational biases, i.e., the coupling between action and valence, as well as the role of feedback processing in the FRN/RewP. With this aim, I here present four experimental studies, each designed to address a specific research gap.

Apart from few previous studies showing that motivational biases are typically enhanced in contexts with low outcome controllability (Csifcsák et al., 2020; Dorfman & Gershman, 2019; Raab et al., 2024; but see Sedlinská et al., 2023), they tend to be overall remarkably robust and only hardly sensitive to contextual manipulation (e.g., Ereira et al., 2021; Guitart-Masip et al., 2011; Peterburs et al., 2021; Weber et al., 2022). Identifying contextual factors that effectively attenuate (or even override) motivational biases is therefore not only important to elevate the understanding of the nature of motivational biases, but may additionally have important clinical implications. Notably, motivational biases have been shown to be altered across several mental disorders including anxiety (Mkrtchian et al., 2017; Ousdal et al., 2018), schizophrenia (Albrecht et al., 2016), as well as addiction (Chen et al., 2023; Liu et al., 2025), and have been

shown to be predictive of recovery from depression (Huys et al., 2016) and relapse in alcohol dependence (Garbusow et al., 2016; Sommer et al., 2020).

Within this dissertation, I considered the following contextual factors that may affect the expression of motivational biases. First, **Study I** examined the effect of emotional compared to neutral facial cues. **Study II** investigated whether motivational biases depend on feedback learning, specifically whether feedback was presented immediately after decision-making, or after a slight temporal delay. Finally, in **Study IV**, motivational biases were compared between active and observational learning.

In addition, while motivational biases have yet been predominantly understood as a Pavlovian response bias and its neural correlates have been primarily investigated in response to Pavlovian cues (e.g., Cavanagh et al., 2013; Guitart-Masip et al., 2011; Guitart-Masip, Huys, et al., 2012), the involvement of outcome evaluation and feedback processing has been widely neglected. Although feedback processing has been assessed by a few fMRI (e.g., Guitart-Masip et al., 2011; Guitart-Masip, Huys, et al., 2012) and ERP studies (Albrecht et al., 2016; Csifcsák & Mittner, 2026), they mainly focused on basic effects of outcome valence coding, and crucially did not examine whether feedback processing depended on whether outcomes were obtained through action or inaction. Given recent evidence of biased instrumental learning, with facilitated learning from rewarded action and disrupted learning from punished inaction (e.g., Swart et al., 2017), as well as independent findings of action-biased feedback processing (e.g., Bikute et al., 2022), it is therefore important to consider also feedback processing as a source of motivational biases.

As a consequence, this dissertation aimed to address this gap, with **Study II** and **Study IV** investigating whether motivational biases are associated with action-biased feedback processing in the ERP.

Moreover, with this dissertation, it was aimed to shed light on the clinical relevance of learning and decision-making, by examining disorder-related alterations, here exemplified by OCD. Crucially, despite overlap in neural mechanisms involved in OCD and motivational biases, whether and how these biases are altered in OCD is not yet fully understood. While PIT studies have suggested attenuated motivational biases in (sub)clinical OCD (Krypotos & Engelhard, 2020; Peng et al., 2022; but see Marzuki et al., 2024), convincing evidence from the orthogonalized go/nogo task—allowing incidental Pavlovian

and instrumental learning—is still lacking. In addition to that, while a recent dimensional study did not find OCD symptoms to predict motivational biases in a non-clinical sample (Scholz et al., 2026), it remains to be clarified whether motivational biases are altered in clinical OCD.

Despite previous inconsistencies, but given the assumed pathophysiology with dysregulated CSTC circuitry and hyperactivity of the direct "go" pathway (e.g., Pauls et al., 2014), it may be conceivable that motivational biases in clinical OCD are exaggerated. **Study IV** was dedicated to test this hypothesis.

Furthermore, while error processing and the ERN have been extensively studied in OCD (Norman et al., 2019; Riesel, 2019), research on feedback processing and the FRN/RewP appears relatively understudied. Critically, in contrast to the ERN, there is currently no clear picture on whether and how feedback processing and the FRN/RewP are altered in OCD (Endrass et al., 2013; Luo et al., 2020; Nieuwenhuis, Nielen, et al., 2005).

This dissertation hence aimed to extend research on feedback processing in OCD. Hence, while **Study III** generally assessed feedback processing during a (non-Pavlovian) instrumental learning task, **Study IV** investigated feedback processing underlying motivational biases in OCD.

Finally, while prior research in OCD has largely focused on active task contexts, in which participants make their own decisions and hence learn from feedback on their own choices, it is currently unknown how learning, decision-making and feedback processing are affected in observational learning contexts. This question is, however, particularly relevant given evidence of an altered sense of agency in OCD (Borrelli et al., 2024; Gentsch et al., 2012; Grossmann et al., 2025; Szalai, 2019), as well as findings suggesting altered affective responses to others in OCD (Jansen et al., 2020). Moreover, while OCD has been linked to striatal dysfunction (Burguiere et al., 2015), learning from observation has been assumed to rely less strongly on the striatum (Kobza & Bellebaum, 2015; Kobza et al., 2012).

Aiming to shed light on whether and how agency affects learning, decision-making and feedback processing in OCD, **Study III** and **Study IV** hence compared active and observational learning in OCD.

2 Study Summaries

General procedures

Participants

All studies presented in this dissertation were conducted at the Department of Biological Psychology at Heinrich Heine University Düsseldorf. Note, however, that Study I was additionally conducted at a second testing site, the ISM Institute for Systems Medicine at MSH Medical School Hamburg. While Studies I and II included healthy participants only, Studies III and IV additionally involved clinical participants and were conducted in parallel using the same recruited sample. Within this data collection process, two OCD patients were assessed at a collaborating psychotherapeutic practice in Krefeld.

All presented studies were approved by the Ethics Committee of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University Düsseldorf and conformed to the Declaration of Helsinki (Study I received additional ethical clearance by the Ethics Board of the MSH Medical School Hamburg). Written informed consent was obtained from all participants prior to participation and participants were reimbursed either through monetary compensation or course credit. All participants had normal or corrected-to-normal vision and were naïve to the study's intent.

Orthogonalized go/nogo task

Aiming to examine motivational biases, Studies I, II and IV were all based on the same computerized, orthogonalized go/nogo task (Guitart-Masip et al., 2011). Within this task, cue valence ("win" vs. "avoid-losing") and the required instrumental response ("go" vs. "nogo") are decoupled, resulting in four cued learning conditions: go to win (GW), go to avoid-losing (GAL), nogo to win (NGW), and nogo to avoid-losing (NGAL). While the innate Pavlovian response conflicts with the required instrumental response in GAL and NGW, these conditions have sometimes been referred to as Pavlovian-conflict conditions, whereas GW and NGAL constitute Pavlovian non-conflict conditions (e.g., Albrecht et al., 2016; Cavanagh et al., 2013).

In the basic version of the task (see Figure 2), each trial begins with the presentation of a single cue, corresponding to one of the four learning conditions. Following a brief fixation period, an open white circle appears either on the left or right side of the computer screen. Participants are required to

either press the button corresponding to the location of the circle ("go") or to withhold a button press ("nogo"). After another fixation period, symbolic feedback reveals the consequence of the participant's decision. A green upward pointing arrow indicates a gain of 10 points ("win"), a red downward pointing arrow indicates the loss of 10 points ("loss"), and a yellow horizontal bar indicates no change in the current score ("draw"). Finally, another fixation period occurs as an intertrial interval before the next trial starts.

Importantly, for each learning cue only two possible outcomes are available: one favorable and one unfavorable. For GW and NGW, "win" is the favorable outcome and "draw" is the unfavorable outcome. Conversely, for GAL and NGAL, "draw" is the favorable outcome and "loss" is the unfavorable outcome. Accordingly, depending on cue valence, "draw" can either indicate reward omission (GW/NGW) or loss avoidance (GAL/NGAL), and hence can either be favorable or unfavorable.

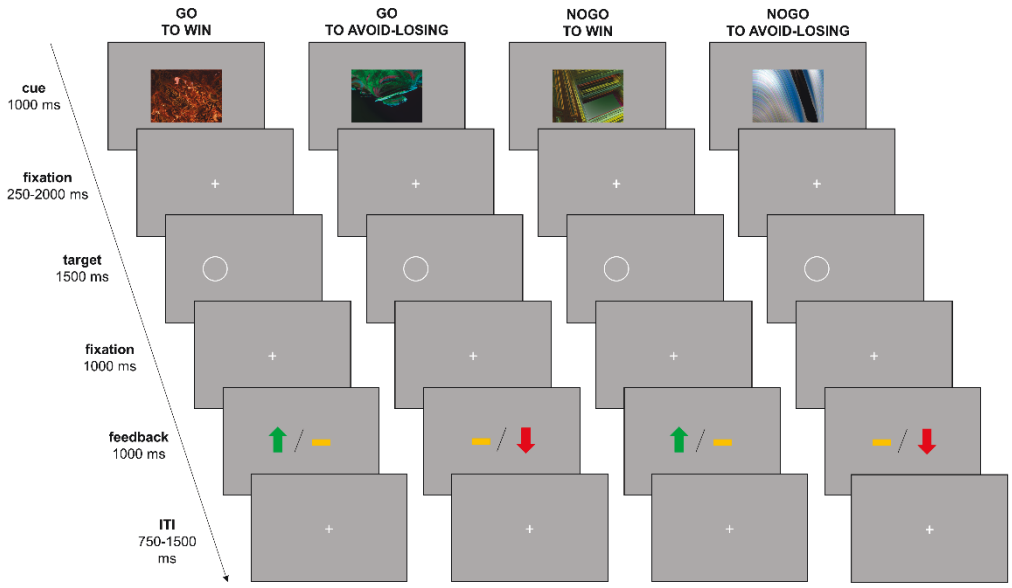


Figure 2. Schematic of the orthogonalized go/nogo paradigm.

Unbeknownst to the participants, feedback in this task is probabilistic. Showing the required response (i.e., "go" in GW/GAL and "nogo" in NGW/NGAL) results in the favorable outcome with a probability of 80% and in the unfavorable outcome with a probability of 20%, whereas showing the non-required response reverses these probabilities such that the unfavorable outcome occurs with a probability of 80% and the favorable outcome with a

probability of 20%. Participants are generally instructed to collect as many points as possible, i.e., to maximize reward and minimize loss.

In all studies employing the orthogonalized go/nogo task (Studies I, II and IV), data quality was ensured by verifying that participants (1) exhibited less than 25% invalid button presses (Scholz et al., 2022), (2) did not perseverate on the same response in more than 85% of trials (cf. Weber et al., 2022) and (3) performed above chance-level in the easiest condition GW (Weber et al., 2022).

EEG recording and data processing

Studies II-IV involved EEG acquisitions. In all these studies, EEG data were acquired from 29 scalp sites, i.e., FCz (used as online reference), F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, PO10, O1, Oz, and O2, via active Ag/AgCl electrodes that were attached to an elastic cap and positioned according to the extended 10–20 system (Chatrian et al., 1988; Chatrian et al., 1985). Electrode site AFz was used as the ground electrode, and two electrodes were attached to the mastoids for offline re-referencing. Horizontal and vertical electrooculogram was measured via additional electrodes placed lateral to the left outer canthus and above the left eye (Fp1), respectively. EEG data were recorded at a 1000 Hz sampling rate, amplified using a BrainAmp DC amplifier and recorded using BrainVision Recorder software (Brain Products GmbH, Germany). Impedances were kept below 20 kΩ.

All studies involved standard EEG preprocessing using BrainVision Analyzer software (Brain Products GmbH, Germany), including re-referencing to the mastoid channels, data filtering (0.1-30 Hz bandpass, 50 Hz notch), a semi-automatic ocular correction independent component analysis as well as segmentation with baseline correction and automatic artifact rejection. For the artifact rejection the following criteria were used to exclude segments: (1) amplitudes exceeding ±100 μV, (2) voltage steps above 50 μV, (3) voltage differences of 200 μV (within 200 ms) and (4) activity below 0.5 μV (within 100 ms).

Statistical modeling

In all presented studies, statistical analyses were carried out using (generalized) linear mixed-effects models ([G]LMMs) in R (R Core Team, 2021). These models offer several advantages over more traditional analyses of variance (Brown, 2021; Volpert-Esmond et al., 2021): First, they allow modeling both categorical

and continuous predictors simultaneously and warrant the possibility of single-trial analyses. Importantly, such single-trial analyses have been specifically recommended for ERP research, which has traditionally relied on trial averaging (Volpert-Esmond et al., 2018). Second, they allow including random effects that can account for variability across different levels of groups or clusters (e.g., participants or measurement electrodes). Finally, (G)LMMs have been shown to be relatively robust to missing data and imbalanced data sets.

In all (G)LMMs reported across all studies, it was initially attempted to fit a maximal random effects structure, including by-participant random intercepts and slopes for all within-participant main effects and interactions, following (Barr, 2013). However, if the maximal model failed to converge, the random effects structure was simplified as supported by the data. Across all studies, statistical significance was evaluated using a threshold of $p < .050$.

Study I: Emotional cues reduce Pavlovian interference in feedback- based go and nogo learning

This section is based on the following research article published in "Psychological Research" and reprinted in the Appendix under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0):

Vahedi, J., Mundorf, A., Bellebaum, C., & Peterburs, J. (2024). Emotional cues reduce Pavlovian interference in feedback-based go and nogo learning. *Psychological Research*, *88*, 1212-1230. https://doi.org/10.1007/s00426-024-01946-9

Rationale and hypotheses

As outlined in the Introduction, learning and decision-making are shaped by motivational biases, where reward-predictive cues promote approach ("go") tendencies ("go") and punishment-predictive cues promote avoidance ("nogo") tendencies (e.g., Guitart-Masip, Duzel, et al., 2014). Notably, valence-dependent modulations of response tendencies, similar to motivational biases, have also been reported for the emotional domain. Whereas positive emotional stimuli (e.g., a smiling face) facilitate approach responses, negative emotional stimuli (e.g., a frowning face) facilitate avoidance responses (e.g. Chen & Bargh, 1999; Krieglmeyer et al., 2010; Phaf et al., 2014; Seibt et al., 2008; Seidel et al., 2010; see also Cacioppo et al., 1999 and Lang, 1995).

Study I therefore investigated the effect of emotional facial cues on the expression of motivational biases. Specifically, it was examined whether motivational biases are modulated when the Pavlovian response tendency associated with the valence of the emotional facial cue aligned with or conflicted with the required instrumental response, compared to a neutral face condition. This study thus focused on the conceptualization of motivational biases representing a Pavlovian response bias on action selection.

Three groups of participants were tested in a novel emotional variant of the orthogonalized go/nogo task. In an emotional-congruent group (CON), positively valenced (happy) faces cued conditions requiring action invigoration (GW and GAL), whereas negatively valenced (angry) faces cued conditions requiring action suppression (NGW and NGAL). In an emotional-incongruent group (INC), this assignment was reversed. A third group completed the task using neutral facial cues, as a baseline (NEU).

It was hypothesized that general task performance would be increased in CON relative to NEU. Because GW and NGAL are typically learned particularly well, with GW often at ceiling (Peterburs et al., 2022), this manipulation was expected to particularly boost learning in the Pavlovian-conflict conditions, GAL and NGW, thereby attenuating motivational biases. Conversely, general task performance was expected to be decreased in INC relative to NEU and, if primarily affecting learning in Pavlovian-conflict conditions, to increase motivational biases.

Methods

Participants

In total, data from 121 healthy student volunteers from two test sites, Heinrich Heine University Düsseldorf and MSH Medical School Hamburg, entered the analyses. Participants were recruited via public advertisements and/or social media and randomly assigned to one of three experimental groups: emotional-congruent (CON; $n = 40$), emotional-incongruent (INC; $n = 40$), or neutral (NEU; $n = 41$). The sample size was determined based on previous studies on motivational biases (e.g. Cavanagh et al., 2013; Ereira et al., 2021; Guitart-Masip, Huys, et al., 2012; Peterburs et al., 2021). Overall, participants were mostly young ($M = 22.25$; SD = 3.15), female (68%), and right-handed (86%), with an average IQ ($M = 102.78$, $SD = 10.82$), as assessed using the Mehrfachwahl-Wortschatz-Test B (MWT-B; Lehrl et al., 1995; Merz et al., 1975). The experimental groups did not differ significantly in any of these variables. None of the participants reported a history of mental disorders and/or current psychotropic medication.

Experimental task and procedure

Participants completed a novel emotional variant of the orthogonalized go/nogo task. Deviating from the original task design, that typically employs abstract neutral cues (e.g., fractal stimuli), the current task adaptation used facial cues, obtained from the FACES database (Ebner et al., 2010). Facial stimuli depicted the same four individuals (two young females and two young males), broadly matched for perceived age, attractiveness, and distinctiveness, but differing in emotional valence (i.e., happy, angry or neutral).

Crucially, experimental groups differed in how facial cues were assigned to the trial conditions. In CON, valence-dependent Pavlovian responses aligned with the required instrumental response, such that happy faces cued GW and GAL,

and angry faces cued NGW and NGAL. Conversely, in INC, Pavlovian responses conflicted with the required instrumental response, such that angry faces cued GW and GAL, and happy faces cued NGW and NGAL.

Moreover, the task used in Study I comprised both learning blocks including trial-by-trial feedback (as described under General Procedures) and test blocks, in which trials ended after the decision-stage, i.e., before providing feedback, hence allowing to assess the stability of motivational biases in the absence of trial-by-trial feedback. Nonetheless, participants were encouraged to continue performing like in learning blocks, as points were still awarded also in test blocks. The task comprised eight blocks, including four learning blocks, each followed by a test block, with 40 trials per block, amounting to 320 trials in total (excluding ten practice trials). Task completion took approximately 35 minutes.

Statistical analysis

Data quality was ensured using the criteria detailed under General procedures. Moreover, Cook's distance (Cook, 1977) was calculated to identify influential observations, indicative of statistical outliers, using a cut-off criterion of = 4/(n - k - 1).[10]

Aggregated choice accuracy data were analyzed using LMM analysis in R, with choice accuracy reflecting the percentage of performing the required instrumental response. Fixed effects included the categorical between-subject predictor *learning condition* (NEU, CON, INC), the within-subject predictors *required response* (go, nogo), *cue valence* (win, avoid-losing), and *block type* (learning block, test block), as well as the continuous predictor *block* (1-8, centered around the task midpoint). A significant *required response* × *cue valence* interaction would hence be indicative of the presence of motivational biases. Significant interaction effects were probed while correcting for *the false discovery rate* (Benjamini & Hochberg, 1995).

Results and discussion

Overall, task performance replicated well-established motivational biases: Participants performed better when executing a response to gain a reward than to avoid punishment (GW > GAL), and when withholding a response to avoid punishment than to gain a reward (NGAL>NGW). This result adds to a large body of research reporting such asymmetric coupling of action and valence in

[10] n = number of observations; k = number of predictors

feedback-based learning (e.g., Cavanagh et al., 2013; Dorfman & Gershman, 2019; Ereira et al., 2021; Guitart-Masip, Duzel, et al., 2014; Guitart-Masip, Huys, et al., 2012; Peterburs et al., 2022; Peterburs et al., 2021; Raab & Hartley, 2020; Scholz et al., 2022).

Moreover, and as expected, learning from emotional compared to neutral facial cues modulated motivational biases. Specifically, motivational biases were attenuated when happy faces cued required "go" responding and angry faces cued required "nogo" responding (CON) compared to learning from neutral facial cues (NEU). This attenuation was driven by a selective performance boost in the Pavlovian-conflict condition NGW, suggesting enhanced goal-directed control. Unexpectedly, however, motivational biases were also attenuated in INC (relative to NEU), i.e., when angry faces cued required "go" responding and happy faces cued required "nogo" responding. In contrast to CON, this was driven by impaired learning in the typically well-learned GW and NGAL conditions.

While generally aligning with previous evidence of valence-dependent approach-avoidance tendencies in the emotional domain (e.g., Marsh et al., 2005; Nikitin & Freund, 2019; Phaf et al., 2014; Seidel et al., 2010), these results suggest that emotional cues may *generally* attenuate motivational biases, irrespective of whether their associated Pavlovian response aligns or conflicts with the required instrumental response. However, although attenuated motivational biases were found both for CON and INC, overall task performance was decreased in INC relative to CON, suggesting a dissociation between goal-directed control and the strength of motivational biases. Accordingly, while emotional cues may generally support Pavlovian-instrumental regulation—possibly mediated through increased motivational significance and/or arousal compared to neutral cues—facilitating goal-directed control may depend on more specific response biasing, in this study induced by cue-response congruency.

Finally, although emotional cues resulted in attenuation of motivational biases, this manipulation did not suffice to overcome them. These findings therefore add to previous work emphasizing the robustness of motivational biases and that they are particularly difficult to overcome (Ereira et al., 2021; Peterburs et al., 2021).

Conclusion

Study I demonstrates that motivational biases can be attenuated when learning from emotional facial cues. Whether this attenuation is adaptive and supports goal-directed behavior was dependent on the congruency between the emotional valence of the cue and the required instrumental response. These findings therefore suggest a dissociation between goal-directed control and the strength of motivational biases. The newly adapted paradigm presented in this study provides evidence for an easy-to-implement behavioral intervention capable of modulating otherwise robust motivational biases and may therefore be useful for future research, e.g., in clinical populations characterized by enhanced motivational biases.

Study II: Motivational biases in go and nogo learning from immediate versus delayed feedback

This section is based on the following research article published in "European Journal of Neuroscience" and reprinted in the Appendix under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0):

Vahedi, J., Schneider, S., Swiatek, L., Peterburs, J., & Bellebaum, C. (2026). Motivational Biases in Go and Nogo Learning From Immediate Versus Delayed Feedback. *European Journal of Neuroscience*, *64*(8), e70717. https://doi.org/10.1111/ejn.70717

Note: This article was published after submission of the present dissertation but prior to its official approval for printing.

Rationale and hypotheses

Motivational biases have been linked to the dopaminergic modulation of the striatum (cf. Guitart-Masip, Duzel, et al., 2014; Richter et al., 2014), although it remains debated whether these biases reflect Pavlovian-biased action selection (Guitart-Masip, Huys, et al., 2012), biased instrumental learning (de Boer et al., 2019), or both (Swart et al., 2017). Importantly, striatal involvement during learning has been shown to depend on feedback timing: Learning from immediate feedback more strongly engages the striatum, whereas learning from delayed feedback more strongly engages the hippocampus (Foerde & Shohamy, 2011; Hinneberg & Hegele, 2022). Such a shift in the neural systems underlying feedback-based learning has also been reflected in the FRN/RewP, with gradually decreasing outcome valence coding as feedback delay increases (Peterburs et al., 2016). Given that motivational biases may reflect biased instrumental learning (Swart et al., 2017) and arise through striatal mechanisms (Guitart-Masip, Duzel, et al., 2014; Richter et al., 2014), with striatal involvement appearing most pronounced when feedback is immediate (Foerde & Shohamy, 2011), Study II investigated whether motivational biases are modulated by feedback timing.

Moreover, if motivational biases reflect biased instrumental learning, with facilitated learning from rewarded action and impaired learning from punished inaction (Swart et al., 2017), this may be manifested in action-biased feedback processing. While previous work indeed showed enhanced FRN/RewP outcome valence coding for actions over inactions (Bikute et al., 2022; Di Bernardi Luft et

al., 2024; Yeung et al., 2005), which would generally align with biased instrumental learning, these studies implemented (in)actions as involuntary non-choices and not in relation with motivational biases. Accordingly, Study II examined whether action-biased feedback processing in the FRN/RewP underlies motivational biases, as would be conceivable if they reflect biased instrumental learning.

Two groups of participants completed a modified orthogonalized go/nogo task, either learning from immediate or delayed feedback, while EEG was recorded. Generally, it was hypothesized that motivational biases reflect biased instrumental learning, and that computational modeling of choice behavior would favor a model assuming facilitated learning from rewarded action and/or impaired learning from punished inaction (Swart et al., 2017).

In addition, assuming that delayed feedback may reduce striatal involvement and shift learning toward more declarative, possibly more goal-directed control (Foerde & Shohamy, 2011), motivational biases were hypothesized to be attenuated when learning from delayed relative to immediate feedback. However, because of their robustness (e.g., Peterburs et al., 2021) and evidence indicating shared neural mechanisms for immediate and delayed feedback (Weber & Bellebaum, 2024; Weismüller et al., 2018) motivational biases may not be overridden but persist across feedback timings.

Finally, it was expected that biased learning would be reflected in action-biased feedback processing in the FRN/RewP, e.g., enhanced outcome valence coding and/or PE coding for action versus inaction, particularly for immediate feedback (Bikute et al., 2022). Exploratory analyses were conducted on the P3, for which similarly action-biased feedback processing was conceivable (Schevernels et al., 2016).

Methods

Participants

In total, data from 56 healthy student volunteers were included in the analyses. Participants were recruited through public advertisements and/or social media and randomly assigned to one of two experimental conditions: one that involved learning from immediate (n=28), and one from delayed feedback (n=28). The sample size was based on previous ERP studies on feedback processing (Bellebaum & Colosio, 2014; Weber & Bellebaum, 2024) and prior

studies reporting behavioral modulation of motivational biases (de Boer et al., 2019; Guitart-Masip, Chowdhury, et al., 2012). Overall, participants were mostly young (M = 21.47; SD = 3.68), female (82%), and right-handed (88%), with an average IQ (M = 106.87, SD = 8.17), as assessed by the MWT-B (Lehrl et al., 1995; Merz et al., 1975). The experimental groups did not differ significantly in any of these variables. None of the participants reported a history of mental disorders and/or psychotropic medication.

Experimental task and procedure

Participants completed a modified orthogonalized go/nogo task, either learning from immediate or delayed feedback. Four fractal stimuli (obtained from https://github.com/smathot/materials_for_P0010.5; Mathôt et al., 2015) were selected that cued conditions GW, GAL, NGW, NGAL, respectively. While retaining the general task structure, the modified orthogonalized go/nogo task used in Study II differed from the basic version described under General procedures in several respects. Specifically, the participant's choice was visually confirmed by presenting a hand symbol below the white circle on the corresponding side of a "go" choice, or by presenting a crossed-out hand symbol in the middle of the screen in case of a "nogo" choice. Most importantly, however, trial timings differed. While the immediate feedback group received feedback 500 ms after choice confirmation, the delayed feedback group received feedback after 6,500 ms. Importantly, to compensate for differential trial lengths between feedback timings, the intertrial interval was extended by additional 6,000 ms in the immediate feedback group, ensuring comparable overall task duration. The experiment comprised four blocks of 40 trials each, amounting to 160 trials in total (excluding five practice trials). Task completion took approximately 35 minutes.

EEG recording and data processing

EEG recording and preprocessing was performed as described under General procedures, including re-referencing to the mastoid channels, data filtering and ocular correction independent component analysis. Notably, feedback-locked segments, each representing a single-trial, were eventually extracted from -200 to 600 ms relative to feedback (win, loss), using the 200 ms pre-feedback interval for baseline correction. Importantly, consistent with Albrecht et al. (2016) and given that action-biased feedback processing should primarily emerge for win and loss feedback, draw trials were not considered in the EEG

analyses. Finally, automatic artifact rejection was applied before exporting the remaining segments for further data processing.

EEG data were analyzed at the single-trial level and focused on the FRN/RewP and P3, scored in a fronto-central (Fz, FCz, FC1, FC2) and centro-parietal (Cz, CP1, CP2, Pz) electrode cluster, respectively. ERP component scoring was performed using a data-driven approach. For each ERP component, a composite waveform was created by averaging the win- and loss-related grand average (GA) signals across electrodes of its respective cluster. Next, peak detection was performed on the composite waveform within a priori, literature-backed search windows. The FRN/RewP peak was defined as the local minimum between 200-350 ms post-feedback (Faßbender et al., 2023) in the fronto-central composite waveform, whereas the P3 peak was defined as the local maximum between 250-500 ms post-feedback (Polich, 2007) in the centro-parietal composite waveform. Each ERP component was eventually scored as the mean amplitude within ±30 ms of the identified peak latency at each electrode of the respective cluster and on each single-trial per participant. Consistent with Weber and Bellebaum (2024) and visual inspection of the GA waveforms indicating slight timing differences between immediate and delayed feedback, this ERP scoring procedure was applied separately for each feedback timing.

Importantly, this procedure may have the advantage of providing a common extraction window for a given ERP component while remaining agnostic to the presence and direction of condition-dependent ERP effects. As a consequence, this procedure may hence be preferred over related procedures relying on peak estimates derived from a difference waveform, as it avoids circularity by defining the extraction time window independently of the observed differences between wins and losses (cf. Luck & Gaspelin, 2017). Hence, this procedure may be less likely to capitalize on noise and inflate false-positive findings.

Computational modeling

A series of increasingly complex RL models was fitted to test for the presence of biased instrumental learning, roughly following Swart et al. (2017). In all models, choice probabilities were calculated based on state-action weights $W_t(a_t, s_t)$ and an inverse temperature parameter $\beta \in (0, +\infty)$, i.e.,

$$p(a_t|\, s_t) = \frac{\exp\big(\beta * W_t(a_t, s_t)\big)}{\sum_{a'} \exp(\beta * W_t(a', s_t))}$$

In the most parsimonious model M0, $W_t(a_t, s_t)$ reflected typical state-action values and hence equaled $Q_t(a_t, s_t)$. Q-values were updated based on the PE, i.e., the difference between the received feedback $r \in \{-1,0,1\}$ (indicating loss, draw, and win, respectively) and the current Q-value, and a learning rate $\varepsilon \in [0, 1]$, i.e.,

$$Q_t(a_t, s_t) = Q_{t-1}(a_t, s_t) + \varepsilon\,(r_t - Q_{t-1}(a_t, s_t))$$

Model M1 assumed choice behavior was additionally shaped by a general go bias parameter $b \in (-\infty, +\infty)$, implemented by updating $W_t(a_t, s_t)$, i.e.,

$$W_t(a_t, s_t) = \begin{matrix} Q_t(a_t, s_t) + b & if\ go \\ Q_t(a_t, s_t) & else \end{matrix}$$

Model M2 additionally assumed a Pavlovian (response) bias parameter $\pi \in (-\infty, +\infty)$, i.e.,

$$W_t(a_t, s_t) = \begin{matrix} Q_t(a_t, s_t) + b + \pi V_t(s_t) & if\ go \\ Q_t(a_t, s_t) & else \end{matrix}$$

where V-values were updated analogously to Q-values, but independently of the response, i.e.,

$$V_t(s_t) = V_{t-1}(s_t) + \varepsilon(r_t - V_{t-1}(s_t))$$

Models M3-M5 involved different parametrizations of an instrumental learning bias parameter $k \in (-\infty, +\infty)$. At the conceptual level, this parameter was used as a bonus term applied to the learning rate for rewarded go choices and/or as a penalty term applied to the learning rate for punished nogo choices[11], i.e.,

$$\varepsilon = \begin{cases} \varepsilon + k & if\ a = go\ and\ r = win \\ \varepsilon - k & if\ a = nogo\ and\ r = loss \\ \varepsilon & else \end{cases}$$

Model M3, hence included an instrumental learning bias for both rewarded go and punished nogo, whereas model M4 only assumed facilitated learning from rewarded go ($k_{rewardedGo}$) and M5 only impaired learning from punished nogo ($k_{punishedNogo}$). In models M6-M8, both a Pavlovian response bias and one of the parametrizations of an instrumental learning bias were assumed. For all models, Q- and V-values were initialized at the value of 0.

[11] Because adding or subtracting k could push ε outside its mathematical bounds (i.e., [0,1]), ε was optimized in an unconstrained space, i.e., $\varepsilon \in (-\infty, +\infty)$, but mapped onto [0,1] via inverse logit transformation (Algermissen et al., 2024; Swart et al., 2018; Swart et al., 2017).

Models were fitted via the *fmincon* function in MATLAB (MathWorks Inc., USA) and compared to identify the model that best captured the observed choice data. For each model, choice probabilities were used to calculate the NLL,

$$NLL = -\sum_t \log(p(a_t|\, s_t))$$

which was then used to calculate the Bayesian information criterion (BIC),

$$BIC = 2NLL + n_{params} \log(N)$$

where n_{params} is the number of free model parameters and N the number of observations. The model with the lowest (mean) BIC value was considered the overall best-fitting model.

Statistical analysis

Prior to statistical analyses, it was ensured that participants included in the analyses met the data quality criteria detailed under General procedures.

Single-trial choice accuracy data were analyzed using GLMM analysis in R, with choice accuracy defined as whether the required instrumental response was selected. Fixed effects included the categorical between-subject predictor *feedback timing* (immediate, delayed) as well as the within-subject predictors *required response* (go, nogo) and *cue valence* (win, avoid-losing). A significant *required response* × *cue valence* interaction would hence be indicative of the presence of motivational biases.

Feedback processing was examined via two complementary LMM analyses on single-trial FRN/RewP or P3 amplitudes, respectively. In both analyses, fixed effects included the categorical between-subject predictor *feedback timing* (immediate, delayed) as well as the within-subject predictors *response type* (go, nogo) and *outcome valence* (win, loss). Importantly, note that the predictor *response type* coded the actual rather than required response and given that biased instrumental learning should primarily affect processing of win and loss feedback, draw trials were not considered. To examine the representation of PEs, the absolute value of Q (i.e., $|Q|$), obtained via latent variable inference from the winning RL model, was added as a continuous predictor (Burnside et al., 2019; Fischer & Ullsperger, 2013; also see Caplin & Dean, 2008), where a significant *outcome valence* × $|Q|$ interaction would be indicative for the encoding of signed PEs. With these predictors, action-biased feedback processing would be reflected in the *response type* × *outcome valence* (× $|Q|$) interaction effect. We

ensured to include a minimum of ten trials (see Bellebaum & Daum, 2008; Ichikawa et al., 2010) for each outcome valence × response type combination. Significant interaction effects were probed while correcting for the *false discovery rate* (Benjamini & Hochberg, 1995).

Results and discussion

Motivational biases were generally replicated, but no significant differences were observed between learning from immediate and delayed feedback. This finding was unexpected, given that motivational biases have been linked to the striatum (e.g., de Boer et al., 2019; Guitart-Masip, Duzel, et al., 2014; Perosa et al., 2020; Richter et al., 2014), which has been indicated to be less strongly involved in learning from delayed feedback (Foerde & Shohamy, 2011; Hinneberg & Hegele, 2022; Lighthall et al., 2018). While this finding may challenge the role of the striatum in motivational biases, it may also be explained by shared mechanisms involved in learning from both immediate and delayed feedback (cf. Weber & Bellebaum, 2024; Weismüller et al., 2018) and therefore extends previous evidence highlighting motivational biases as robust and difficult to modify (e.g., Ereira et al., 2021; Peterburs et al., 2021).

Moreover, despite recent evidence suggesting a contribution of biased instrumental learning to motivational biases (Algermissen et al., 2024; de Boer et al., 2019; Swart et al., 2018; Swart et al., 2017), RL modeling revealed that motivational biases were overall better explained in terms of a Pavlovian response bias on action selection (M2), therefore challenging biased instrumental learning as a *substantial* mechanism to motivational biases. However, prior evidence for biased instrumental learning was mainly based on a designated adaptation of the orthogonalized go/nogo task which may better disentangle Pavlovian from instrumental contributions to learning and decision-making (Algermissen et al., 2024; Swart et al., 2018; Swart et al., 2017; but see de Boer et al., 2019). Moreover, there was some variance in which RL model predicted actual decision-making best. Although it can therefore not be excluded that biased instrumental learning contributed to motivational biases, the results suggest that a Pavlovian response bias may be a more robust mechanism.

Aligning with the limited support for biased instrumental learning, neither the FRN/RewP nor the P3 reflected action-biased feedback processing. Still, this finding contrasted with previous studies (Bikute et al., 2022; Di Bernardi Luft et

al., 2024; Schevernels et al., 2016; Yeung et al., 2005), which implemented actions and inactions as forced non-choices, thereby suggesting that these findings may not extend to contexts in which actions and inactions are chosen voluntarily. Interestingly, however, the FRN/RewP reflected a -PE for immediate but not delayed feedback, whereas the P3 signaled a +PE independently of feedback timing. Together with results from Weber and Bellebaum (2024) and Weismüller et al. (2018), these results therefore suggest that, despite differential mechanisms for immediate and delayed feedback, there are also similarities.

Conclusion

Study II found motivational biases across learning from immediate and delayed feedback, suggesting that these biases are not a mere feature of implicit, striatal-based learning but also extend to more declarative learning from delayed feedback. These motivational biases were overall best accounted for by a Pavlovian response bias rather than biased instrumental learning. Given that also the FRN/RewP and P3 did not reflect action-biased feedback processing, these findings may challenge the role of biased learning and feedback processing during the emergence of motivational biases.

Study III: Altered reward processing in obsessive-compulsive disorder: Insights from active and observational learning

This section is based on the following research article published in "Psychophysiology" and reprinted in the Appendix under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0):

Vahedi, J., Bahic, A., Chaliani, I., Schilbach, L., Ciupka-Schön, B., Bellebaum, C., Pietrowsky, R., & Peterburs, J. (2025). Altered Reward Processing in Obsessive–Compulsive Disorder: Insights From Active and Observational Learning. *Psychophysiology*, *62*(9), e70142. https://doi.org/10.1111/psyp.70142

Rationale and hypotheses

Whereas the ERN has been thoroughly investigated in OCD and consistently found to be enhanced (Riesel, 2019), FRN/RewP studies in OCD are relatively scarce. Although the FRN/RewP may also reflect reward processing (Holroyd et al., 2008; Proudfit, 2015), an influential account suggests that the FRN/RewP elicited by negative feedback reflects an extension from internal to external error processing (Holroyd & Coles, 2002). In support of this notion, the neural source of both the ERN and FRN/RewP has been localized in the MCC (Debener et al., 2005; Fu et al., 2019; Hauser et al., 2014; Oerlemans et al., 2025). However, previous FRN/RewP studies in OCD have yielded highly inconsistent results (Endrass et al., 2013; Luo et al., 2020; Nieuwenhuis, Nielen, et al., 2005). Given the reliable evidence for a hyperactive ERN in OCD (Riesel, 2019) and aiming to expand previous FRN/RewP findings in OCD, Study III investigated whether the processing of errors as indicated by negative performance feedback during learning is likewise altered in OCD.

Moreover, while feedback processing typically involves monitoring the consequences of one's own decisions, it can also involve monitoring others' outcomes through observation. Given that the striatum is considered less strongly involved in observational learning (Bellebaum, Jokisch, et al., 2012; Kobza et al., 2012), alongside the role of the striatum in OCD pathophysiology (Burguiere et al., 2015), OCD-related alterations in feedback processing and instrumental learning may depend on agency. However, this has not yet been investigated.

Participants completed an active and observational version of a probabilistic learning task, while EEG was recorded (Bellebaum & Colosio, 2014). It was

hypothesized that OCD patients would show impaired learning performance, particularly for active learning, possibly manifesting in enhanced choice perseveration (Moritz & Pohl, 2009). Assuming hyperactive error processing extends to feedback processing during learning, the FRN/RewP was expected to be more negative to negative feedback in OCD, although the direction of FRN/RewP alterations remained speculative given previous inconsistent findings.

Methods

Participants

In total, data from 83 participants were included in the analyses: 27 OCD patients, 27 HCs and 29 patients with social anxiety disorder (SAD), who served as a clinical control group. The sample size was determined based on a previous EEG study that compared OCD patients with both SAD patients and HCs (Endrass et al., 2014).

Patients were recruited from collaborating healthcare facilities as well as local self-help groups. The Structured Clinical Interview for DSM-5—Clinician Version (SCID-5-CV; First et al., 2016, German Version: Beesdo-Baum et al., 2019) was conducted to confirm that patients met the diagnostic criteria for OCD or SAD, respectively. Importantly, patients must *not* present comorbid OCD and SAD, a lifetime history of substance use disorder, bipolar disorder or psychotic symptoms. Patients with other comorbid disorders (mostly affective disorders) and current psychopharmacological treatment (mostly selective serotonin reuptake inhibitors) were included in the analyses.

HCs were recruited via public advertisement and/or social media and must not present a history of mental or neurological disorders (including a family history of OCD) and/or current psychotropic medication. These eligibility criteria were checked via a custom screening tool based on the SCID-5.

Overall, participants were mostly young (M = 31.93; SD = 11.14), female (64%), and right-handed (89%), with an average IQ (M = 112.90 , SD = 14.84), as assessed using the MWT-B (Lehrl et al., 1995; Merz et al., 1975). The diagnostic groups did not differ significantly in any of these variables.

Experimental task and procedure

Participants completed both an active and observational version of a probabilistic feedback learning task, first introduced by Frank et al. (2004) and

extended for observational learning by Bellebaum, Rustemeier, et al. (2012), which consisted of different types of blocks.

In learning blocks, participants were presented with one of three stimulus pairs, each consisting of modified Japanese characters, on each trial (A/B, C/D, E/F). In the active task version, participants were asked to select one of the paired stimuli via button press, whereas in the observational task version participants observed the recorded choice of a previous participant, indicated by a hand symbol. After a short delay, participants received symbolic feedback indicating either a win of 20 points or a loss of 10 points, contingent on their own or the observed choice, respectively. However, unknown to the participants, each stimulus was assigned a distinctive reward probability which was reciprocal within each stimulus pair (A/B = 80%/20%, C/D = 70%/30%; E/F = 60%/40%), such that the selection of the stimulus associated with the higher (lower) reward probability not always resulted in positive (negative) feedback.

Subsequent test blocks were nearly identical to the learning phase. Importantly, however, participants had to actively choose between stimuli, both in the active and observational task version and trial-by-trial feedback was omitted, as compared to learning blocks. Nonetheless, participants were instructed to continue selecting the stimuli they anticipated would maximize reward, based on knowledge gained through previous learning blocks. Hence, test blocks allowed the assessment of learning performance across both the active and observational task version.

Task versions were completed in separate sessions using distinctive stimulus sets. Task order, i.e., whether to start with the active or observational version in the first session, was counterbalanced. Each task comprised nine blocks with a total of 400 trials (excluding ten practice trials), with four learning blocks of 60 trials each, alternating with four test blocks of 30 trials each, and followed by a final transfer block of 40 trials.[12] Task completion took approximately 30 minutes.

[12] In the transfer block, participants selected between new combinations of stimuli, pairing stimulus A (80% reward probability) and stimulus B (20% reward probability) with all stimuli from the other stimulus pairs. However, the transfer block will not be further discussed here.

Exploratory computational modeling

To explore PE representation in feedback processing (see Statistical analysis), exploratory computational modeling was performed on behavioral choice data from both active and observational learning. Computational modeling involved fitting different RL models to the participants behavioral data and comparing their model fits (based on the BIC) to determine which model best accounted for actual choice behavior in test and transfer trials (cf. Schultner et al., 2024). In contrast to Study II, which aimed to examine the latent computational mechanisms underlying decision-making, the primary purpose of RL modeling in Study III was the estimation of PEs. The best-fitting model included dual learning rates for positive and negative feedback, an inverse temperature parameter, and a choice-induced preference change parameter, that was used to update action values even in the absence of feedback (cf. Ptasczynski et al., 2022).

EEG recording and data processing

EEG recording and preprocessing followed the procedures outlined under General procedures and included re-referencing to the mastoid channels, data filtering and ocular correction independent component analysis. Feedback-locked segments, derived from learning trials, were extracted from -200 to 600 ms relative to feedback (win, loss), using the 200 ms pre-feedback interval for baseline correction. Automatic artifact rejection was applied before exporting the data for further processing.

EEG data were analyzed at the single-trial level and focused on feedback processing as indexed by the FRN/RewP. The FRN/RewP was scored in a fronto-central electrode cluster (Fz, FCz, FC1, FC2, Cz) using a data-driven approach, as described in Study II. First, a composite waveform was created by averaging the win- and loss-related GA signals, pooled across electrodes. Next, this composite waveform was used to search the FRN/RewP peak, defined as the local minimum between 200-350 ms post-feedback (Faßbender et al., 2023). Finally, the FRN/RewP was scored as the mean amplitude within ±30 ms relative to the identified peak latency from the composite waveform, at each electrode and each single trial per participant. Because visual inspection indicated slight latency differences in the FRN/RewP for active and observational learning, this procedure was applied separately for each agency condition. A supplementary P3 analysis was conducted using the same ERP

scoring procedure but applied to a centro-parietal electrode cluster (Cz, CP1, CP2, Pz), and an a priori search window of 290-450 ms post-feedback (van Dinteren et al., 2014) to identify the P3 peak (local maximum).

Statistical analysis

Single-trial choice accuracy data were analyzed using a GLMM, where correct choices reflected selecting the stimulus linked to the higher reward probability. In order to compare choice accuracies between active and observational learning, this analysis was hence restricted to trials from test blocks. Fixed effects included the categorical between-subject predictor *group* (OCD, HC, SAD), the within-subject predictor *agency* (active, observational), and the continuous predictors *reward contingency* (A/B: 80%, C/D: 70%, E/F: 60%, coded as −1, 0, 1), and *block* (1-4, centered around its midpoint, i.e., 2.5).

A second GLMM was specified to examine win-stay/lose-shift behavior, assessed via analyzing single-trial choice shifting behavior, reflecting whether participants repeated or switched their previous choice when the same stimulus pair was encountered again. Because participants' own decision-making led to feedback only in learning blocks during active learning, this analysis was restricted to trials from active learning blocks. Fixed effects included the categorical between-subject predictor *group* (OCD, HC, SAD) and the within-subject predictors *previous outcome valence* (win, loss) and *previous outcome authenticity* (authentic, misleading). Notably, *previous outcome authenticity* was implemented as—given the probabilistic design—staying after wins and shifting after losses was only adaptive when feedback was indeed authentic (i.e., aligned with the choice accuracy, see also Kirschner et al., 2024). Additionally, *block* (1-4, centered around 2.5) was included as a continuous within-subject predictor.

Feedback processing was analyzed using an LMM on single-trial FRN/RewP amplitudes. Fixed effects included the categorical between-subject predictor *group* (OCD, HC, SAD) and the within-subject predictors *agency* (active, observational), and *outcome valence* (win, loss).

A second (model-based) LMM was specified to confirm that potential processing differences did not simply reflect differences in learning and reward expectancies. To this end, the original model-free LMM, reported above, was extended by including $|PE|$ derived from exploratory computational modeling as a continuous within-subject predictor. This model hence allowed testing for

the presence of both unsigned PEs (main effect $|PE|$) and signed PEs (*outcome valence* × $|PE|$ interaction effect). Note that although this approach is different from that described for Study II, it has been used in previous studies to disentangle effects of outcome valence and general expectancy (see e.g., Weber & Bellebaum, 2024). Supplementary LMM analyses of the P3 were conducted using the same predictors described above. Significant interaction effects were probed while correcting for *the false discovery rate* (Benjamini & Hochberg, 1995).

Results and discussion

As expected, OCD patients showed impaired learning performance, while this was especially pronounced for the easiest-to-learn stimulus pair with the highest reward contingency. Notably, learning impairments in OCD did not depend on agency, therefore showing for the first time that learning impairments in OCD are not limited to active learning but extend to observational learning.

Unexpectedly, however, OCD patients showed more indecisive rather than perseverative decision-making, with increased maladaptive shifting particularly following positive feedback. This finding may relate to uncertainty induced through the probabilistic task design. Specifically, OCD patients have been suggested to show increased perseveration only under low uncertainty but increased indecisiveness under high uncertainty (Apergis-Schoute et al., 2024; Fradkin et al., 2020).

The FRN/RewP differentiated wins and losses more strongly in OCD patients compared to HCs during active—but not observational—learning. Unexpectedly, however, this was driven by OCD patients showing a more positive FRN/RewP to wins, suggesting altered reward rather than punishment processing in OCD. Altered FRN/RewP amplitudes have previously often been interpreted in terms of disrupted outcome prediction (O'Toole et al., 2012). Accordingly, because OCD patients showed impaired learning and experienced wins less frequently, wins may have been more surprising, which could hence account for the differential sensitivity to reward in OCD. However, model-based FRN/RewP analyses did not provide evidence for altered PE processing and OCD patients showed a more positive FRN/RewP response to wins, even after accounting for the PE, suggesting broader differences in reward sensitivity in OCD.

Following current interpretations of the FRN/RewP as a reward-sensitive RewP (Proudfit, 2015), increased positivity to wins would hence suggest hyperactive reward processing in OCD. Consistent with this interpretation, but on a theoretical note, repetitive behaviors and/or mental acts in OCD have been theorized to persist because they are excessively rewarding (see Bragdon et al., 2023). These findings therefore suggest that aside from aberrant error processing, also reward processing may contribute to the pathophysiology of OCD.

Notably, enhanced outcome valence coding in OCD, with greater positivity to wins, was primarily observed for active learning, aligning with the idea that with reduced striatal involvement in observational learning (Bellebaum, Jokisch, et al., 2012; Kobza et al., 2012), aberrant striatal functioning in OCD (Burguiere et al., 2015) may primarily interfere with active learning. However, note that after controlling for the PE, altered reward processing in OCD was found independent of agency. Comparisons between OCD and SAD patients revealed only nuanced differences between OCD and SAD patients, that were overall rather subtle and related to slight differences in task performance and choice shifting behavior, suggesting that the reported differences may not be particularly characteristic of OCD. Supplementary P3 analyses showed attenuated P3 outcome valence coding in OCD, particularly for active learning.

On a more general note, the FRN/RewP was found to encode both a -PE and +PE, only for active but not observational learning, replicating previous results by Burnside et al. (2019). Supplementary P3 analyses, however, indicated that whereas the P3 signaled both +PEs and -PEs for active learning, it signaled a +PE but no -PE also for observational learning.

Conclusion

Study III found impaired learning and increased indecisiveness in OCD, while showing that impaired learning was not limited to active learning but extended to observational learning. This was accompanied by enhanced FRN/RewP outcome valence coding with more positive amplitudes to wins, primarily for active learning, suggesting altered reward—rather than punishment—processing in OCD.

Study IV: Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder

This section is based on the following research article provided in the Appendix, which has been submitted for publication and is currently under review:

Vahedi, J., Bahic, A., Chaliani, I., Schilbach, L., Ciupka-Schön, B., Bellebaum, C., Pietrowsky, R., & Peterburs, J. (2026). Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder. *Manuscript submitted for publication*

Rationale and hypotheses

Altered motivational biases have been generally linked to maladaptive behavior and observed across numerous mental disorders (Albrecht et al., 2016; Chen et al., 2023; Ousdal et al., 2018). However, evidence from OCD is scarce, despite the neural mechanisms involved in motivational biases overlap with those implicated in OCD pathophysiology, such as altered PE signaling (Hauser et al., 2017; Murray et al., 2019; Suzuki et al., 2023) and fronto-striatal dysfunction (e.g., Pauls et al., 2014). Using the PIT paradigm, previous studies have suggested attenuated motivational biases in (sub)clinical OCD (Krypotos & Engelhard, 2020; Peng et al., 2022; but see Marzuki et al., 2024), whereas a recent study employing the orthogonalized go/nogo task did not find motivational biases to depend on OCD-symptoms in subclinical participants (Scholz et al., 2026). Accordingly, whether motivational biases, as assessed by the orthogonalized go/nogo task, are altered in OCD remains to be clarified.

Given the presumed role of the striatum in both motivational biases (cf. Guitart-Masip, Duzel, et al., 2014; Richter et al., 2014) and OCD (Burguiere et al., 2015), and given that the striatum appears less strongly involved in observational learning (Bellebaum, Jokisch, et al., 2012; Kobza et al., 2012), Study IV aimed to test whether motivational biases are altered in OCD and differently modulated depending on agency. Moreover, it was aimed to assess whether and how action-biased feedback processing contributes to motivational biases in OCD by examining the FRN/RewP and P3 while participants completed an active and observational variant of the orthogonalized go/nogo task (Peterburs et al., 2021).

Based on previous evidence (Peterburs et al., 2021), it was hypothesized that motivational biases would emerge across active and observational learning,

although OCD-related alterations in motivational biases may be more strongly pronounced in active learning compared to observational learning. Specifically, it was assumed that dysregulated fronto-striatal circuits, with overactivity of the direct "go" pathway (e.g., Pauls et al., 2014) may lead to enhanced motivational biases in OCD, although previous evidence found motivational biases in OCD to be attenuated (Peng et al., 2022), or unchanged (Scholz et al., 2026). Action-biased feedback processing in the FRN/RewP and/or P3 was expected to contribute to motivational biases, and to be correspondingly increased or attenuated in OCD, again with any alterations in OCD assumed to be most strongly pronounced for active learning.

Methods

Participants

Participants in this study were drawn from the same recruited sample as for Study III, with data from 81 participants included in the analyses: 26 OCD patients, 28 HCs and 27 SAD patients. Note that different group sizes compared to Study III resulted from data exclusions (e.g., due to technical issues or data quality), affecting different participants of the recruited sample. Apart from that, eligibility criteria were the same as for Study III. The sample size was determined based on previous studies on motivational biases in clinical populations (e.g., Montagnese et al., 2020; Ousdal et al., 2018) and previous ERP studies on feedback processing (Bellebaum & Colosio, 2014; Weismüller & Bellebaum, 2016).

Overall, participants were mostly young (M = 32.51; SD = 11.42), female (65%), and right-handed (89%), with an average IQ (M = 113.26, SD = 14.95), as assessed by the MWT-B (Lehrl et al., 1995; Merz et al., 1975). The diagnostic groups did not differ significantly in any of these variables.

Experimental task and procedure

Participants completed both an active and observational version of the orthogonalized go/nogo task, similar to that described in (Peterburs et al., 2021). As described in the basic task description, this task involved four cued conditions: GW, GAL, NGW and NGAL.

However, deviating from the basic task description provided under General procedures, the task used in Study IV not only comprised learning blocks with trial-by-trial feedback, but also test blocks, in which trials ended before

feedback was provided, i.e., after the decision stage. Crucially, while test blocks were identical between the active and observational task version, learning blocks differed.

Specifically, in the active task version participants performed learning blocks themselves, where feedback was provided on their own choices. By contrast, in learning blocks of the observational task version, participants observed the recorded choice of a previous participant indicated by a hand symbol in case of a "go" choice or the non-appearance of a hand symbol in case of a "nogo" choice. Hence, for observational learning, feedback was vicarious and referred to the choice made by the observed participant.

For a comparable assessment of task performance between task versions, subsequent test blocks required active decision-making in both the active and observational task version. Accordingly, participants of both task versions had to choose between "go" and "nogo", while feedback was omitted. Yet, participants were instructed to choose the response they anticipated would maximize reward and minimize loss, based on knowledge gained through previous learning blocks.

Task versions were completed in separate sessions using unique stimulus sets. Whether participants first completed the active or observational task version was counterbalanced between participants. Each task version comprised eight blocks, with four learning blocks, each followed by a test block, with 40 trials per block, amounting to 320 trials in total (excluding ten practice trials). Task completion took approximately 35 minutes.

EEG recording and data processing

The EEG recording and preprocessing complied to the procedures under General procedures, including re-referencing to the mastoid channels, data filtering and ocular correction independent component analysis. Given the substantial overlap in task design, segmentation and ERP scoring procedures were nearly identical to those reported for Study II. Feedback-locked segments (=single-trials), derived from learning trials, were extracted from -200 to 600 ms relative to feedback (win, loss), using the 200 ms pre-feedback interval for baseline correction. In accordance with Study II, only win and loss feedback was considered, given that biased instrumental learning and hence action-biased feedback processing should primarily manifest for non-neutral feedback.

Segments containing artifacts were removed using automatic artifact rejection, before exporting the data for further processing.

As described in more detail for Study II, EEG data were analyzed at the single-trial level, focusing on the fronto-central FRN/RewP (Fz, FCz, FC1, FC2) and centro-parietal P3 (Cz, CP1, CP2, Pz). As for Studies II and III, a data-driven approach was used for ERP component scoring. Therefore, for each electrode cluster, a composite waveform was created representing the average of the win- and loss-related GA signals, pooled across electrodes. Next, the fronto-central composite waveform was used to search the FRN/RewP peak, defined as the local minimum between 200-350 ms post-feedback (Faßbender et al., 2023), whereas the P3 peak was searched as the local maximum between 250-500 ms post-feedback (Polich, 2007) in the centro-parietal composite waveform. Finally, ERP components were scored as the mean amplitude within ±30 ms relative to the identified peak latency from the respective composite waveform, at each electrode and each single-trial per participant. As, similar to Study III, visual inspection indicated slight latency differences in the FRN/RewP and P3 between active and observational learning, the above procedure was applied separately for each agency condition.

Statistical analysis

Prior to statistical analyses, it was ensured that participants included in the analyses met the data quality criteria detailed under General procedures.

As for Study II, single-trial choice accuracy data were analyzed using a GLMM in R, with choice accuracy defined as the selection of the required instrumental response. Fixed-effects included the categorical between-subject predictor *group* (OCD, HC, SAD) as well as the within-subject predictors *agency* (active, observational), *required response* (go, nogo) and *cue valence* (win, avoid-losing). With these predictors, a significant *required response* × *cue valence* interaction effect would hence indicate the presence of motivational biases.

Feedback processing was examined via two complementary LMM analyses on single-trial FRN/RewP or P3 amplitudes, respectively. Fixed-effects included the categorical between-subject predictor *group* (OCD, HC, SAD) as well as the within-subject predictors *agency* (active, observational), *response type* (go, nogo), and *outcome valence* (win, loss). In order to account for unspecific temporal effects, two additional predictors were added as continuous covariates of no interest: *block* and (within-block) *trial number* (both centered before inclusion).

Note, however, that these predictors were only included as fixed main effects, i.e., not in interaction with the predictors of interest to prevent model overfitting. As explained in more detail in Study II, analyses on feedback processing were restricted to non-neutral feedback, i.e., trials with win and loss feedback. It was ensured to include a minimum of ten trials for each combination of predictors (see Bellebaum & Daum, 2008; Ichikawa et al., 2010). Significant interaction effects were resolved with Holm-adjusted *p*-values (Holm, 1979) to correct for multiple comparisons.

Results and discussion

Although motivational biases were overall attenuated for observational compared to active learning, they were not found to be altered in OCD. Although unexpected, this finding aligns well with recent evidence suggesting that motivational biases may be unaffected in OCD (Marzuki et al., 2024; Scholz et al., 2026), despite being linked to fronto-striatal dysregulation (Pauls et al., 2014). It has been suggested that motivational biases arise through multiple mechanisms, i.e., a Pavlovian response bias and/or biased instrumental learning (de Boer et al., 2019; Guitart-Masip, Huys, et al., 2012; Swart et al., 2017). Importantly, however, whereas prior research found instrumental learning to be disrupted in OCD (Gillan et al., 2011), Pavlovian associative learning appears rather preserved (Myles et al., 2025). It may therefore be possible that motivational biases were primarily driven or maintained by the unaltered Pavlovian system in OCD.

Interestingly, however, although no alterations in motivational biases were found for OCD, feedback processing in the FRN/RewP showed altered sensitivity to self- versus other related outcomes, indicative of disrupted self-other monitoring. While post-hoc evaluation tentatively suggested that this effect was driven by altered processing of vicarious feedback, it did not survive Holm correction. Still, this finding broadly aligns with evidence of inflated responsibility and control beliefs (Reuven-Magril et al., 2008; Salkovskis et al., 2000) as well as heightened affective responses when observing others (Jansen et al., 2020), cautiously suggesting increased empathic engagement during observational learning in OCD. Notably, however, FRN/RewP alterations in OCD did not involve altered outcome valence coding nor were alterations found for the later P3. Comparisons between OCD and SAD patients revealed largely similar results. However, altered self-other distinction in the FRN/RewP in OCD was also found in comparison to SAD.

On a more general note, similar as for Study II, there was no evidence for action-biased feedback processing in the FRN/RewP. Yet, the P3 showed overall enhanced outcome valence coding following actions versus inactions, which, however, likely reflected a general action bias rather than biased instrumental learning. It could therefore not be supported that motivational biases involve action-biased feedback processing as would be suggested if these biases reflect biased instrumental learning.

Conclusion

Study IV failed to demonstrate that motivational biases are altered in OCD, while showing that motivational biases may be overall reduced for observational compared to active learning. Moreover, although feedback processing in neither the FRN/RewP nor P3 provided evidence for action-biased feedback processing, OCD may be associated with disrupted self-other monitoring, reflected in the FRN/RewP, which may be a particularly specific characteristic of OCD.

3 General Discussion

In this dissertation, I have presented four experimental studies, which aimed to provide an integrated perspective on how learning and feedback processing are shaped by task context, while primarily focusing on motivational biases. Two studies (Studies I and II) were conducted in healthy individuals, whereas the remaining two (Studies III and IV) additionally involved patients with OCD as well as a clinical control group of SAD patients, to assess clinical implications and explore specificity of findings for OCD. Participants were tested using well-established experimental paradigms, while the research presented in this dissertation adopted complementary methodologies including behavioral approaches, computational modeling and EEG, alongside advanced statistical modeling through (single-trial) mixed-effects model analyses.

It was found that, albeit robust, motivational biases were attenuated through emotional cues (Study I) and observational learning (Study IV). Yet, integrated evidence from Studies II and IV did not provide convincing support for a putative role of action-biased feedback processing underlying motivational biases. Aiming to assess clinical implications, Study III revealed impaired instrumental learning across both active and observational learning in OCD. This was accompanied by altered reward processing in the FRN/RewP, particularly for active learning. By contrast, examining motivational biases in Study IV neither showed alterations in motivational biases or overall instrumental learning, nor altered reward processing in OCD. Instead, evidence pointed to altered self-other distinction during feedback processing in patients with OCD. General implications of these findings are discussed in the following sections.

Insights into the nature of motivational biases

Context-dependent alterations of motivational biases

Given previous work highlighting the robustness of motivational biases (e.g., Ereira et al., 2021; Weber et al., 2022), one objective of this dissertation was to identify contextual factors that modulate their expression. In line with this objective, results demonstrated context-induced attenuation of motivational biases through emotional facial cues (Study I) and observational learning (Study IV).

This finding is interesting because both emotional facial cues and observational learning affect cognitive-affective engagement during learning, yet in opposite directions. Specifically, emotional facial stimuli have been shown to enhance arousal and attentional allocation (Duval et al., 2013; Sawada & Sato, 2015), indicative of increased cognitive-affective engagement. Conversely, relative to active learning, observational learning may involve overall reduced cognitive-affective engagement.

Although it may therefore seem contradictory that both emotional facial cues and observational learning attenuated motivational biases, this pattern may reflect the multifaceted nature of motivational biases, which appears to arise from multiple dissociable mechanisms. For instance, motivational biases were previously found to reflect both a Pavlovian response bias on action selection as well as biased instrumental learning (Algermissen et al., 2024; Swart et al., 2018; Swart et al., 2017). Yet, motivational biases may involve even more mechanisms, such as a recently proposed *Pavlovian persistence bias*, reflecting the tendency to persist with behavior in response to reward-predictive cues and shift behavior in response to punishment-predictive cues (Algermissen et al., 2024; Koutsoumpari et al., 2026). Accordingly, while both emotional facial cues and observational learning attenuated motivational biases, they may have affected different mechanisms.

Notably, in Study I, emotional facial cues primarily aimed to affect action selection in accordance with a Pavlovian response bias, i.e., positive emotional valence was expected to favor action invigoration, whereas negative emotional valence was expected to favor action suppression (cf. Cacioppo et al., 1999; Lang, 1995). Although this pattern was not observed across all cue conditions, the effects that did emerge were consistent with these predictions.

By contrast, Study IV focused more on instrumental aspects of motivational biases. Accordingly, whereas active learning relies on ascribing value to one's own responses by their outcomes, observational learning alters this instrumental contingency and requires inferring action values from observed choices and vicarious outcomes. Related to that, it has been shown that the striatum is less strongly involved in observational compared to active learning (Bellebaum et al., 2016; Kobza & Bellebaum, 2015; Kobza et al., 2012). Given the suggested role of the striatum in motivational biases (e.g., de Boer et al., 2019; Perosa et al., 2020), attenuation of motivational biases is hence not surprising. Moreover, this finding is particularly reasonable if motivational biases truly

arise through biased instrumental learning. Accordingly, when participants do not engage in action selection by themselves during learning, the typical learning advantage for rewarded actions and disadvantage for punished inaction should not emerge. In partial support for that, Study IV indeed found that attenuated motivational biases in observational learning were driven by impaired performance in the GW condition.

Nonetheless, while theoretically reasonable, it must be noted that converging evidence from Studies II and IV provided overall only limited support for a substantial role of biased instrumental learning to motivational biases. Moreover, deviating from the findings of Study IV, a previous study found motivational biases to be comparable between active and observational learning (Peterburs et al., 2021), which is why it was originally hypothesized that observational learning may not affect motivational biases. However, while these findings may challenge a substantial contribution of the proposed asymmetric learning from rewarded actions and punished inactions (Swart et al., 2017), they may not preclude the possibility that observational learning may have affected instrumental learning in another way that ultimately led to the attenuation of motivational biases.

It therefore appears likely that the attenuation of motivational biases through emotional facial cues and through observational learning have been driven through at least partially distinct mechanisms. Accordingly, these findings suggest that motivational biases may be multifaceted rather than reflecting a single mechanism.

Robustness of motivational biases

In contrast to the findings presented above, Study II failed to reveal that motivational biases were modulated by feedback timing. Moreover, although attenuated in Studies I and IV, motivational biases were not overcome. Instead, they persisted across all task contexts considered within this dissertation, strengthening the notion that they are overall fairly robust and especially difficult to overcome (see e.g., Asci et al., 2019; Ereira et al., 2021; Weber et al., 2022).

This robustness may be rooted in evolution. Indeed, Pavlovian approach and avoidance, in particular, have been deemed evolutionary sensible default responses to potentially rewarding and threatening stimuli, respectively (cf. Dayan et al., 2006; Rangel et al., 2008). Although not explicitly linked to

evolution, Dorfman and Gershman (2019) have suggested that such Pavlovian mechanisms become particularly influential in uncontrollable environments, which resonates well with evidence suggesting motivational biases to be relatively enhanced under low (outcome) controllability (Csifcsák et al., 2020; Raab et al., 2024). Additionally, the robustness of motivational biases may be warranted by its aforementioned multifaceted nature which likely involves multiple dissociable mechanisms (Guitart-Masip, Huys, et al., 2012; Koutsoumpari et al., 2026; Swart et al., 2017).

Importantly, although motivational biases were found to be attenuated in Studies I and IV, this attenuation was only adaptive in Study I while using emotional facial cues, and specifically when the response tendency associated with the emotional valence of the cue aligned with the required instrumental response (CON). Conversely, when the response tendency associated with the emotional valence of the cue conflicted with the required instrumental response (INC), or following observational learning, the attenuation of motivational biases was maladaptive. Accordingly, while the adaptive attenuation of motivational biases in CON resulted from improved performance in conflict condition NGW, the maladaptive attenuation of motivational biases in INC was due to decreased performance in non-conflict conditions GW and NGAL. Similarly, maladaptive attenuation of motivational biases in observational learning was driven by impaired performance in the non-conflict condition GW. This further suggests that overcoming motivational biases via the implementation of goal-directed control in Pavlovian-instrumental conflict is particularly hard to achieve. Instead, motivational biases can be decreased at the expense of general performance, emphasizing that attenuated motivational biases do not necessarily reflect enhanced goal-directed control. Accordingly, the findings highlight motivational biases as a dynamic construct, spanning both facilitatory and impairing influences, which requires dissociating the strength of motivational biases and general performance when assessing goal-directed behavior.

Taken together, despite evidence for its sensitivity to contextual modulation (see Studies I and IV), motivational biases appear overall vastly stable and interventions for overcoming them have yet to be identified. These findings therefore suggest motivational biases as a particularly robust hallmark of learning and decision-making and that assessing goal-directed control over

motivational biases requires dissociating motivational bias strength and general task performance.

Role of feedback processing in motivational biases

Given the putative involvement of reward-related striatal modulation (cf. Guitart-Masip, Duzel, et al., 2014; Richter et al., 2014) and the proposed role of biased instrumental learning in motivational biases (Swart et al., 2017), one objective of this dissertation was to investigate the role of feedback processing in the emergence of these biases. Specifically, it was hypothesized that feedback processing would be biased toward outcomes following actions versus inactions, corresponding to facilitated learning from rewarded action and impaired learning from punished inaction that is assumed to underlie an instrumental learning bias (Swart et al., 2017). Importantly, however, neither Study II nor Study IV provided convincing evidence for such action-biased feedback processing.

This finding was surprising, given that previous studies have linked the FRN/RewP to enhanced feedback processing for actions relative to inactions (Bikute et al., 2022; Di Bernardi Luft et al., 2024; Yeung et al., 2005). However, whereas the orthogonalized go/nogo task, employed in Studies II and IV, required *voluntary* decisions between action and inaction, these previous studies implemented action and inaction as *involuntary* non-choices. Drawing from evidence suggesting that action is typically preferred over inaction (Sunderrajan & Albarracin, 2021), particularly inactions may have been extrinsically rather than intrinsically motivated in these prior studies. Against this background, previous reports of enhanced outcome valence coding for actions relative to inactions resemble findings comparing feedback processing between active and observational learning, for which similar effects on outcome valence coding have been reported (Bellebaum & Colosio, 2014; Bellebaum et al., 2010). Studies II and III therefore suggest that feedback processing in the FRN/RewP does not depend on the response type when *voluntarily* choosing between action and inaction. This finding is also broadly in line with evidence suggesting voluntary inaction as a mode of action (Kühn & Brass, 2009).

In contrast to the FRN/RewP, the P3 showed differences in the processing of feedback following action and inaction. However, these findings were rather subtle and inconsistent across Studies II and IV. Accordingly, while Study IV showed that outcome valence coding was indeed enhanced for outcomes

following action versus inaction, assessing action effects separately for positive and negative outcome valence failed to provide significant results. This is different from a previous study by Schevernels et al. (2016) who reported a corresponding action effect for positive feedback.

Crucially, and as stated before, the hypothesis of action-biased feedback processing was primarily motivated by findings suggesting motivational biases to reflect biased instrumental learning with facilitated learning from rewarded action and impaired learning from punished inaction (Algermissen et al., 2024; de Boer et al., 2019; Swart et al., 2018; Swart et al., 2017). However, at least for Study II, computational modeling revealed that motivational biases were overall better explained by a Pavlovian response bias rather than by involving biased instrumental learning. While this does not necessarily preclude any contribution of an instrumental learning bias, particularly given that there were interindividual differences in model fits, this may suggest motivational biases to be more robustly shaped by a Pavlovian response bias rather than by biased instrumental learning. Accordingly, failing to provide evidence for action-biased feedback processing may have resulted from only minor contribution of biased instrumental learning to motivational biases.

On a critical notice, although both the FRN/RewP and P3 are considered well-established markers of feedback processing (San Martín, 2012), failing to detect action-biased feedback processing in these measures does not mean that feedback processing is not biased toward actions in brain regions that are not captured by the FRN/RewP and/or P3.

Taken together, it could not be shown that motivational biases were reflected in action-biased feedback processing. While motivated by findings suggesting that motivational biases are substantially shaped by biased instrumental learning, the results presented in this dissertation challenge these findings by showing that motivational biases are most robustly shaped by a Pavlovian response bias. As action-biased feedback processing has also been reported outside the context of motivational biases, these findings may have important implications for the study of feedback processing in the voluntary selection of action and inaction.

Re-considering the role of the striatum in motivational biases

A striking commonality across Studies II and IV was that they involved conditions that have previously been linked to altered striatal activity. Specifically, learning from delayed compared to immediate feedback as well as

from observed, vicarious compared to own, self-referential feedback have been linked to relatively reduced striatal engagement (Bellebaum, Jokisch, et al., 2012; Foerde & Shohamy, 2011). Moreover, OCD has been linked to altered striatal functioning (Burguiere et al., 2015). Yet, while motivational biases were attenuated during observational compared to active learning, no differences were found between motivational biases following immediate versus delayed feedback. Finally, motivational biases further appeared unaltered in OCD. Given the putative role of the striatum in driving motivational biases, it was therefore surprising that motivational biases were only partially sensitive to these conditions.

Importantly, however, motivational biases have not been exclusively related to the striatum but also been linked to several other brain regions. For instance, recent findings by Queirazza et al. (2023) have suggested motivational biases to arise through the vmPFC, with synergistic Pavlovian-instrumental effects relying on limbic structures including the amygdala and hippocampus. Moreover, using simultaneous EEG-fMRI, Algermissen et al. (2024) demonstrated that biased PE signals underlying motivational biases emerged in the MCC before the striatum, hence again suggesting non-striatal influences to motivational biases. Finally, evidence from transcranial ultrasound stimulation recently suggested a causal role of both the MCC and the anterior insula in motivational biases (Koutsoumpari et al., 2026). Accordingly, these findings collectively suggest that motivational biases involve a distributed network of brain regions.

This does not necessarily mean that the striatum does not contribute to motivational biases at all. For instance, albeit striatal activity may be relatively reduced when learning from delayed compared to immediate feedback or during observational compared to active learning, it is not absent in these conditions. Motivational biases could thus rely on striatal mechanisms that are preserved across the processing of immediate and delayed feedback and self-referential versus vicarious feedback, as well as for OCD and HC (cf. Weber & Bellebaum, 2024; Weismüller et al., 2018).

A critical point of discussion is, however, that findings of relatively reduced striatal engagement for delayed and vicarious feedback primarily relate to outcome evaluation rather than action selection. Specifically, while learning from delayed relative to immediate and self-referential relative to vicarious feedback have shown differences in feedback processing, behavioral task performance, at least in healthy participants, is typically not affected

(Bellebaum & Colosio, 2014; Weismüller & Bellebaum, 2016). If motivational biases primarily reflect a Pavlovian response bias on action selection, as discussed above, it would thus be reasonable that they were not (or only marginally) affected by these conditions. Accordingly, the striatum may still contribute to motivational biases, yet not during learning but rather during action selection. Note, however, that previous fMRI evidence has failed to demonstrate striatal encoding of cue valence, as would be predicted by a Pavlovian response bias (Guitart-Masip, Huys, et al., 2012), while particularly unaltered motivational biases in OCD would still challenge a substantial striatal role, given its strong association with altered striatal functioning (Burguiere et al., 2015).

Taken together, motivational biases were shown to be relatively insensitive to conditions that have been linked to altered striatal activity. Together with findings suggesting a distributed network of areas involved in motivational biases, findings from Studies II and IV challenge the role of the striatum in driving motivational biases. Because striatal involvement was, however, not directly assessed in this dissertation, these interpretations remain speculative.

Alterations in learning and feedback processing in OCD

Another objective of this dissertation was to assess clinical implications, i.e., whether and how learning, decision-making and feedback processing are altered in OCD. While Study III indicated that OCD patients showed impaired learning (across both active and observational learning) and more indecisive decision-making in an instrumental probabilistic feedback learning task, Study IV suggested that motivational biases were unaltered in OCD. Most particularly, yet unexpectedly, findings presented in this dissertation provide novel evidence for altered sensitivity to reward (Study III) and disrupted self-other monitoring in feedback processing (Study IV) in OCD.

Altered processing of and sensitivity to reward

Study III revealed several alterations in the sensitivity to positive feedback in OCD. OCD patients showed learning impairments particularly for high-contingent learning pairs with high reward probability, as well as increased choice shifting following positive feedback. Moreover, OCD patients showed altered reward processing, expressed in a more positive FRN/RewP to positive feedback compared to HCs, particularly for active learning. This finding was unexpected given that OCD has been primarily associated with alterations in

the processing of negative valence (Dzinalija et al., 2025; Norman et al., 2019; Riesel, 2019). Under the RewP account (Proudfit, 2015), the absence of alterations in punishment processing reflected in the FRN/RewP would be expected, suggesting that the FRN/RewP elicited by negative feedback may simply reflect a baseline N2. Nevertheless, the involvement of the OFC and striatum in the pathophysiology of OCD (see e.g., Menzies et al., 2008) makes also alterations in processing positive valence and reward reasonable. Specifically, under the account of the RewP (Proudfit, 2015), a more positive FRN/RewP to win feedback may be indicative of hyperactive reward processing, possibly indicating increased salience of rewards due to biased attentional processing of threat-related stimuli (cf. Moritz & Pohl, 2009). Yet, given the impaired learning from high-contingent pairs and increased shifting following positive feedback, such enhanced sensitivity to reward may still be detrimental if not translated properly into behavior.

While evidence for altered reward processing in OCD is still emerging (see e.g., Bragdon et al., 2023; Shephard et al., 2021), prior research provides also evidence for hypoactive reward processing, specifically during reward anticipation (Figee et al., 2011) but also during reward receipt (Koch et al., 2018; Remijnse et al., 2006). Reduced sensitivity to reward feedback could therefore contribute to feelings of incompleteness and not-just-right experiences (Coles et al., 2003; Coles et al., 2005), as well as to difficulties to stop ongoing behaviors (Hinds et al., 2012; Wahl et al., 2008), as a reward would normally indicate that a response has been successfully completed. Such reduced rather than enhanced sensitivity to rewards appears particularly compatible with the behavioral findings from Study III, in which reduced reward responsiveness could have contributed to impaired learning and increased choice shifting following rewards.

Taken together, these findings suggest alterations in reward rather than punishment processing in OCD. Although the more positive FRN/RewP in OCD may suggest enhanced reward sensitivity, the behavioral findings could also be explained by reduced sensitivity to positive feedback. These findings hence motivate future studies to further clarify the role of reward processing in OCD.

Agency: Disrupted self-other distinction in feedback processing

As noted before, research on OCD has yet focused exclusively on active learning contexts (e.g., Endrass et al., 2014; Nieuwenhuis, Nielen, et al., 2005). However, previous research has linked OCD to an altered sense of agency (e.g., Szalai, 2019) with altered social functioning (Jansen et al., 2020). Further building on evidence of striatal dysfunction in OCD (Burguiere et al., 2015) and reduced striatal involvement in observational learning (Kobza & Bellebaum, 2015; Kobza et al., 2012), Studies III and IV aimed to investigate the role of agency in OCD by extending research to observational learning contexts.

Behaviorally, learning performance overall did not appear to be differentially modulated by agency in OCD. Using an instrumental learning task, Study III found learning impairments across both active and observational learning in OCD, thereby demonstrating that these deficits are not a mere feature of active learning contexts. Furthermore, although Study IV found generally attenuated motivational biases in observational compared to active learning, agency did not differentially affect motivational biases nor general learning performance in OCD.

Notably, however, agency effects were found at the neural level during feedback processing. Study III revealed enhanced FRN/RewP outcome valence coding, with more positive amplitudes to rewards, for active but not observational learning, aligning with the general hypothesis that due to aberrant striatal functioning in OCD (Burguiere et al., 2015) and reduced striatal recruitment in observational learning (Kobza & Bellebaum, 2015; Kobza et al., 2012), OCD-related alterations should primarily emerge during active learning. By contrast, Study IV demonstrated that while the FRN/RewP in HCs distinguished between own and vicarious feedback, this distinction was not found in OCD patients, thereby suggesting alterations in self-other monitoring. This finding may be attributable to alterations in the processing of vicarious rather than self-referential feedback. However, this was supported only by trend-level significance such that this interpretation warrants caution. Nonetheless, such altered processing of vicarious feedback would be plausible in light of previous evidence suggesting heightened affective responses during social observation (Jansen et al., 2020) along evidence of inflated responsibility and control beliefs (Reuven-Magril et al., 2008; Salkovskis et al., 2000). Accordingly, these characteristics may have contributed to heightened cognitive-affective engagement during learning in OCD patients, even when

feedback was vicarious and beyond their control. Again, as post-hoc evaluations could not reliably detect whether this effect was driven by alterations in the processing of self-referential and/or vicarious feedback, this interpretation remains speculative.

Taken together, these findings show for the first time that impaired instrumental learning in OCD is not restricted to active learning contexts but may extend also to observational learning. Moreover, while alterations in feedback processing during instrumental learning were particularly pronounced during active learning, alterations in feedback processing associated with motivational biases cautiously hinted at differences that may instead be more pronounced during observational learning. Extending research in OCD to observational task contexts therefore appears promising to gain more comprehensive insights into the neurocognitive profile of OCD.

Context dependence and cognitive inflexibility

On a critical note, the finding of altered reward processing observed in Study III could not be replicated in Study IV, nor could the finding of altered self-other distinction, reported in Study IV, be replicated in Study III. Moreover, while instrumental learning performance was found to be impaired in OCD patients in Study III, it was preserved in Study IV. This discrepancy in findings is particularly noteworthy given that both Studies III and IV were based on the same recruited sample and hence cannot be attributed to random differences between samples.

It is therefore likely that these discrepancies (at least partly) arose due to differences in the employed experimental paradigms. Study III used a (non-Pavlovian) instrumental probabilistic learning task that required decision-making (or its observation) between two active response options, each of which was associated with either reward or punishment at a varying probability. By contrast, Study IV used a Pavlovian-instrumental task with fixed reward probabilities, which included decisions between an active ("go") and passive ("nogo") response option (or their observation). Depending on their respective context, decisions either resulted in reward or omitted reward, or punishment or omitted punishment, respectively.

Importantly, the immediate threat of punishment was substantially higher in Study III compared to Study IV. Given recent evidence from healthy individuals suggesting that punishments can affect reward learning and processing

(Carvalheiro et al., 2026), this may also account for OCD patients, particularly based on evidence of biased attentional processing of threat-related stimuli in OCD (cf. Moritz & Pohl, 2009). Moreover, learning contexts with varying reward probabilities, as in Study III, may carry increased uncertainty, while OCD has been specifically linked to heightened intolerance of uncertainty (Gentes & Ruscio, 2011; Knowles & Olatunji, 2023). Accordingly, altered reward processing in OCD, as found in Study III, may therefore primarily emerge in situations with increased threat of punishment and/or high outcome uncertainty. Yet in other situations, OCD patients may be less self-focused and show other alterations, e.g., enhanced empathic distress and affective responding (Jansen et al., 2020; Salazar Kämpf et al., 2022), possibly contributing to disrupted self-other monitoring, as observed in Study IV.

This interpretation highlights the role of context dependence of OCD-related alterations in learning, decision-making, and their underlying neural mechanisms. This interpretation is not implausible. For instance, Apergis-Schoute et al. (2024) demonstrated that, while OCD patients showed increased perseverative decision-making in a deterministic reversal task with low outcome uncertainty, the same OCD patients showed more indecisive decision-making in a probabilistic reversal task with high outcome uncertainty. Notably, this finding is consistent with the results from Study III showing increased choice vacillation as well as with other evidence showing increased indecisiveness in OCD during decision-making under uncertainty (Hauser et al., 2017; Kanen et al., 2019; Pushkarskaya et al., 2015). Context dependence may also extend to motivational biases: while PIT studies have reported attenuated motivational biases in OCD (Krypotos & Engelhard, 2020; Peng et al., 2022; but see Marzuki et al., 2024), combined evidence from Scholz et al. (2026) and Study IV suggests intact motivational biases using an orthogonalized go/nogo paradigm.

Moreover, context-dependent alterations in OCD have also been reported at the neural level. For instance, although OCD has been robustly linked to ERN enhancement (Riesel, 2019), Riesel et al. (2019) found that this effect could only be replicated when emphasizing speed over accuracy in the task instructions of a flanker task. Beyond that, ERN enhancement in OCD appears to be limited to situations involving response conflict, with no evidence of ERN enhancement in low-response-conflict situations, such as feedback-based learning tasks (Gründler et al., 2009; Nieuwenhuis, Nielen, et al., 2005; Riesel, 2019). Finally,

such context dependence may also account for the heterogeneity in FRN/RewP findings in OCD, such that feedback processing may also depend on whether it is investigated in a probabilistic (reversal) learning or gambling paradigm (Endrass et al., 2013; Luo et al., 2020; Nieuwenhuis, Nielen, et al., 2005).

Taken together, these findings may therefore suggest that OCD-related alterations in learning, decision-making and their underlying neural mechanisms are prone to task context. Rather than general alterations, OCD patients may be inflexible in adjusting to certain tasks or contexts. This idea broadly aligns with the notion suggesting cognitive inflexibility as a substantial underlying factor in OCD (Gruner & Pittenger, 2017).

Comparison with SAD and contribution of transdiagnostic mechanisms

Comparisons between OCD and SAD patients were rather exploratory and aimed to assess whether the observed alterations in learning, decision-making and feedback processing were OCD-specific or generalized to a phenotypically overlapping but nosologically distinct disorder. Overall, these comparisons revealed only minor differences between disorders, suggesting the contribution of transdiagnostic, disorder-general mechanisms. This finding is not unreasonable given that OCD and SAD do not only show considerable overlap in symptoms (Carpita et al., 2020) but also in their pathophysiology. For instance, both disorders have been linked to altered striatal (Burguiere et al., 2015; Manning et al., 2015) and cingulate functioning (Nutt et al., 1998; Phan et al., 2005), as well as to enhanced error processing as reflected in the ERN (Endrass et al., 2014). Moreover, like OCD, also SAD has been linked to intolerance of uncertainty (Boelen & Reijntjes, 2009; Tolin et al., 2003).

Notably, however, although overall differences between OCD and SAD patients were rather subtle, the observed findings, interpreted above, appeared more pronounced in OCD. In particular, altered self-other distinction during feedback processing was not only found in comparison to HCs but also to SAD patients, suggesting that this finding may be particularly characteristic of OCD. Yet, this interpretation warrants caution, as assessing disorder-specificity requires comparisons with more than a single clinical control group.

Insights into the functional significance of the FRN/RewP

While overall replicating well-established findings that the FRN/RewP is sensitive to outcome valence (e.g., Miltner et al., 1997), feedback timing (e.g.,

Weismüller & Bellebaum, 2016), and agency (e.g., Bellebaum et al., 2010), the findings presented in this dissertation may also offer additional insights into the functional significance of the FRN/RewP, particularly regarding its role in reflecting PEs.

Specifically, an important point of debate is whether the FRN/RewP reflects signed (Holroyd & Coles, 2002; Holroyd et al., 2008), or unsigned PEs (cf. Alexander & Brown, 2011). Evidence from Studies II and III converges to support the former, showing that the FRN/RewP primarily reflects signed rather than unsigned PEs. While previous reports suggesting that the FRN/RewP reflects signed PEs have often been confounded by valence, as PEs were not assessed separately for positive and negative feedback (e.g., Fischer & Ullsperger, 2013; Frömer et al., 2021), Studies II and III provide evidence that the FRN/RewP reflects signed PEs while disentangling the effects of expectancy and valence (see also Röhlinger et al., 2025; Weber & Bellebaum, 2024).

Another point of debate relates to the question whether the ERP signal in the 200-350 ms time window post-feedback reflects a punishment-sensitive FRN, as proposed by the RL-theory (Holroyd & Coles, 2002), or is driven by a RewP, where the neural response to punishment feedback merely represents a baseline N2 (Holroyd et al., 2008; Krigolson, 2018; Proudfit, 2015). This question is not straightforward to answer. However, whereas Study II showed FRN/RewP encoding of -PEs only, suggesting sensitivity primarily to punishment feedback, Study III found encoding of both +PEs and -PEs, which may suggest sensitivity to both reward and punishment. Notably, however, the encoding of both +PEs and -PEs could still be accommodated within a strict RewP account, where -PE signaling may not reflect sensitivity to punishment but unvalenced surprise in the N2 (Ullsperger, 2024). By contrast, the RL theory along its early adaptation could account for both the selective encoding of -PEs and the encoding of both +PEs and -PEs (Holroyd & Coles, 2002; Nieuwenhuis et al., 2004).

Notably, the discrepancies in findings between Studies II and III concerning whether the FRN/RewP reflects -PEs and/or both +PEs and -PEs is in line with considerable heterogeneity of reported FRN/RewP findings in the literature. Some studies found the FRN/RewP to primarily encode -PEs (Chase et al., 2011; Huvermann, Berlijn, Thieme, et al., 2025), whereas others found it to encode primarily +PEs (Kirsch et al., 2022; Weber & Bellebaum, 2024), or both -PEs and +PEs (Albrecht et al., 2026; Röhlinger et al., 2025). Moreover, some studies have also reported the FRN/RewP to reflect unsigned rather than signed PEs (e.g.,

Hauser et al., 2014; Talmi et al., 2013). Adaptive coding accounts may provide an explanation for this heterogeneity. Specifically, it has been suggested that the signals reflected by the MCC are highly context-sensitive and reflect those most informative for implementing cognitive control and/or adjusting behavior under the current task demands (Heilbronner & Hayden, 2016). Originating in the MCC (Hauser et al., 2014; Luu et al., 2003; Oerlemans et al., 2025), the FRN/RewP may therefore sometimes reflect -PEs, +PEs, both, or even unsigned PEs, depending on which kind of PE signal is most informative in a given task context (cf. Heilbronner & Hayden, 2016). Aligning with the idea of such context dependency, Studies II and III used fundamentally different tasks, not only differing in the response requirements (Study II required both go and nogo responses, whereas Study III required an active response between two choice alternatives) but also with regard to the possible outcomes on a given trial (Study II involved either win versus no-win or loss versus no-loss outcomes, whereas every trial in Study III could result in either a win or a loss). Such details in task design may hence contribute to the heterogeneous PE coding in the FRN/RewP. On a critical note, however, although such an adaptive coding account may be tempting, it is particularly difficult to falsify, as inconsistent findings could always be attributed to context dependence.

Still, although such adaptive coding may be realized while the FRN and RewP reflect the same overarching mechanism, it remains possible that they reflect distinct (Proudfit, 2015) or valence-opposing (Nieuwenhuis et al., 2004) mechanisms. Using time-frequency analysis, Hoy et al. (2021) indeed revealed distinct valence-dependent mechanisms underlying the FRN/RewP, with frontal theta underlying punishment processing linked to the FRN, and posterior delta underlying reward processing linked to the RewP. Moreover, evidence from Bai et al. (2015) indicated a valence-dependent, temporal dissociation of PE signals, where they observed -PE encoding selectively during early feedback processing, within the classical FRN/RewP time window, and +PE encoding only later, within a classical P3 time window.

Such (spatio)temporal dissociation between -PE and +PE encoding broadly matches the findings observed in Studies II and III, which showed -PE effects primarily in the earlier FRN/RewP time window, whereas +PE effects persisted into later time windows and/or most consistently emerged as late as within the P3 time window. Importantly, findings from this dissertation extend previous evidence by showing also functional differences. Specifically, whereas +PE

encoding in the later P3 time window was flexible, emerging across immediate and delayed feedback (Study II) and active and observational learning (Study III), -PE encoding in the FRN/RewP time window rather appeared more restricted, primarily emerging for immediate feedback (Study II) and during active learning (Study III). Accordingly, -PE effects on the FRN/RewP were primarily observed in contexts requiring rapid cognitive control and/or behavioral adjustment, typical for MCC functioning, whereas prolonged +PE effects more broadly supported learning, potentially further involving memory updating and P3-related processes (Polich, 2007; Ullsperger, Fischer, et al., 2014). These findings therefore contribute to previous evidence, suggesting different (spatio)temporal profiles of -PE and +PE processing in the ERP (Bai et al., 2015; Hoy et al., 2021), cautiously suggesting opposing ERP mechanisms for reward and punishment that may sometimes overlap in the time window between 200-350 ms. However, future research using designated methodologies, such as principal component (Proudfit, 2015) or time-frequency analyses (Hoy et al., 2021) are needed to further disentangle the mechanisms in the ERP response to feedback.

Limitations

Limitations in the recruited samples

The research presented in this dissertation is not without limitations. Healthy samples recruited for Studies I and II primarily consisted of young and female university students, which may therefore not be representative to generalize to the general population. This is particularly because motivational biases have been shown to alter across the age span (Betts et al., 2020; Chen et al., 2018; Raab & Hartley, 2020) and be differentially sensitive to contextual influences depending on the age group (Raab et al., 2024).

While samples in Studies III and IV were more diverse, a major limitation in these studies was that most OCD (and SAD) patients had at least one comorbid disorder, predominantly an affective or anxiety disorder, and that most patients were receiving medication, primarily selective serotonin reuptake inhibitors, at the time of testing. Crucially, pharmacological treatment has been shown to modulate motivational biases (Guitart-Masip, Economides, et al., 2014; Scholz et al., 2022; Swart et al., 2017), while DA drug treatment was shown to remediate PE processing in OCD patients (Murray et al., 2019), hence potentially affecting both behavior and feedback processing.

Limitations in task design

Although based on a well-established paradigm (Guitart-Masip et al., 2011), the modified versions of the orthogonalized go/nogo task contained several deviations from the original task, even in their baseline conditions, thereby limiting comparability with previous work. For instance, both Studies I and IV contained (active) test blocks without feedback that followed learning blocks with feedback, thereby interrupting continuous learning. While this was necessary for Study IV to enable comparison of motivational biases between active and observational learning (Peterburs et al., 2021), this also meant that motivational biases were assessed after rather than during learning, resembling a limitation commonly faced in the classical PIT paradigm (see Introduction). Yet, even when both learning and test blocks are assessed, there may be unintended interaction effects, such that e.g., learning blocks bias performance in test blocks and test blocks bias performance in learning blocks.

Although Study II did not contain such test blocks, the immediate feedback condition, which served as the baseline, used unusually long intertrial intervals to compensate for task duration induced by the delayed feedback condition. While the overall result patterns observed using these modified task versions generally aligned with previous work, it cannot be ruled out that these methodological decisions in task design may have subtly affected learning and decision-making in an unintended way.

Moreover, as with other learning tasks, the orthogonalized go/nogo task may have some limitations regarding the number of trials available for analyzing feedback processing. This is because task performance naturally results in uneven and, in some cases, limited numbers of trials across conditions (e.g., particularly for rewarded nogo choices), potentially introducing frequency effects on feedback processing (Krigolson, 2018).

Last, Studies III and IV were based on virtual observation, which may have compromised the ecological validity of results, particularly regarding social inferences about OCD, e.g., altered self-other monitoring. Although Peterburs et al. (2021) showed similar effects on task performance for virtual and in-person observational learning in a healthy sample, this may be different in OCD. Assessing OCD in terms of a disorder of social interaction (cf. Schilbach, 2016) hence requires more naturalistic and ecologically valid environments, e.g., social observation and/or interaction.

Conclusion

In conclusion, the studies presented in this dissertation highlight the importance of context in learning, decision-making, and feedback processing. While motivational biases were shown to be attenuated by emotional cues and observational learning, they remained generally robust and difficult to overcome. Moreover, although likely involving multiple mechanisms, motivational biases appeared to primarily reflect a Pavlovian response bias rather than biased instrumental learning. Consistent with this, motivational biases were not reflected in action-biased feedback processing. Context dependence was particularly evident in OCD, with impaired learning and altered reward processing observed in an instrumental probabilistic feedback learning task, whereas motivational biases and learning were unaltered in an orthogonalized go/nogo task, although individuals with OCD showed altered self-other distinction during feedback processing.

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Affidavit

Eidesstattliche Erklärung gemäß § 5 der Promotionsordnung vom 15.06.2018 der Mathematisch-Naturwissenschaftlichen Fakultät der Heinrich-Heine-Universität Düsseldorf:

Ich versichere an Eides Statt, dass die Dissertation von mir selbständig und ohne unzulässige fremde Hilfe unter Beachtung der „Grundsätze zur Sicherung guter wissenschaftlicher Praxis an der Heinrich-Heine-Universität Düsseldorf“ erstellt worden ist. Die Dissertation wurde in der vorliegenden oder ähnlichen Form noch bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Düsseldorf, den _____ _____

Datum Julian Vahedi

Declaration of AI use

Während der Erstellung dieser Arbeit wurden generative KI (ChatGPT, OpenAI) sowie KI-basierte Anwendungen (DeepL Write, DeepL SE) als Hilfsmittel genutzt, um sprachliche Fehler zu erkennen und Lesbarkeit einzelner Textpassagen zu verbessern. Nach der Nutzung dieser Anwendungen habe ich die entsprechenden Textpassagen sorgfältig und kritisch überprüft sowie bei Bedarf weiterführend überarbeitet und übernehme die volle Verantwortung für den Inhalt dieser Dissertation.

Düsseldorf, den

Datum	Julian Vahedi

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APPENDIX

Original article of Study I

Vahedi, J., Mundorf, A., Bellebaum, C., & Peterburs, J. (2024). Emotional cues reduce Pavlovian interference in feedback-based go and nogo learning. *Psychological Research*, *88*, 1212-1230. https://doi.org/10.1007/s00426-024-01946-9

I was the first and corresponding author of this article. I contributed to the conceptualization and development of the paradigm, created the experimental setup and adapted existing code for the experimental task. I contributed to and supervised data acquisition at the testing site at Heinrich Heine University Düsseldorf. I contributed to the methodology, wrote all code for, and conducted the data (pre)processing, statistical analyses and data visualization. I interpreted the results, wrote the initial draft of the manuscript and collaborated with all co-authors on the final version of the manuscript.

Original article of Study II

Vahedi, J., Schneider, S., Swiatek, L., Peterburs, J., & Bellebaum, C. (2026). Motivational Biases in Go and Nogo Learning From Immediate Versus Delayed Feedback. *European Journal of Neuroscience*, *64*(8), e70717. https://doi.org/10.1111/ejn.70717

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I was the first and corresponding author of this article. I contributed to the conceptualization and development of the paradigm, created the experimental setup and adapted existing code for the experimental task. I contributed to the methodology, wrote all code for data (pre)processing, RL modeling, statistical analyses and data visualization. I contributed to and supervised data acquisition, EEG data preprocessing and statistical analyses of behavioral data. I conducted the RL modeling and statistical analyses of EEG data, and visualized the results. I interpreted the results, wrote the initial draft of the manuscript and collaborated with all co-authors on the final version of the manuscript.

Original article of Study III

Vahedi, J., Bahic, A., Chaliani, I., Schilbach, L., Ciupka-Schön, B., Bellebaum, C., Pietrowsky, R., & Peterburs, J. (2025). Altered Reward Processing in Obsessive–Compulsive Disorder: Insights From Active and Observational Learning. *Psychophysiology*, *62*(9), e70142. https://doi.org/10.1111/psyp.70142

I was the first and corresponding author of this article. I created the experimental setup and adapted existing code for the experimental task. I planned and conducted data acquisition, including eligibility screening and clinical interviews. I contributed to the methodology, wrote all code for, and conducted the data (pre)processing, RL modeling, statistical analyses and data visualization. I interpreted the results, wrote the initial draft of the manuscript and collaborated with all co-authors on the final version of the manuscript.

Original article of Study IV

Vahedi, J., Bahic, A., Chaliani, I., Schilbach, L., Ciupka-Schön, B., Bellebaum, C., Pietrowsky, R., & Peterburs, J. (2026). Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder. *Manuscript submitted for publication*

I was the first and corresponding author of this article. I created the experimental setup and adapted existing code for the experimental task. I planned and conducted data acquisition, including eligibility screening and clinical interviews. I contributed to the methodology, wrote all code for, and conducted the data (pre)processing, statistical analyses and data visualization. I interpreted the results, wrote the initial draft of the manuscript and collaborated with all co-authors on the final version of the manuscript.

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RESEARCH

Emotional cues reduce Pavlovian interference in feedback-based go and nogo learning

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Abstract

It is easier to execute a response in the promise of a reward and withhold a response in the promise of a punishment than vice versa, due to a conflict between cue-related Pavlovian and outcome-related instrumental action tendencies in the reverse conditions. This robust learning asymmetry in go and nogo learning is referred to as the Pavlovian bias. Interestingly, it is similar to motivational tendencies reported for affective facial expressions, i.e., facilitation of approach to a smile and withdrawal from a frown. The present study investigated whether and how learning from emotional faces instead of abstract stimuli modulates the Pavlovian bias in reinforcement learning. To this end, 137 healthy adult participants performed an orthogonalized Go/Nogo task that fully decoupled action (go/nogo) and outcome valence (win points/avoid losing points). Three groups of participants were tested with either emotional facial cues whose affective valence was either congruent (CON) or incongruent (INC) to the required instrumental response, or with neutral facial cues (NEU). Relative to NEU, the Pavlovian bias was reduced in both CON and INC, though still present under all learning conditions. Importantly, only for CON, the reduction of the Pavlovian bias effect was adaptive by improving learning performance in one of the conflict conditions. In contrast, the reduction of the Pavlovian bias in INC was completely driven by decreased learning performance in non-conflict conditions. These results suggest a potential role of arousal/salience in Pavlovian-instrumental regulation and cue-action congruency in the adaptability of goal-directed behavior. Implications for clinical application are discussed.

Introduction

In order to optimize our behavior during decision-making, we have to select actions that most likely lead to favorable outcomes and avoid actions resulting in unfavorable consequences. Thus, adaptive behavior requires integrating our past experiences with actions and their consequences to maximize rewards and minimize losses in the future. Decision-making in everyday life often requires choosing between executing a specific action (*go*) and withholding an action (*nogo*). For instance, when standing at a busy intersection, we would ideally cross the road only when no vehicles are approaching, thus stop and wait until the road is empty and can be safely crossed.

Early behaviorist theories predicted that individuals generally align their behavior to the best outcome (e.g. Thorndike, 1927). Notably, not all contingencies between (in) actions and their consequences are learned equally well. Under the influence of Pavlovian learning, associations between cues and their expected outcomes seem to trigger actions in a stereotyped and valence-dependent manner: the expectation of reward facilitates action invigoration, whereas the expectation of punishment facilitates the inhibition of action, which has been referred to as *Pavlovian bias* in the literature (see e.g. Cavanagh et al., 2013; Guitart-Masip et al., 2011, 2012, 2014a; Peterburs et al., 2021, 2022).

The Pavlovian bias has been typically studied using a feedback-based Go/Nogo learning task first described by Guitart-Masip et al. (2011). This task orthogonalizes action and outcome valence, resulting in four experimental conditions: pressing a button in order to obtain a reward (go to win), pressing a button in order to avoid punishment (go to

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avoid-losing), withholding a button press in order to obtain a reward (nogo to win), and withholding a button press in order to avoid punishment (nogo to avoid-losing). Go to avoid-losing and nogo to win are often referred to as conflict conditions, while go to win and nogo to avoid-losing are referred to as non-conflict conditions (e.g. Albrecht et al., 2016; Cavanagh et al., 2013). Participants' learning performance is typically better for non-conflict relative to conflict conditions, i.e., better for go to win compared to go to avoid-losing, and for nogo to avoid-losing compared to nogo to win. This asymmetric coupling of action and outcome valence reflecting Pavlovian learning biases seems to be quite robust and has been repeatedly demonstrated in a variety of experimental studies (e.g. Cavanagh et al., 2013; Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Peterburs et al., 2021).

Crucially, action selection is not fully determined by either instrumental or Pavlovian learning but rather from a combination of both (Dorfman & Gershman, 2019; O'Doherty, 2016). Instrumental control of action based on learning from performance feedback is rather slow but highly flexible as it enables goal-directed behavior. In contrast, Pavlovian control of action is fast and reflexive but also more rigid. Hence, the Pavlovian bias might be particularly useful when the Pavlovian responses are in alignment with the required instrumental response (e.g., approaching food), but can hinder optimal decision-making when Pavlovian responses conflict with the required instrumental response. In evolutionary terms, automatic, prepotent Pavlovian responses might have been advantageous, particularly in new and uncertain environments, because they served as a quickly available decision heuristic (Boureau et al., 2015; Dayan & Seymour, 2009; Rangel et al., 2008). Nonetheless, to ensure adaptive behavior, both instrumental and Pavlovian learning systems need to be carefully balanced.

Accordingly, Pavlovian bias abnormalities have been linked to maladaptive behaviors including impulsivity (Eisinger et al., 2020) and are associated with numerous (neuro-) psychiatric conditions, including anxiety (Peterburs et al., 2022) and traumatic stress (Ousdal et al., 2018), schizophrenia (Albrecht et al., 2016), and Parkinson's disease (Eisinger et al., 2020; Wagenbreth et al., 2015). For depression, results have been inconsistent, with Nord et al. (2018) reporting enhanced and Moutoussis et al. (2018b) reporting intact Pavlovian biases. Differences have also been reported for different age groups, indicating that adolescents exhibit reduced Pavlovian control over action compared with children and young adults, possibly facilitating exploration and openness to new experiences (Raab & Hartley, 2020). Interestingly, as age progresses in adulthood, Pavlovian biases have been found to decrease again, with the effect particularly driven by a decrease in Pavlovian facilitation of action in the promise of reward (Chen et al., 2018). Note, however, that Betts et al. (2019) found no modulatory effect of age on the Pavlovian bias but increased bias towards action in children and adolescents and decreased reward and punishment sensitivity in midlife and older adults. Beyond that, higher IQ has been shown to be associated with weaker Pavlovian influence (Moutoussis et al., 2018a).

The neural source of the Pavlovian bias has often been linked to the striatum along with its key neuromodulator dopamine (de Boer et al., 2019; Guitart-Masip et al., 2011, 2012; Richter et al., 2014; Swart et al., 2017). However, results of Guitart-Masip et al. (2014b) indicated a reduced Pavlovian bias after boosting dopamine levels using levodopa that could not be attributed to striatal dopaminergic activity, but was rather explained by a potential involvement of the prefrontal cortex in overcoming Pavlovian biases. This assumption was supported by findings of Cavanagh et al. (2013) who could show that midfrontal oscillatory theta power was associated with greater ability to overcome the Pavlovian biases on the inter- as well as intraindividual level, indicating that prefrontal control mechanisms are capable of resolving conflicting action requirements. In line with that, a recent study by Kim et al. (2023) provided causal evidence for a prefrontal role in overcoming Pavlovian-instrumental conflicts by showing reduced Pavlovian bias after anodal transcranial direct current stimulation over the dorsolateral prefrontal cortex.

Recent investigations have focused on how Pavlovian influences on instrumental learning can be manipulated or overcome. Motivated by findings indicating a reduced role of the striatum in observational learning (e.g. Bellebaum et al., 2012; Kobza et al., 2012), Peterburs et al. (2021) compared learning performance in a modified orthogonalized Go/Nogo task among active and observational learners, but found comparable Pavlovian bias in both groups. Similarly, the Pavlovian bias was hardly modifiable in a recent series of experiments by Ereira et al. (2021). Here, five groups of participants underwent three days of training in different variants of an orthogonal Go/Nogo task that varied in the response domain (motoric vs. semantic), in stimulus presentation (single vs. massed), and in gamification (no gamification vs. gamification). All subjects underwent a consecutive test session on the third day of training. Only in the semantic task version with massed stimulus presentation and gamification a training-induced reduction of the Pavlovian bias, that even persisted in an independent task, could be observed. The Pavlovian bias remained robust under all other training conditions.

In the standard orthogonalized Go/Nogo task, neutral cues, often abstract visual stimuli such as fractal images, are used which are then assigned positive or negative valence through the process of learning (Guitart-Masip et

al., 2011, 2012; Peterburs et al., 2021). However, for emotional-affective stimuli, valence does not require previous learning. Valence-action biases similar to the Pavlovian bias in reinforcement learning have been assumed for the emotional domain, with positive emotional valence favoring response invigoration and negative emotional valence favoring withdrawal behavior (Cacioppo et al., 1999; Lang, 1995). This contingency between valenced emotional stimuli and approach/avoidance has been supported by several studies (e.g. Chen & Bargh, 1999; Krieglmeyer et al., 2010; Phaf et al., 2014; Seibt et al., 2008; Seidel et al., 2010). Faster response times (RTs) have been reported for congruent valence-action pairings, i.e., when approaching positive emotional stimuli and avoiding negative emotional stimuli, compared with incongruent valence-action pairings, i.e., when approaching negative emotional stimuli and avoiding positive emotional stimuli (Krieglmeyer et al., 2010; Phaf et al., 2014; Seidel et al., 2010). However, it must be noted that these findings were based on studies in which participants were required to show an active response for both approach and avoidance. Emotion effects on action execution and action suppression have been typically investigated using emotional variants of Go/Nogo tasks (e.g. Schrammen et al., 2020), reporting more commission errors to positive than to negative facial stimuli as well as increased RTs to negative compared to positive facial stimuli (Hare et al., 2005; Schulz et al., 2007).

Whether and how emotional valence affects the Pavlovian bias has not been fully answered yet. Asci et al. (2019) studied the effects of task-irrelevant emotional background stimuli on action-valence compatibility effects in an equiprobable Go/Nogo task. However, while there was evidence for reward-related facilitation of action over inaction, the authors did not find any modulatory effect of emotional background. In a more recent study, Weber et al. (2022) studied the effect of video-based induction of positive and negative affect on Pavlovian biases. Strikingly, the results revealed that induced affect did not have an effect on overall approach or avoidance tendencies, and therefore did not modulate the Pavlovian bias.

However, both of these studies used emotional manipulations with rather low salience, as emotional stimuli or affect were introduced in a task-irrelevant manner. Rotteveel and Phaf (2004) suggested that affective cues have to be consciously processed in order to bias action tendencies. Beyond that, it should be noted that emotional stimuli and induced affect do not necessarily affect approach and avoidance behavior in the same direction. While negative emotional stimuli such as angry faces are generally associated with avoidance behavior, induced negative affect, especially experienced anger, might be more strongly related to approach behavior (Carver & Harmon-Jones, 2009; Harmon-Jones, 2003).

Taking this into account, using emotional stimuli and implementing emotional valence more saliently, e.g., by using emotional instead of neutral cues, may be better suited to uncover emotionality effects on the Pavlovian bias. In this context, emotional faces may be of particular interest as facial expressions play a vivid role in social interactions. A smile, i.e., a happy face, automatically evokes approach, while a frown, i.e., an angry face, triggers withdrawal behavior (Marsh et al., 2005; Nikitin & Freund, 2019; Seidel et al., 2010). Facial stimuli have been successfully used as feedback stimuli in a social task variant of the orthogonalized Go/Nogo task, indicating that emotional faces are capable of signaling reward and punishment (Thompson & Westwater, 2017). There is also evidence that brain areas activated by the perception of happy faces overlap with reward-related areas of the basal ganglia (Chakrabarti et al., 2006), which, depending on whether the emotional valence matches or opposes the required instrumental response, may facilitate or hinder learning.

The aim of the present study was to investigate whether the Pavlovian bias can be modulated by social affective cues in an emotional variant of the orthogonalized Go/Nogo task. In this task, facial stimuli were used as Pavlovian cues (as opposed to social feedback). Previous findings indicate that non-conflict conditions (i.e., go to win and nogo to avoid-losing) are already relatively easy to learn, with at least go to win often resulting in a ceiling effect (e.g., see Peterburs et al., 2022). Therefore, we hypothesized emotional manipulations to have an asymmetric effect on task performance, expecting a greater influence on conflict conditions (i.e., go to avoid-losing and nogo to win) relative to non-conflict conditions. In particular, go to win may only be hardly modifiable (if at all). In contrast, whether and how emotional manipulations will affect task performance for nogo to avoid-losing is more speculative. On the one hand, task performance may be hardwired and resistant to emotional manipulations, as assumed for go to win. On the other hand, nogo to avoid-losing could be susceptible to emotional manipulations in the same way as is supposed for conflict conditions.

Consequently, we hypothesized that learning from a facial cue whose motivational prospect was congruent with the required instrumental action (i.e., emotional-congruent; happy face for go response, angry face for nogo response) should facilitate learning by particularly boosting performance in conflict conditions (go to avoid-losing and nogo to win). As a result, the Pavlovian bias should decrease or even disappear compared to a task version with neutral facial cues. In contrast, we expected that learning from facial cues whose motivational prospect was incongruent with the

required instrumental action (i.e., emotional-incongruent; happy face for nogo response, angry face for go response) should hinder learning. However, whether and how this manipulation affects the Pavlovian bias is more speculative. As assumed for the emotional-congruent learning condition, learning may be relatively unaffected in the non-conflict conditions (go to win, nogo to avoid-losing), due to the relative ease and robustness of learning. For go to avoid-losing and nogo to win, learning performance should decrease. Thus, the Pavlovian bias should be enhanced compared to a task version with neutral facial cues. Alternatively, it is also conceivable that learning performance will be equally impaired in all conditions, resulting in reduced learning performance overall but comparable Pavlovian bias relative to the neutral task version. On a statistical level, the hypothesized modulation of the Pavlovian bias would correspond to an interaction effect between the factors learning condition, required action and outcome valence.

Last, in an exploratory analysis, we investigated a potential link between the Pavlovian bias and reward and punishment sensitivity, as individual differences in reward and punishment have shown to be associated with striatal activation during reward and avoidance learning (Kim et al., 2015). Reward and punishment sensitivity were measured via self-report using the behavioral inhibition system/behavioral activation system (BIS/BAS) scales (Carver & White, 1994).

Materials and methods

Participants

Sample size was roughly estimated based on previous studies that employed the orthogonalized Go/Nogo task which collected data from between around 20 and 50 participants (e.g. Cavanagh et al., 2013; Ereira et al., 2021; Guitart-Masip et al., 2012; Peterburs et al., 2021). Thus, we aimed at a sample size of approximately 40 participants per experimental group (after exclusions), which we assumed to have sufficient statistical power to detect potential effects related to our manipulations. Consequently, a total of 137 young and healthy volunteers participated in the study (see Table S1) that were recruited at two test sites, Heinrich-Heine University Düsseldorf, Germany (HHU; $n=66$), and MSH Medical School Hamburg, Germany (MSH; $n=71$) by public advertisement and/or social media. At each test site, participants were randomly assigned to one of three experimental groups: emotional-congruent (CON; $n=43$), emotional-incongruent (INC; $n=48$), or neutral (NEU; $n=46$).

Importantly, a simulation-based sensitivity power analysis conducted in R using the *simr* package (Green & MacLeod, 2016) based on the final sample size (i.e. after exclusions) attested sufficient statistical power (=80%) to detect an (unstandardized) effect size of $\beta=25.3$ for the three-way interaction between the factors learning condition, action and valence, used to operationalize the modulation of the Pavlovian bias effect by emotional cues (see Figure S1). Details on the sensitivity power analysis can be found in the Supplementary Material.

Participants were only eligible for participation if they reported no history of psychiatric or neurological disorders and were currently not taking any psychotropic medication. All participants had normal or corrected-to normal vision and were naïve to the study's intent. Written informed consent was obtained from all participants prior to their participation. The study procedures conformed to the Declaration of Helsinki and had received ethical clearance by the Ethics Board of the Faculty of Mathematics and Natural Sciences at Heinrich-Heine-University, Germany, and the Ethics Board of the MSH Medical School Hamburg, Germany.

IQ estimates were obtained from each participant using a short multiple-choice vocabulary test (Mehrfachwahl-Wortschatz-Test B, MWT-B; Merz et al., 1975), consisting of 37 items. Each item contained a row of five words and participants had to correctly identify the real word among four pseudowords. Using norm tables, the sum scores were translated into IQ estimates, which have been shown to correlate fairly high with global IQ scores obtained by more elaborate intelligence tests (Lehrl et al., 1995). Participants also completed BIS/BAS scales (Carver & White, 1994; German version: Strobel et al., 2001). This 20-item self-report questionnaire assesses the dispositional sensitivity to punishment (BIS scale; 7 items) and reward (BAS scale; 13 items) based on Gray's *Reinforcement Sensitivity Theory* (Gray, 1982, 1987). Note that the present study only used BIS and BAS total scores, as the German version does not confirm the full four dimensional structure of the original BIS/BAS scales (Strobel et al., 2001).

Data exclusion (for details, see Data Analysis) left a sample of 121 participants (CON: $n=40$; INC: $n=40$; NEU: $n=41$) for statistical analyses (see Table 1). There were no differences between experimental groups with respect to age ($p=.649$), verbal IQ ($p=.525$) and BIS ($p=.967$). However, BAS scores did differ between experimental groups ($p=.047$), with slightly higher BAS scores in INC relative to CON ($p=.041$) but no difference between CON and NEU ($p=.535$) and INC and NEU ($p=.736$).

Experimental task

Participants performed an emotional variant of the orthogonalized Go/Nogo task first described by Guitart-Masip et al. (2011). In this task, action (*go*, *nogo*) and outcome valence

Table 1 Sample characteristics after exclusions

	CON ($n=40$)	INC ($n=40$)	NEU ($n=41$)
Demographic characteristics			
mean (*SD*) age in years	22.08 (3.06)	21.95 (2.64)	22.56 (3.59)
sex (female/male), *n*	27/13	27/13	28/13
handedness (left/right/n.a.), *n*	6/34/0	3/34/3	2/36/3
Mean (*SD*) score			
verbal IQ	101.45 (11.69)	103.95 (9.96)	103.59 (10.14)
BIS	20.45 (4.11)	20.25 (3.94)	20.37 (3.75)
BAS	39.23 (5.88)	41.85 (3.82)	40.63 (4.10)

Note. Demographic data and questionnaire scores are provided. Abbreviations are used as follows: CON = emotional-congruent group, INC = emotional-incongruent group, NEU = neutral group, SD = standard deviation, n.a. = not available; BIS = Behavioral Inhibition System, BAS = Behavioral Activation System

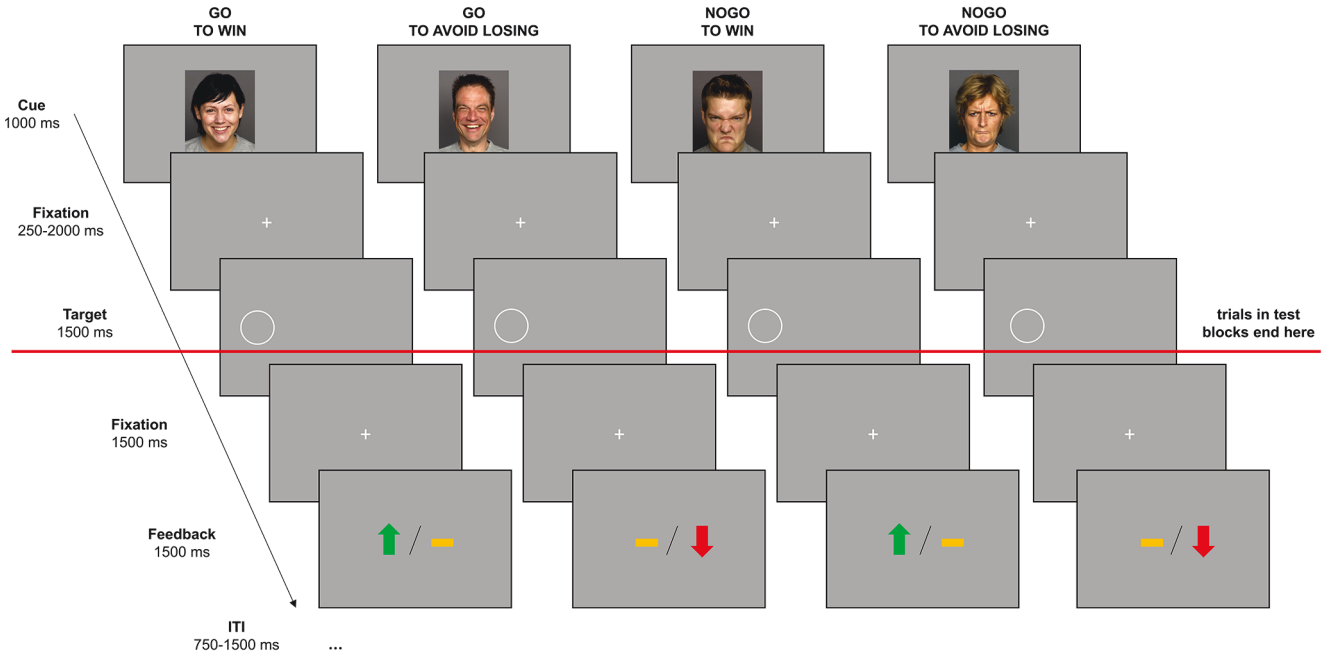


Fig. 1 Experimental paradigm. Each trial started with one of four possible facial cues indicating one of the four experimental conditions (go to win, go to avoid losing, nogo to win, nogo to avoid losing). After a variable fixation phase, a white circle appeared either on the left or right side of the screen and participants were required to decide to either press the button corresponding to the side on which the circle appeared (go) or withhold the button press (nogo). After a short delay, symbolic feedback was provided: a green upward pointing arrow indicated winning ten points, a red downward pointing arrow indicated losing ten points, and a yellow horizontal bar indicated a draw (no points lost or won). Note that the task contained two block types, training and test blocks. Feedback was only provided in training blocks but not in test blocks. Facial cues were obtained from FACES database (Ebner et al., 2010). Note that this figure contains facial stimuli that are publicly available via the FACES platform. These faces do not correspond to the stimuli used in this study, except for their valence assignment

(*win*, *avoid-losing*) are fully decoupled in a balanced two-by-two design, resulting in four experimental conditions: go to win (GW), go to avoid-losing (GAL), nogo to win (NGW), and nogo to avoid-losing (NGAL). Figure 1 illustrates the time course and sequence of stimulus presentation in one trial of the task for these four experimental conditions. Each trial started with the presentation of a specific learning cue, i.e., one out of four facial stimuli for each experimental condition. For participants assigned to CON, the affective valence of the facial cue *matched* the associated action tendency that was required in that specific condition, i.e., GW and GAL were each indicated by a happy face, and NGW and NGAL were each indicated by an angry face. For participants assigned to INC, the affective valence of the facial cue *contradicted* the associated action tendency that was required in that specific condition, i.e., GW and GAL were each indicated by an angry face, and NGW and NGAL were each indicated by a happy face. Neutral faces served as learning cues for participants in the neutral learning

condition. Stimulus assignment depending on learning condition is visualized in Fig. 2.

Each facial cue was displayed for 1000 milliseconds (ms), followed by a fixation cross for 250 to 2000 ms. Subsequently, an open white circle (target stimulus) was presented either on the left or right side of the screen for 1000 ms. Participants had to decide between responding (*go*) or not responding (*nogo*), and in case of choosing to respond, pressing the response button that indicated the location of the open circle (i.e., pressing the left/right CTRL button on a standard USB-keyboard when the open circle had appeared on the left/right). Button presses had to be made within 1000 ms. If participants chose not to respond, they had to simply let the response period pass. If participants accidentally pressed the wrong button, opposite to the actual side of the open circle, the trial was aborted and participants received explicit feedback that an invalid response had been made. When participants had made a valid decision, i.e., they had either indicated the correct side of the open circle or had not responded at all, another fixation cross was displayed for 1000 ms before symbolic feedback was provided. A green upward pointing arrow indicated that participants gained ten points (*win*), a red downward pointing arrow indicated that participants lost ten points (*loss*), and a yellow horizontal bar indicated that points had neither been gained nor lost (*draw*). Based on this performance feedback, participants could learn which action (*go*, *nogo*) for which learning cue was most likely associated with which outcome (*win*, *draw*, *loss*). Participants were explicitly instructed to use this performance feedback to maximize gains and minimize losses.

Importantly, for each learning cue, there was one favorable and one unfavorable outcome. In GW and NGW trials, the favorable outcome was to gain points (*win*) and the unfavorable outcome was to neither win nor lose points (*draw*). In GAL and NGAL trials, the favorable outcome was to avoid losing points (*draw*) and the unfavorable outcome was to lose points (*loss*). Responses that were associated with the best possible outcome in a given trial were classified as correct responses. Importantly, correct responses led to the favorable outcome in 80% of trials, while in the other 20%, participants received the unfavorable outcome (analogously, incorrect responses also led to favorable outcomes in 20% of trials, while in the other 80%, participants were presented the unfavorable outcome).

In total, the task comprised eight experimental blocks of 40 trials (ten for each trial type), amounting to 320 trials in total. Trial order was randomized within blocks. Following the procedures used in previous studies (Peterburs et al., 2021, 2022), there were two types of blocks, training blocks and test blocks, that were presented in alternate order. Training blocks and test blocks were nearly identical, except that in in training blocks, participants received performance-related symbolic feedback for each decision (as described above), while in test blocks, trials ended after the participant's choice, thus no feedback was presented. Between blocks, participants could take a short rest and were informed about their current score. Unlike in the original task, described by Guitart-Masip et al. (2011), and following Peterburs et al. (2022), we implemented test blocks without feedback in order to assess the current state of learning that was not influenced by trial-by-trial adjustments to the

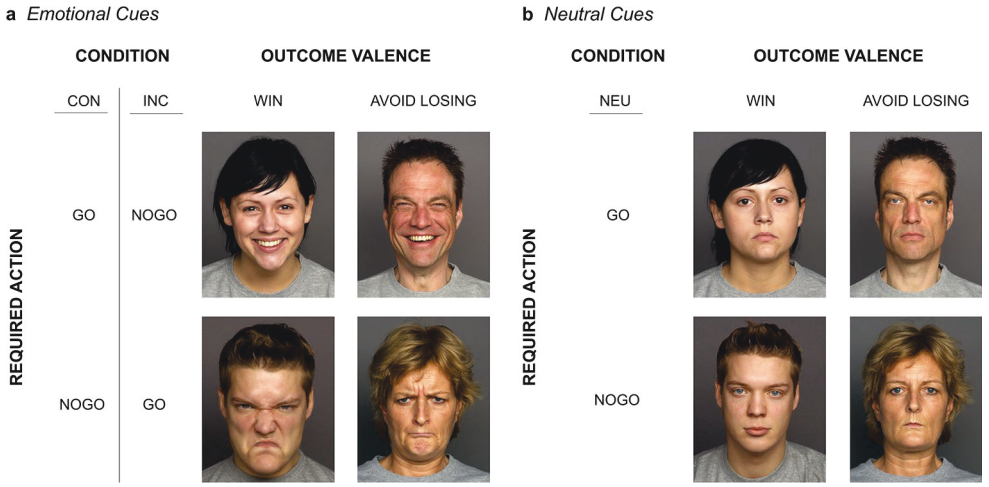


Fig. 2 Facial stimuli were obtained from FACES data base (Ebner et al., 2010) and consisted of two sets (**a** and **b**) of photographs of four young adults (two females, two males). (**a**) shows the cues used for the two emotional learning conditions. For the emotional-congruent learning condition (CON), cues showing happy face expressions were used for the go conditions and cues showing angry face expressions were used for the nogo conditions. For the emotional-incongruent learning condition (INC), cues showing happy face expressions were used for the nogo conditions and cues showing angry face expressions were used for the go conditions. (**b**) shows the facial cues used for the neutral learning condition. Note that this figure contains facial stimuli that are publicly available via the FACES platform. These faces do not correspond to the stimuli used in this study, except for their valence assignment

probabilistic performance feedback and therefore allowed testing the stability of learning in the absence of feedback. Note, however, that in contrast to Peterburs et al. (2022), we included all trials, i.e., both from training and test blocks, in the statistical analyses.

Presentation software (version 20.1, Neurobehavioral Systems, Inc., Albany, CA, USA) was used for stimulus presentation and response recording. Participants received either course credit or monetary compensation for taking part in this study. Task completion took around 35 min.

Stimulus selection

Cue stimuli consisted of colored images of adult faces and were obtained from the FACES database (Ebner et al., 2010; https://faces.mpdl.mpg.de/imeji/). We selected four pairs of images of individuals. For each pair, one image shows an emotional (positive, i.e. happy, or negative, i.e. angry) and one image a non-emotional (neutral) face expression, resulting in two sets of four facial stimuli each, one emotional set and one neutral set. Importantly, both stimulus sets contained images of the same individuals, differing only in face emotionality, i.e., emotional vs. neutral. The emotional stimulus set contained images of four young adults (of similar age as our study participants), two males and two females: two (one male and one female) with a happy and two (one male and one female) with an angry facial expression. The non-emotional stimulus set contained images of the same young adults, all four with a neutral facial expression. Facial stimuli were selected based on ratings of an independent sample of 154 adults on perceived facial expression, perceived age, attractiveness, and distinctiveness provided by Ebner et al. (2010) and Ebner et al. (2018), with the selected images rated as similar as possible according to those variables. Stimulus assignment to the experimental conditions within each stimulus set was randomized. For illustrative purposes, exemplary facial cues that are publicly available via the FACES platform are presented in Fig. 2. Additional information about the selected stimuli including filenames as well as stimulus ratings are provided in the Supplementary Material.

Data analysis

Before analyzing the data, we performed three quality control tests to prevent including participants with low compliance and/or motivation. First, participants with more than 25% invalid button presses, that is button presses that were too slow or indicated the opposite location of the target stimulus (open circle), were excluded in accordance with Scholz et al. (2022). Second, we excluded participants choosing the same action option (*go* or *nogo*) in more than 85% of trials as this indicated failure to understand the task instructions of using both response options properly, similar to Weber et al. (2022). Finally, we excluded participants with choice accuracy below-chance level (according to a one-tailed binomial test against chance, $\alpha = .05$) in GW trials, i.e., the easiest condition (see Weber et al., 2022), as previous findings indicated a ceiling effect for GW learning (e.g. Peterburs et al., 2022; Peterburs et al., 2021). Based on those criteria, data from 15 participants were excluded from further analyses: 12 participants showed perseverative responding for either go or nogo, five participants' performance was below chance level in the easiest condition (GW), and one participant had incomplete data due to technical problems during data acquisition. Beyond that, we removed invalid trials, i.e., button presses outside the RT window (> 1000 ms) or button presses indicating the opposite location of the target stimulus (open circle) prior to data analysis. By applying these criteria, 3.51% of trials were removed.

We performed a linear mixed-effects (LME) model analysis on aggregated choice accuracy data using the *lme4* package in R (Bates et al., 2014). As categorical fixed-effect predictors, we included the between-subjects factor learning condition (*neutral* [= reference level], *congruent*, *incongruent*) as well as the within-subject factors action (*go* [= reference level], *nogo*), outcome valence (*win* [= reference level], *avoid-losing*), and block type (*training* [= reference level], *test*). Contrast weights of categorical predictors were set using deviation coding. Block (1–8) was implemented as a continuous predictor to assess effects of task duration and was centered and scaled to the grand mean. Aggregated accuracy in percent was set as the dependent variable. Pavlovian bias was quantified as the effect of a two-way interaction between action and outcome valence.

We used the *bobyqa* algorithm for parameter optimization. The maximal number of iterations was set to 10e6. LME models were fitted using a restricted maximum likelihood approach, as proposed by Luke (2017). Degrees of freedom and *p*-values were calculated using the likelihood ratio test method that was based on type III sums of squares. The *lmerTest* package (Kuznetsova et al., 2017) was used to calculate *p*-values based on Satterthwaite's approximation of degrees of freedom. We attempted to incorporate maximal random-effects structure with all within-subjects effects and interactions as random slopes and random intercepts per participant (Barr, 2013). Since the full model with a maximal random-effects structure resulted in a singular fit, we simplified the model manually via stepwise elimination of random effects. The simplified LME model for choice accuracy data that still reached convergence was specified as follows:

$$choice\ accuracy \sim learning\ condition * action * valence * blocktype * block + (1 + action * valence * block + action : block\ type\ |\ participant)$$

In order to identify statistical outliers, we calculated Cook's distance using the influence.ME package. In case participants exceeded the Cook's distance cut-off criterion of 4/(n - k − 1), with n = number of participants and k = number of fixed effects including the intercept as well as all main and interaction effects, they were excluded and the LME model was refitted for the remaining participants. Cook's distance indicated that one participant from INC had to be excluded. Refitting the LME model specified above for the remaining 121 participants (see Table 1 for sample characteristics after exclusions) resulted in a singular fit. We therefore further simplified the random effects structure until the model converged. The final LME model for choice accuracy data was specified as follows:

$$choice\ accuracy \sim learning\ condition * action * valence * block\ type * block + (1 + action * valence * block + block\ type\ |\ participant)$$

Pairwise comparisons for the three-level factor learning condition as well as significant interaction effects were resolved via the R package *emmeans* (Lenth, 2022). To elucidate three-way or higher-order interactions involving the interaction effect between action and valence, in which all involved factors were categorical, we additionally explored *Pavlovian congruency gain indexes*, similar to Wagenbreth et al. (2015). Note that in this context the term congruency denotes what we refer to as Pavlovian conflict. Following that *Pavlovian congruency gains* reflect the gain in accuracy for win compared to avoid-losing trials as calculated by subtracting accuracies of avoid-losing from win conditions. This value is typically positive for go trials (because GW > GAL) and negative for nogo trials (because NGAL > NGW). Note that, except for interaction effects involving the predictors action and valence, we will only report significant interaction effects of factors which are not included in higher-order interactions. For all reported statistical analyses, the threshold for statistical significance was set to $p = .05$. For follow-up comparisons, adjusted p-values using false-discovery-rate (FDR) correction for multiple comparisons are reported (Benjamini & Hochberg, 1995). Note that we report unstandardized effect size estimates by providing β coefficients for each statistical test. In addition, we report complementary standardized effect size estimates for significant main and interaction effects using partial eta squared (η_p^2) implemented in the *effectsize* package in R (Ben-Shachar et al., 2020). Model specification and results for the analyses of RTs and rating data are reported in the Supplementary Material.

Finally, we assessed whether reward and punishment sensitivity as measured using the BIS/BAS scales moderated the Pavlovian bias in an exploratory analysis. To this end, we calculated Spearman rank-order correlations between participant-wise random slopes for the action × valence interaction effect and BIS and BAS scores, similar to Weber et al. (2022).

Results

Linear mixed-effects model analysis of choice accuracy data

General effects on learning performance

The inferential statistics for all fixed effects of the LME model analysis are listed in Table 2. LME model analysis of choice accuracy revealed significant main effects of block, $F(1, 118) = 39.03$, $p < .001$, $\eta_p^2 = 0.25$ (95%-CI 0.13–0.37), and block type, $F(1, 121.05) = 7.40$, $p = .007$, $\eta_p^2 = 0.06$ (95%-CI 0-0.15), indicating that accuracy linearly increased throughout the task, $\beta = 3.13$ ($SE = 0.50$), and that overall performance was better in test compared to training blocks, $\beta = 1.70$ ($SE = 0.62$). Furthermore, results yielded a significant main effect of action, $F(1, 118.98) = 120.40$, $p < .001$, $\eta_p^2 = 0.50$ (95%-CI 0.38–0.60), with better overall performance in go relative to nogo conditions, $\beta = -20.22$ ($SE = 1.84$). Importantly, there was a significant main effect of learning condition, $F(2, 118.72) = 4.38$, $p = .015$, $\eta_p^2 = 0.07$ (95%-CI 0-0.16). Pairwise comparisons indicated better learning performance in CON relative to INC, $\beta = 7.81$ ($SE = 2.64$), $p = .011$, FDR-corrected. There were no significant differences in overall learning performance between CON and NEU, $p = .153$, FDR-corrected, or INC and NEU, $p = .153$, FDR-corrected. Results for the analysis of RTs and rating data are reported in the Supplementary Material.

Modulation of Pavlovian biases by emotional cues

Crucially, we found an action × valence interaction effect, reflecting the Pavlovian bias, $F(1, 118.99) = 92.59$, $p < .001$, $\eta_p^2 = 0.44$ (95%-CI 0.31–0.54). Performance was better for GW relative to GAL, $\beta = -15.21$ ($SE = 1.88$), $t(119.90) = -8.09$, $p < .001$, FDR-corrected, and for NGAL relative to NGW, $\beta = 20.16$ (SE = 2.87), $t(118.81) = 7.01$, $p < .001$, FDR-corrected. Importantly, the observed Pavlovian bias effect was modulated by the factor learning condition as reflected in a significant learning condition × action ×

Table 2 Inferential statistics for the fixed effects of the linear-mixed effects model of choice accuracy

Fixed effect	β	SE	df	*F* / *t*	*p*
(intercept)	65.90	1.07	118.72	61.45	<.001***
learning condition			**2, 118.72**	**4.38**	**.015***
NEU vs. CON	*4.04*	*2.62*	*118.72*	*1.54*	*.126*
NEU vs. INC	*-3.77*	*2.62*	*118.72*	*-1.44*	*.153*
action	**-20.22**	**1.84**	**1, 118.98**	**120.40**	**<.001*****
valence	2.48	1.59	1, 119.33	2.43	.121
block type	**1.70**	**0.62**	**1, 121.05**	**7.40**	**.007****
block	**3.13**	**0.50**	**1, 118**	**39.03**	**< .001*****
learning condition:action			2, 118.98	1.81	.167
NEU vs. CON	*8.44*	*4.51*	*118.98*	*1.87*	*.063*
NEU vs. INC	*2.83*	*4.51*	*118.98*	*0.63*	*.531*
learning condition:valence			2, 119.33	2.08	.130
NEU vs. CON	***-7.89***	***3.88***	***119.33***	***-2.03***	***.044****
NEU vs. INC	*-4.44*	*3.88*	*119.33*	*-1.14*	*.255*
action:valence	**35.37**	**3.68**	**1, 118.99**	**92.59**	**<.001*****
learning condition:block type			2, 121.05	0.27	.760
NEU vs. CON	*1.12*	*1.52*	*121.05*	*0.74*	*.463*
NEU vs. INC	*0.67*	*1.52*	*121.05*	*0.44*	*.661*
action:block type	**8.25**	**1.09**	**1, 2767.67**	**57.72**	**<.001*****
valence:block type	-0.75	1.09	1, 2767.67	0.48	.488
learning condition:block			2, 118	<0.01	1.000
NEU vs. CON	*-0.01*	*1.22*	*118.00*	*-0.01*	*.993*
NEU vs. INC	*-0.01*	*1.22*	*118.00*	*-0.01*	*.994*
action:block	**2.74**	**1.28**	**1, 120.05**	**4.57**	**.034***
valence:block	1.16	0.77	1, 123.78	2.28	.133
block type:block	**-1.42**	**0.54**	**1, 2767.67**	**6.86**	**.009****
learning condition:action:valence			**2, 118.99**	**7.28**	**.001****
NEU vs. CON	***-28.67***	***8.98***	***118.99***	***-3.19***	***.002*****
NEU vs. INC	***-30.51***	***8.98***	***118.99***	***-3.40***	***.001*****
learning condition:action:block type			2, 2767.67	1.75	.173
NEU vs. CON	*-3.58*	*2.66*	*2767.67*	*-1.35*	*.178*
NEU vs. INC	*1.24*	*2.66*	*2767.67*	*0.47*	*.641*
learning condition:valence:block type			2, 2767.67	0.04	.961
NEU vs. CON	*0.39*	*2.66*	*2767.67*	*0.15*	*.885*
NEU vs. INC	*0.75*	*2.66*	*2767.67*	*0.28*	*.779*
action:valence:block type	**12.43**	**2.17**	**1, 2767.67**	**32.74**	**<.001*****
learning condition:action:block			2, 120.05	0.50	.605
NEU vs. CON	*2.91*	*3.13*	*120.05*	*0.93*	*.354*
NEU vs. INC	*0.41*	*3.13*	*120.05*	*0.13*	*.897*
learning condition:valence:block			2, 123.78	1.76	.176
NEU vs. CON	*-2.58*	*1.88*	*123.78*	*-1.37*	*.173*
NEU vs. INC	*-3.38*	*1.88*	*123.78*	*-1.79*	*.076*
action:valence:block	**4.08**	**1.87**	**1, 121.89**	**4.77**	**.031***
learning condition:block type:block			2, 2767.67	0.40	.671
NEU vs. CON	*-1.13*	*1.33*	*2767.67*	*-0.85*	*.396*
NEU vs. INC	*-0.24*	*1.33*	*2767.67*	*-0.18*	*.859*
action:block type:block	**-4.99**	**1.09**	**1, 2767.67**	**21.12**	**<.001*****
valence:block type:block	-0.49	1.09	1, 2767.67	0.21	.650
learning condition:action:valence:block type			2, 2767.67	0.85	.428
NEU vs. CON	*-6.86*	*5.31*	*2767.67*	*-1.29*	*.197*
NEU vs. INC	*-4.21*	*5.31*	*2767.67*	*-0.79*	*.429*
learning condition:action:valence:block			2, 121.89	0.31	.731
NEU vs. CON	*0.07*	*4.57*	*121.89*	*0.02*	*.988*
NEU vs. INC	*3.18*	*4.57*	*121.89*	*0.70*	*.487*
learning condition:action:block type:block			2, 2767.67	0.52	.593

Table 2 (continued)

Fixed effect	β	SE	df	*F* / *t*	*p*
NEU vs. CON	*-0.37*	*2.66*	*2767.67*	*-0.14*	*.890*
NEU vs. INC	*2.16*	*2.66*	*2767.67*	*0.81*	*.417*
learning condition:valence:block type:block			2, 2767.67	0.65	.524
NEU vs. CON	*-2.61*	*2.66*	*2767.67*	*-0.98*	*.327*
NEU vs. INC	*-2.62*	*2.66*	*2767.67*	*-0.99*	*.324*
action:valence:block type:block	-4.01	2.17	1, 2767.67	3.41	.065
learning condition:action:valence:block type:block			2, 2767.67	0.76	.469
NEU vs. CON	*4.36*	*5.31*	*2767.67*	*0.82*	*.412*
NEU vs. INC	*6.39*	*5.31*	*2767.67*	*1.20*	*.229*

Note. SE = standard error, df = degrees of freedom; the *t*-statistic rather than the *F*-statistic is provided for contrasts related to the three-level predictor learning condition (corresponding rows are italicized); statistically significant results are highlighted in bold

*$p < .05$, **$p < .01$, ***$p < .001$

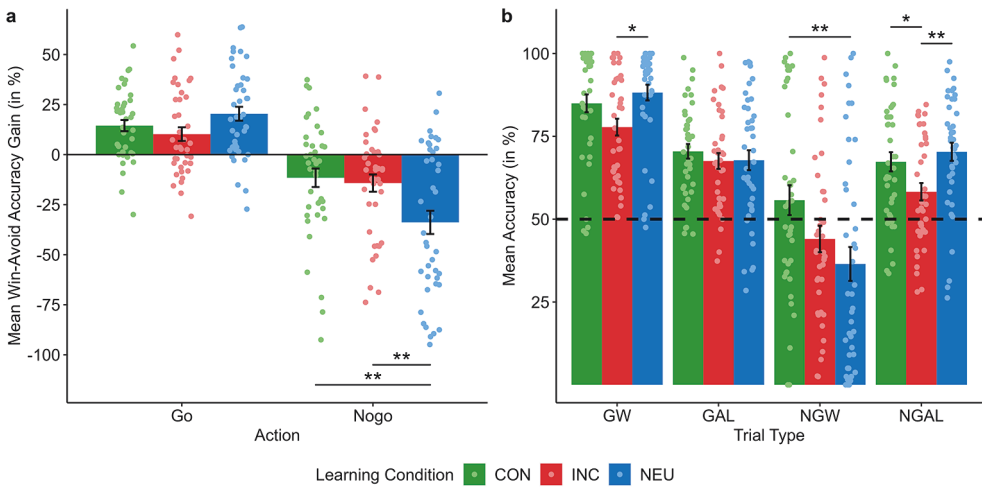


Fig. 3 Pavlovian bias modulated by learning condition. (**a**) Mean Pavlovian congruency gain indexes for go (left) and nogo trials (right) according to learning condition (green bars = emotional-congruent learning condition, red bars = emotional-incongruent learning condition, blue bars = neutral learning conditions). Scores represent the interaction between action and valence in choice accuracy (difference of win and avoid-losing). The lighter shaded dots represent subject-level choice accuracies. Error bars are represented as the standard error of the mean. (**b**) Mean accuracy across all trials is plotted for each experimental condition (GW = go to win, GAL = go to avoid losing, NGW = nogo to win, NGAL = nogo to avoid losing), according to learning condition (green bars = emotional-congruent learning condition, red bars = emotional-incongruent learning condition, blue bars = neutral learning conditions). The lighter shaded dots represent subject-level choice accuracies. Error bars are represented as the standard error of the mean. *$p < .05$, **$p < .01$, ***$p < .001$

valence interaction effect, $F(2, 118.99) = 7.28$, $p = .001$, $\eta_p^2 = 0.11$ (95%-CI 0.02–0.22) (see Fig. 3).

To resolve this interaction, we first checked whether the action × valence interaction was evident in each learning condition. Results revealed that the action × valence interaction effect emerged under all three learning conditions (all $ps < 0.001$, FDR-corrected, all $\eta_p^2 \geq 0.11$). Notably, the interaction coefficient was significantly higher for NEU, β = 55.09 (*SE* = 6.31), relative to both CON, β = 26.42 (*SE* = 6.39), $t(118.99) = 3.19$, $p = .003$, FDR-corrected, and INC, β = 24.58 (*SE* = 6.39), $t(118.99) = 3.40$, $p = .003$, FDR-corrected. Interaction coefficients did not differ between CON and INC, $p = .840$, FDR-corrected.

To further characterize the effect of learning condition on the action × outcome interaction effect, we next compared *Pavlovian congruency gain indexes*, quantified as the gain in accuracy for win minus avoid-losing, separately for go and nogo between learning conditions (see Fig. 3a). For go, gain indexes did not differ between learning conditions, all $ps \geq 0.061$, FDR-corrected. However, for nogo, absolute values for the (negative) gain indexes were reduced for CON relative to NEU, $\Delta_{win-avoid}$ = -22.22 (*SE* = 7.03), $t(118.81)$ = -3.16, $p = .006$, FDR-corrected, and for INC relative to NEU, $\Delta_{win-avoid}$ = -19.69 (*SE* = 7.03), $t(118.81)$ = -2.90, $p = .009$, FDR-corrected. There was no difference between CON and INC, $p = .721$, FDR-corrected.

As a last step, we explored what caused these differences among learning conditions by comparing learning performance for each action-valence combination between learning conditions (see Fig. 3b). For GW, INC showed

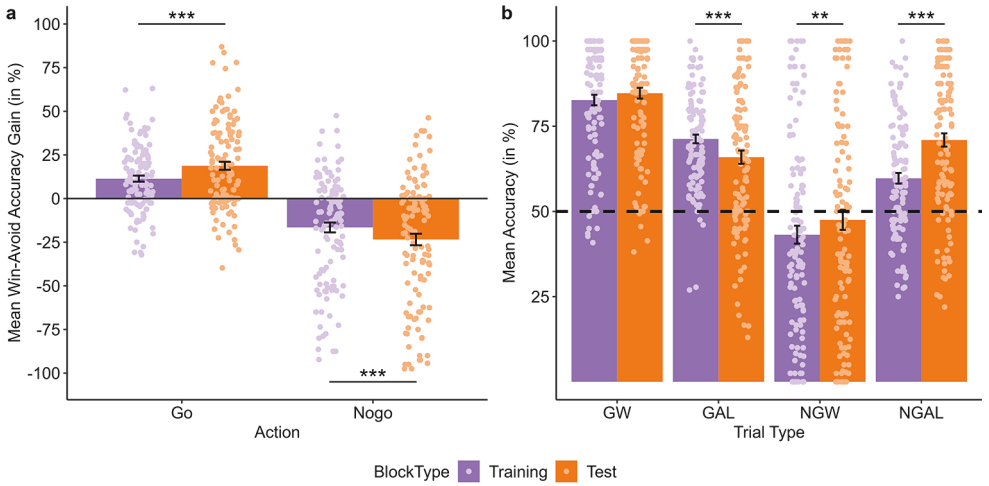


Fig. 4 Pavlovian bias modulated by block type. (**a**) Mean Pavlovian congruency gain indexes for go (left) and nogo trials (right) according to block type (purple bars = training blocks, orange bars = test blocks). Scores represent the interaction between action and valence in choice accuracy (difference of win and avoid-losing). The lighter shaded dots represent subject-level choice accuracies. Error bars are represented as the standard error of the mean. Error bars are represented as the standard error of the mean. (**b**) Mean accuracy across all trials is plotted for each experimental condition (GW = go to win, GAL = go to avoid losing, NGW = nogo to win, NGAL = nogo to avoid losing), according to block type (purple bars = training blocks, orange bars = test blocks). The lighter shaded dots represent subject-level choice accuracies. Error bars are represented as the standard error of the mean. Error bars are represented as the standard error of the mean. *p < .05, **p < .01, ***p < .001

significantly decreased learning performance compared to NEU, β = -10.59 (*SE* = 3.69), $t(119.56) = 2.95$, $p = .011$, FDR-corrected, while there was no difference in learning performance between INC and CON, $p = .073$, FDR-corrected, and NEU and CON, $p = .343$, FDR-corrected. Similarly, for NGAL, learning performance was significantly decreased in INC relative to NEU, β = -12.20 (*SE* = 3.89), $t(119.32) = 3.14$, $p = .007$, FDR-corrected, and CON, β = 9.35 (*SE* = 3.92), $t(119.32) = 2.39$, $p = .028$, FDR-corrected. However, differences in learning performance between NEU and CON were again non-significant, $p = .465$, FDR-corrected. Contrary to that, learning performance did not differ between learning conditions for GAL (all $ps \geq 0.664$, FDR-corrected). Finally, results indicated improved NGW learning performance for CON compared to NEU, β = 19.37 (*SE* = 6.47), $t(118.48) = -3.00$, $p = .010$, FDR-corrected, but no differences between CON and INC ($p = .106$, FDR-corrected) or NEU and INC ($p = .249$, FDR-corrected).

In summary, the Pavlovian bias effect emerged under all learning conditions but was reduced in both CON and INC relative to NEU, particularly for nogo-learning. Crucially, while the reduced Pavlovian bias found in CON was driven by improved learning performance in NGW, the reduced Pavlovian bias effect in INC was rooted in impaired learning performance in GW and NGAL.

Complementary results

Increased Pavlovian biases in the absence of feedback Beyond that, results revealed an action × valence × block type interaction effect, $F(1, 2767.67) = 32.74$, $p < .001$, $\eta_p^2 = 0.01$ (95%-CI 0.01–0.02; see Fig. 4).The action × valence interaction effect was significant for both block types (both $ps < .001$, FDR-corrected, both $\eta_p^2 \geq 0.29$). However, the interaction coefficient was larger for test, β = 41.58 (*SE* = 3.83, compared with training blocks, β = 29.15 (*SE* = 3.83), $t(2767.67) = 5.72$, $p < .001$. Comparing Pavlovian congruency gain indexes separately for go and nogo between block types revealed increased (absolute) gain indexes in test relative to training blocks for both go, $\Delta_{win-avoid} = 6.97$ (SE = 1.54), $t(2767.67) = 4.54$, $p < .001$, and nogo conditions, $\Delta_{win-avoid} = -5.46$ (*SE* = 1.54), $t(2767.67) = -3.56$, $p < .001$ (see Fig. 4a). Comparing block types at each action-valence combination further indicated increased learning performance in test relative to training blocks in NGAL, β = 8.56 (*SE* = 1.13), $t(1052.62) = 7.58$, $p < .001$, FDR-corrected, and NGW, β = 3.09 (SE = 1.13), $t(1052.62) = 2.74$, $p = .008$, FDR-corrected. In contrast, GAL learning performance was increased in training relative to test blocks, β = -5.92 (*SE* = 1.13), $t(1052.62) = -5.24$, $p < .001$, FDR-corrected (see Fig. 4b). There was no difference between block types for GW, $p = .351$, FDR-corrected.

In summary, the Pavlovian bias was increased, in test blocks, i.e. in the absence of feedback for both go and nogo learning. Importantly, accuracy was decreased in GAL, but increased in NGAL and NGW in test relative to training blocks.

Effects of the continuous factor block on learning performance Furthermore, LME model analysis revealed an action × valence × block interaction effect, $F(1, 121.89) = 4.77$, $p = .031$, $\eta_p^2 = 0.04$ (95%-CI 0-0.12). Slope estimates for the block factor were significant for GW, NGW and NGAL, all $ps \leq 0.033$, FDR-corrected, but not GAL, $p = .149$, FDR-corrected, indicating accuracy increases across blocks in all learning conditions, $\beta s \geq 2.20$ ($SEs \leq 0.1.28$), except GAL. Subsequent comparisons of slope estimates for each action-valence combination revealed that the increase in accuracy across blocks was strongest in NGAL, $\beta = 6.10$ ($SE = 0.97$), thus greater relative to NGW, $\beta = 2.90$ ($SE = 1.28$), $t(121.75) = -2.38$, $p = .038$, FDR-corrected, GAL, $\beta = 1.32$ ($SE = 0.91$), $t(121.19) = -3.29$, $p = .008$, FDR-corrected, and GW, $\beta = 2.20$ ($SE = 0.85$), $t(121.94) = -2.97$, $p = .011$, FDR-corrected. All other comparisons did not reach statistical significance (all $ps \geq 0.491$, FDR-corrected).

There was also an action × block type × block interaction effect, $F(1, 2767.67) = 21.12$, $p < .001$, $\eta_p^2 = 0.01$ (95%-CI 0-0.02). For go conditions, slope estimates for the predictor block indicated accuracy increases across test, $\beta = 2.30$ ($SE = 0.80$), $p = .009$, FDR-corrected, but not training blocks, $p = .129$, FDR-corrected, though slope estimates did not significantly differ from each other, $t(2767.67) = 1.40$, $p = .162$. For nogo conditions, slope estimates for the predictor block indicated accuracy increases across both training, $\beta = 6.46$ ($SE = 0.99$), $p < .001$, FDR-corrected, and test blocks, $\beta = 2.54$ ($SE = 0.99$), $p = .011$, FDR-corrected, with greater increases over blocks for training relative to test blocks, $t(2767.67) = -5.10$, $p < .001$.

In summary, choice accuracy linearly increased throughout the task for all experimental conditions, except for GAL, with the largest increase in accuracy across blocks for NGAL. Crucially, increases in learning performance for go conditions were only observed in test but not training blocks, while for nogo conditions accuracy increased across both training and test blocks.

Relationship between BIS/BAS and the Pavlovian bias

Relationships between reward and punishment sensitivity and the Pavlovian bias were explored via Spearman rank-order correlations between participants' BIS/BAS scores and participant-wise random slopes for the action × valence interaction effect. However, results did not reveal significant correlations, $r(119) \leq |0.046|$, all $ps \geq 0.920$, FDR-corrected. Importantly, calculating correlations separately for each learning condition also failed to reveal a significant relationship between BIS/BAS scores and random slopes for the action × valence interaction, CON: $r(38) \leq |0.159|$, all $ps \geq 0.490$, FDR-corrected, INC: $r(38) \leq |0.349|$, all $ps \geq 0.082$, FDR-corrected, NEU: $r(39) \leq |0.242|$, all $ps \geq 0.380$, FDR-corrected.

Discussion

In the present study, we aimed to test whether and how the Pavlovian bias in feedback-based learning can be modulated by social affective cues. Participants were tested using a variant of the orthogonalized Go/Nogo task which fully decoupled action and outcome valence. Importantly, participants learned action-outcome contingencies either from neutral (NEU) or emotional facial cues, for which action tendencies associated with the affective valence of the facial cue were either congruent (CON) or incongruent (INC) to the required action in order to obtain the best possible outcome on each trial. We hypothesized that when action tendencies associated with the affective valence of the facial cue matched the required instrumental action, the Pavlovian bias would be reduced relative to learning from neutral cues. Conversely, when action tendencies associated with the affective valence of the facial cue contradicted the required instrumental action, we expected the Pavlovian bias to be enhanced relative to learning from neutral cues (although this hypothesis was somewhat more speculative, see above). We assumed emotional faces to primarily affect learning performance in conflict conditions (i.e. GAL and NGW). The results revealed that the Pavlovian bias was present ubiquitously in all three learning conditions. However, contrary to our hypotheses, the Pavlovian bias was reduced in both CON and INC relative to NEU.

As expected, participants learned better to execute a response to obtain a reward than to avoid punishment, and to withhold a response to avoid punishment than to obtain a reward. In line with our hypotheses, this asymmetry observed in instrumental learning, referred to as Pavlovian bias, was evident in each learning condition. This result is largely consistent with previous research reporting a robust Pavlovian bias in various study populations and task contexts (e.g. Cavanagh et al., 2013; Dorfman & Gershman, 2019; Ereira et al., 2021; Guitart-Masip et al., 2012, 2014a; Peterburs et al., 2021, 2022; Raab & Hartley, 2020; Scholz et al., 2022). The Pavlovian bias can be understood as a conflict between hard-wired *Pavlovian control of behavior*, in which the anticipation of valenced outcomes automatically determines the choice of action (i.e., anticipating reward facilitates action invigoration, and anticipating punishment facilitates action inhibition), and flexible *instrumental control of behavior* which slowly but efficiently adjusts our actions to obtain the best possible outcome. At the neural level, this might be rooted in the ventral striatal dopamine

(DA) system, signaling reward prediction errors (Bayer & Glimcher, 2005; Schultz et al., 1997). Accordingly, better-than-expected outcomes elicit increased striatal DA release that facilitates action invigoration, and worse-than-expected outcomes elicit reduced striatal DA release which facilitates action inhibition (Collins & Frank, 2014; Frank et al., 2004; Schultz et al., 1997; Wickens et al., 2007). Accordingly, cues predicting reward would lead to increased firing of DA neurons, thus facilitating *go* responses, and cues predicting punishment would lead to reduced firing of DA neurons, thus facilitating *nogo* responses. Note however, that a role of prefrontal dopamine in the resolution of Pavlovian-instrumental conflicts has also been considered (Scholz et al., 2022), which is in line with previous findings that linked the prefrontal cortex to overcoming Pavlovian biases (Cavanagh et al., 2013; Kim et al., 2023).

Notably, in the present study, the Pavlovian bias was attenuated in CON. This effect was driven by a selective performance boost in the conflict condition NGW that was cued by an angry face. While this result is consistent with our hypotheses, against our expectations the manipulation did not influence learning performance in GAL. Previous research has consistently linked appetitive and aversive stimuli, including facial expressions, with approach and avoidance motivation, respectively (Marsh et al., 2005; Nikitin & Freund, 2019; Phaf et al., 2014; Seidel et al., 2010). Our results demonstrate that during reinforcement learning, at least in the context of nogo learning, maladaptive Pavlovian biases can be reduced by learning from angry facial cues. Findings from Chiu et al. (2014) further suggest that this effect may originate in the motor system, as they could show that aversive cues decreased motor system excitability, therefore biasing nogo behavior in a Go/Nogo task. Beyond that, overcoming Pavlovian biases has been linked to effort-based resolution of motivational conflicts via cognitive control mechanisms (Cavanagh et al., 2013). Emotional valence has been shown to be capable of resolving both emotional and cognitive conflicts (Kanske & Kotz, 2010, 2011; Zinchenko et al., 2015, 2020). Thus, angry faces may have helped resolve the Pavlovian conflict related to NGW. Importantly, the modulatory effect of CON was restricted to nogo, highlighting the robustness of the Pavlovian learning bias in the context of go, consistent with previous studies (e.g. Asci et al., 2019; Ereira et al., 2021; Peterburs et al., 2021; Weber et al., 2022).

Crucially, the Pavlovian bias was not only reduced in CON but also in INC. However, what caused the observed result patterns for CON and INC was fundamentally different. For CON, affective cues supported regulating maladaptive Pavlovian influences by improving performance in the conflict condition NGW, thereby promoting adaptive and goal-directed decision-making (at least in the nogo context). In contrast, for INC, affective cues did not affect learning performance in conflict conditions but rather led to impaired performance in both non-conflict conditions, GW and NGAL, which in turn resulted in a reduced Pavlovian nogo bias. Even though not in line with our hypotheses, it should be noted that this results still confirms the assumed relationship between affective cues and approach-avoidance behavior, with angry faces impairing learning performance in GW and happy faces impairing learning performance in NGAL. In addition, although both CON and INC were associated with comparably reduced Pavlovian biases, global learning success was reduced in INC relative to CON. These findings suggest that reduced Pavlovian biases and adaptive, goal-directed behavior reflected in the global learning performance do not always go hand in hand and should therefore be dissociated.

Taking that into consideration, improved Pavlovian-instrumental regulation observed in both CON and INC relative to NEU was only adaptive in CON but not INC, as only for CON an improvement in instrumental performance in one of the conflict conditions could be detected. Thus, although seemingly similar at first glance, our results indicate opposite effects of CON and INC related to goal-directed behavior.

Strikingly, non-conflict and conflict conditions have been shown to be differently sensitive to emotionally valenced cues in CON versus INC. Why affective cues modulated conflict in CON but non-conflict conditions in INC still remains speculative. One possible reason may be congruency differences between CON and INC related to outcome valence. Thompson and Westwater (2017) demonstrated that happy, neutral, and angry faces can be successfully used as social feedback signalizing win, draw, and loss, respectively. In the present study, however, facial stimuli were implemented as learning cues instead of feedback stimuli. Importantly, congruency was based on whether the valence of the facial cue was in accordance with the required response, thus action-congruent (e.g. happy face for go conditions, i.e. GW and GAL) but not outcome-congruent (which would have used happy faces for win conditions, i.e. GW and NGW). Poorer learning performance for INC in non-conflict conditions GW and NGAL might therefore be explained by the fact that both GW and NGAL were not only action- but also outcome-incongruent, thus further cognitive control would have been needed to resolve two levels of maladaptive conflicts, i.e. both action-incongruencies as well as outcome-incongruencies in those conditions. However, this interpretation only holds for INC. For CON, both non-conflict conditions were not only action- but also outcome-congruent. Thus, according to this interpretation, one would assume task performance to even increase in GW and NGAL due to two levels of facilitation. While it

might be plausible to not find an additional increase in performance in the easiest condition GW, due to a ceiling effect (e.g. Peterburs et al., 2021), our results also did not provide evidence for improved task performance in NGAL.

Lerner et al. (2015) emphasized that emotional valence constitutes only one of multiple dimensions related to emotional processing. A reduced Pavlovian bias for both CON and INC might therefore be better explained by increased arousal in response to the cue and/or increased cue salience which may improve Pavlovian regulation. However, as we have discussed, improved Pavlovian-instrumental regulation seems not always to be adaptive. Thus, cue valence, or cue-action congruency may determine whether the reduction in Pavlovian bias is adaptive or maladaptive with respect to goal-directed behavior. Our results therefore expand previous studies that investigated affective valence as the effect of emotional content (Asci et al., 2019) and induced affect (Weber et al., 2022) on the Pavlovian bias but failed to unveil modulatory effects, potentially as those manipulations did not affect cue salience. Our results suggest that, in order to modulate Pavlovian biases, manipulating both cue valence and stimulus salience may be inevitable, suggesting that modulation of the Pavlovian bias effect may require affective evaluation (see also Eder & Rothermund, 2008; Rotteveel & Phaf, 2004). However, it has to be noted that a potential role of arousal/salience in resolving Pavlovian learning biases is rather speculative, as arousal/salience was neither directly manipulated or rated in the present study nor were arousal ratings collected in the validation study by Ebner et al. (2010).

Previous studies indicated Pavlovian biases to be robust to manipulations (e.g. Asci et al., 2019; Ereira et al., 2021; Peterburs et al., 2021; Weber et al., 2022). Nevertheless, Ereira et al. (2021) could show reduced Pavlovian biases through training in a task variant, that used a semantic response domain, combined with gamification and spaced stimulus presentation. Notably, these results may also be explained by increased arousal/salience related to gamification and the semantic domain that hint at a potential role of arousal/salience in overcoming Pavlovian biases. Crucially, emotional faces do not only differ from neutral faces with respect to arousal and salience, but also in terms of motivational intensity (Harmon-Jones et al., 2012a, 2012b, 2013), i.e. the strength of the urge to approach or avoid. However, note that motivational intensity was found to be closely related to valence (Campbell et al., 2021). Beyond that, emotional faces also seem to differ from neutral faces in terms of the appraisal of affective relevance, which has been shown to underly learning biases in Pavlovian aversive conditioning (Stussi et al., 2018, 2021). Thus, it remains unclear which specific mechanism underlies the observed modulation of the Pavlovian bias, reported in the present study. Additional research with direct manipulation of cue arousal/salience and related concepts including motivational intensity and affective relevance is needed to clarify and further characterize potential modulators of the Pavlovian bias on instrumental learning and to evaluate its clinical potential.

Still, to our knowledge, our results provide first evidence for an easy-to-implement intervention, without the need of additional training, that is capable of diminishing Pavlovian-instrumental interference, reflected in reduced Pavlovian bias on instrumental learning.

Interestingly, Pavlovian bias proved to be higher in test blocks in which participants were not provided feedback for their choices compared with training blocks which contained trial-by-trial feedback. This finding fits well with the theory of Pavlovian-instrumental arbitration, proposed by Dorfman and Gershman (2019). According to this theory, the brain arbitrates between Pavlovian and instrumental control of behavior depending on which can better predict reward. While under Pavlovian control, reward predictions are generated based on stimuli only, reward predictions under instrumental control not only consider stimuli but also actions. Dorfman and Gershman (2019) theorized that if actions do not or unreliably affect consequences and rewards are hence uncontrollable, the brain favors Pavlovian over instrumental control, resulting in increased Pavlovian bias. Indeed, Dorfman and Gershman (2019) found that Pavlovian bias was stronger under conditions of low relative to high reward controllability by manipulating the probability of rewards in a reward-based Go/Nogo task. The arbitration theory has been also linked to learned helplessness, a hypothesized model to underly anxiety and depressive symptoms (Csifcsák et al., 2020; Dorfman & Gershman, 2019; Mineka & Hendersen, 1985).

Completely omitting performance feedback might constitute a similar state of reduced reward controllability. During training blocks, rewards could be directly controlled through one's actions, thus instrumental control was useful to flexibly adjust the current response strategy depending on the previous feedback received. In test blocks, when feedback was omitted, feedback-guided decision-making was not possible anymore, and rewards might have seemed uncontrollable. Note however, that participants were instructed that correct decisions were also rewarded in test blocks. Our finding of increased Pavlovian bias in test blocks compared with training blocks may therefore be explained in terms of stronger reliance on a Pavlovian predictor for rewards under conditions of lower reward controllability (i.e., when actions did not have immediate consequences).

A recent study by Kurtenbach et al. (2022) directly compared task performance during reinforced and non-reinforced periods in a Go/Nogo task. Results indicated a shift in response strategy to a more cautious response style with a

decreased tendency to execute a response in non-reinforced relative to reinforced trials that was accompanied by a general improvement in non-reinforced relative to reinforced trials. Our results also found generally better learning performance for non-reinforced test compared with reinforced training blocks, although Pavlovian bias was increased for those trials. Notably, this again emphasizes that Pavlovian bias does not by implication lead to poorer general learning performance. Our results indicate a similar shift in response strategy, as reported in Kurtenbach et al. (2022). While performance in nogo conditions was increased in test relative to training blocks, the opposite was true for GAL. Thus, performance differences between blocks and enhanced Pavlovian biases in test relative to training blocks may also be explained in terms of a reduced go bias, possibly due to a shift to a more cautious response style.

Limitations and future directions

The present study has three main limitations. First, although the recruited participants were in a similar age range compared with previous studies (e.g. Cavanagh et al., 2013; Guitart-Masip et al., 2012; Peterburs et al., 2021), the results might not be representative. Crucially, Pavlovian bias has been shown to differently affect different age groups, with reduced Pavlovian bias reported for adolescents compared with children and young adults (Raab & Hartley, 2020), as well as a continuous decrease with age in adulthood (Chen et al., 2018). Thus, our study only captures a small section of participants, and it might be interesting to test in the future whether different age groups react differently to emotionality manipulations of the Pavlovian bias. Here, older adults might be of particular interest, given that ageing is associated with enhanced emotional processing as manifested in an attentional "positivity shift" (Carstensen & Mikels, 2005; Mather & Carstensen, 2003). Accordingly, one could speculate that using our task design in older individuals might yield a reduced or even absent Pavlovian bias.

Second, it has to be noted that in our task design, participants learned from facial cues but did not directly respond to the facial stimuli but to a neutral target stimulus (open white circle) after a short delay. Therefore, it might be possible that the observed effects underestimate the reported emotionality effects. Although Chiu et al. (2014) could show that cue valence can bias motor excitability and thus action tendencies even before action selection, future research should test if directly approaching versus avoiding facial cues has the potential to fully overcome the Pavlovian bias.

Third, our data provide evidence for reduced Pavlovian biases on instrumental learning, still whether this effect persists in a standard task remains unclear. Ereira et al. (2021) could show that a training-related reduction of Pavlovian biases even persisted in an independent task. Thus, it might be interesting to follow up whether the observed effects from the emotional variants can also be transferred to the standard version.

We believe that the present findings can have important implications for clinical practice. Pavlovian bias has been assumed to contribute to maladaptive behaviors including drug-seeking and addiction (Everitt et al., 2008; Flagel et al., 2010) as well as pathological gambling (Rutledge et al., 2015). Beyond that, altered Pavlovian bias has been linked to various neuropsychiatric conditions. For instance, the Pavlovian bias has been found to be increased in patients experiencing traumatic stress (Ousdal et al., 2018) and depression (Nord et al., 2018). For depression, an enhanced Pavlovian bias has been even considered predictive of recovery (Huys et al., 2016). Interestingly, reduced Pavlovian bias has been reported in schizophrenia, reflecting poorer learning performance in non-conflict conditions (Albrecht et al., 2016), similar to the result pattern in INC. Importantly, regulation of learning biases such as the Pavlovian bias may help overcome maladaptive behaviors. Our results show that the Pavlovian bias can be effectively reduced by increasing the cue-related arousal or cue salience through the use of social affective cues without the need of extensive training. Whether and how patients may benefit from better Pavlovian bias regulation should be addressed in future research.

Conclusion

In conclusion, Pavlovian bias over instrumental behavior can be effectively reduced through learning from affective facial cues. This effect may be driven by increased cue arousal and/or salience. However, whether a reduced Pavlovian bias is adaptive and hence promotes goal-directed behavior, seems to be determined by cue valence, i.e., the congruency between the cue and action valence. This suggests that cue arousal/salience and cue valence may serve different aspects of learning. While cue arousal and salience may have the potential to improve Pavlovian regulation, cue valence seems to rather affect the adaptiveness related to goal-directed behavior. To our knowledge, our results constitute the first evidence of an easy-to-implement behavioral intervention resulting in reduced Pavlovian bias. However, the underlying mechanisms of this effect still remain unclear. Our findings might yield potential for clinical application in order to better understand how Pavlovian learning biases relate to psychiatric disorders.

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Author contributions J.P., C.B., J.V. conceived of the presented idea. J.V. and A.M. carried out the experiment and analyzed the data. J.V. and J.P. wrote the first draft of the manuscript. All authors discussed the results and contributed to the final manuscript. C.B. and J.P. supervised the project.

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Data availability Data and code to reproduce all analyses in this manuscript can be found on the Open Science Framework (https://osf.io/ayp5x/).

Declarations

Ethical approval All procedures performed in this study were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the present study.

Conflict of interest Authors J.V., A.M., C.B., and J.P. declare that they have no conflicts of interest.

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Motivational Biases in Go and Nogo Learning From Immediate Versus Delayed Feedback

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ABSTRACT

Motivational biases in decision-making describe the phenomenon that individuals are more likely to perform an action to receive a reward and to withhold an action to avoid punishment. These biases likely originate from reward-related modulations of the striatum, presumably reflecting biased action selection and/or learning, the latter with facilitated learning from rewarded actions and impaired learning from punished inactions. As striatal engagement during learning depends on whether feedback is presented immediately or delayed, the present study examined whether motivational biases are similarly sensitive to feedback timing. Moreover, based on the idea that motivational biases arise through biased learning, we tested whether they manifest as biased feedback processing for action over inaction. Fifty-six healthy participants performed an orthogonalized go/nogo task learning whether to execute or withhold a response in both reward obtainment and loss-avoidance contexts—either receiving immediate ($n = 28$) or delayed feedback ($n = 28$). Applying computational modeling of choice behavior and using electroencephalography (EEG), we assessed biased instrumental learning and its neural signature in feedback processing, focusing on the feedback-related negativity/reward positivity and the P3 in the event-related potential (ERP). Behavioral results demonstrated robust motivational biases across learning from immediate and delayed feedback. Importantly, motivational biases were best explained in terms of biased action selection rather than biased learning, aligning with our ERP findings that did not provide evidence for action-biased feedback processing. Taken together, these results highlight motivational biases as a robust hallmark of decision-making, relying on common mechanisms involved in both learning from immediate and delayed feedback.

1 | Motivational Biases in Go and Nogo Learning From Immediate Versus Delayed Feedback

Decision-making is a core aspect of human cognition that requires individuals to flexibly evaluate competing response options and their (anticipated) consequences to ensure adaptive and goal-directed behavior. Everyday life decisions often involve choosing between *action* and *inaction*, that is, executing or withholding a response to achieve a desired outcome. Yet, decision-making shows a surprising inflexibility, with individuals more likely engaging in action execution to obtain a reward and action suppression to avoid punishment—a

Abbreviations: BIC, Bayesian information criterion; BIS/BAS, behavioral inhibition system/behavioral activation system scales; CI, confidence interval; DA, dopamine(rgic); EEG, electroencephalography; ERP, event-related potential; FDR, false discovery rate; FRN, feedback-related negativity; GA, grand average; GAL, go to avoid-losing; GW, go to win; ICA, independent component analysis; MCC, midcingulate cortex; NGAL, nogo to avoid-losing; NGW, nogo to win; NLL, negative log likelihood; RewP, reward positivity; RL, reinforcement learning; RPE, reward prediction error; SESOI, smallest effect size of interest; TOST, two one-sided tests; vEOG/hEOG, vertical/horizontal electro-oculogram.

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phenomenon often referred to as the *Pavlovian bias* (e.g., Cavanagh et al. 2013; Guitart-Masip et al. 2014; Guitart-Masip, Huys, et al. 2012; Vahedi et al. 2024).

While the neural underpinnings of this bias are not yet fully understood, converging evidence suggests that it originates from dopaminergic (DA) modulation of the striatum (Guitart-Masip et al. 2014; also see de Boer et al. 2019; Perosa et al. 2020; Richter et al. 2021; Richter et al. 2014). Seminal work has shown that midbrain DA neurons signal reward prediction errors (RPEs), with phasic bursts in activity for events better (+RPE) and dips below baseline for events worse than expected (−RPE; Bayer and Glimcher 2005; Schultz et al. 1997). In the striatum, +RPE signals are hence theorized to promote action invigoration via the direct ("go") pathway and −RPE signals to promote action suppression via the indirect ("nogo") pathway (Collins and Frank 2014; Frank 2005; Frank et al. 2004).

Still, it remains unclear whether the bias reflects (1) a bias on action selection, where the anticipation of reward or punishment—elicited by Pavlovian cues—triggers action invigoration or suppression (Guitart-Masip, Huys, et al. 2012); (2) biased (instrumental) learning and outcome evaluation, where facilitated learning from rewards following actions may shape the bias that performing an action is more easily associated with reward, while impaired learning from punishments following inactions may underlie the bias that inaction is more easily associated with avoiding punishment (de Boer et al. 2019); or (3) a combination of both (Swart et al. 2017). Recent studies thus referred to such phenomena more generally as *motivational biases* (e.g., Algermissen et al. 2024; Richter et al. 2021; Scholz et al. 2022).

Motivational biases that arise through biased learning may conceivably manifest in feedback processing. A well-established neural marker of feedback processing is a distinctive frontocentral negativity in the event-related potential (ERP) which is more negative for unfavorable compared with favorable feedback (Faßbender et al. 2023; San Martín 2012; Walsh and Anderson 2012). Originally labeled feedback-related negativity (FRN) and linked to punishment processing (Holroyd and Coles 2002; Miltner et al. 1997), the neural response to unfavorable feedback has recently been interpreted as a baseline, superimposed by a reward positivity (RewP) to favorable feedback (Holroyd et al. 2008; Krigolson 2018; Proudfit 2015). As a consequence, the terms FRN and RewP are often used interchangeably (see Faßbender et al. 2023); hence following Weber and Bellebaum (2024), we use the compound term FRN/RewP.

While the FRN/RewP was found to primarily emerge from the midcingulate cortex (MCC; Hauser et al. 2014; Luu et al. 2003; Oerlemans et al. 2025), it may also reflect striatal processing (Becker et al. 2014; Carlson et al. 2011; Foti et al. 2011). Not surprisingly, the FRN/RewP has been shown to reflect +/−RPEs (Fischer and Ullsperger 2013; Ichikawa et al. 2010; Röhlinger, Albrecht, and Bellebaum 2025; Vahedi et al. 2025; Weber and Bellebaum 2024), whereas other studies suggested the FRN/RewP to only reflect RPE magnitude (Ferdinand et al. 2012; Hauser et al. 2014; Talmi et al. 2013). Notably, motivational biases through biased learning imply differences in the processing of feedback obtained through action versus inaction. Indeed, previous FRN/RewP studies have reported reduced feedback valence coding following inaction (Bikute et al. 2022; Di Bernardi Luft et al. 2024; Yeung et al. 2005). However, these studies did not employ conventional feedback-based learning task, as (in)actions were implemented as (forced) non-choices. Hence, although assumed to contribute to motivational biases (Bikute et al. 2022), FRN/RewP evidence from a paradigm explicitly testing such biases and allowing participants to freely choose between action and inaction is still lacking.

Recent work examined whether motivational biases can be modulated by the learning context, but generally found them to be robust and difficult to overcome (e.g., Ereira et al. 2021; Peterburs et al. 2021; Vahedi et al. 2024). While motivational biases may be rooted in the striatum (e.g., de Boer et al. 2019; Guitart-Masip et al. 2014), the (medial) prefrontal cortex has been linked to mediating or overcoming them (Algermissen et al. 2024; Cavanagh et al. 2013; Kim et al. 2023; Ousdal et al. 2018). Moreover, the hippocampus has been associated with arbitrating approach-avoidance conflicts (Bach et al. 2014; Bryant and Barker 2020; Le Duc et al. 2025; for a review see Ito and Lee 2016). Thus, modulating motivational biases may require learning contexts that promote more deliberate and reflective processing.

While striatal recruitment during learning is particularly pronounced when feedback is presented immediately, supporting implicit, nondeclarative learning, the medial temporal lobe (including the hippocampus) is increasingly recruited when feedback is delayed by several seconds, supporting more explicit, declarative learning (Foerde and Shohamy 2011; Hinneberg and Hegele 2022). Consistent with this, FRN/RewP feedback valence coding is typically reduced for delayed compared with immediate feedback (Arbel et al. 2017; Höltje and Mecklinger 2018, 2020; Peterburs et al. 2016; Weismüller and Bellebaum 2016). Accordingly, motivational biases may depend on feedback timing, such that learning from delayed feedback may attenuate the impact of striatum-mediated action biases and shift learning toward more declarative and goal-directed control. Such a shift may therefore support overriding rigid motivational biases. However, although neural systems for processing immediate and delayed feedback may partly dissociate, they also involve common mechanisms (Weismüller et al. 2018; also see Hinneberg and Hegele 2022), as, for example, (+)RPE encoding in the FRN/RewP was reported for both immediate and delayed feedback processing (Weber and Bellebaum 2024). Whether motivational biases are modulated by feedback timing or rely on common, timing-invariant learning mechanisms thus remains to be clarified.

The present study aimed to address this gap by examining modulatory influences of feedback timing on motivational biases, while more generally investigating the role of feedback processing underlying them. To this end, electroencephalogram (EEG) was recorded while young healthy adults completed a modified orthogonalized go/nogo task, commonly used to study motivational biases (see Guitart-Masip et al. 2011), learning from either immediate or delayed feedback. Assuming that learning from delayed feedback recruits more declarative systems possibly promoting more goal-directed control (Foerde and Shohamy 2011; Hinneberg and Hegele 2022), we hypothesized that motivational biases would be reduced relative to learning from immediate feedback.

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However, given previous findings highlighting their robustness (e.g., Peterburs et al. 2021) and partially overlapping mechanisms in learning from immediate and delayed feedback (Weber and Bellebaum 2024; Weismüller et al. 2018), motivational biases may also persist across feedback timings. Moreover, we expected motivational biases to reflect biased (instrumental) learning, such that computational modeling of choice behavior should favor a model assuming facilitated learning from rewarded actions and/or impaired learning from punished inactions (see Swart et al. 2017). Biased learning may manifest in the FRN/RewP as stronger feedback valence coding for feedback following action compared with inaction, with increased positivity for rewards following actions (Bikute et al. 2022). This effect may be more strongly pronounced for immediate feedback. Similarly, RPE signaling in the FRN/RewP may be stronger for action relative to inaction, again especially for immediate feedback. Last, in an exploratory analysis, we also assessed later feedback processing, reflected in the P3 that has been linked to coding of motivational significance and outcome magnitude (San Martín 2012; Wu and Zhou 2009; Yeung and Sanfey 2004), for which similarly biased feedback processing was conceivable (see Schevernels et al. 2016).

2 | Materials and Methods

2.1 | Participants

Previous ERP studies from our group have shown that sample sizes of approximately 25 participants per experimental group are sufficient to reveal group differences in feedback processing (Bellebaum and Colosio 2014; Weismüller and Bellebaum 2016) and to detect trial-level RPE encoding (Röhlinger, Albrecht, Ghio, and Bellebaum 2025; Weber and Bellebaum 2024). We therefore targeted a sample size of around 30 participants, which we assumed to provide sufficient statistical power, even after exclusions. Note that comparable sample sizes have also been successfully used to identify group differences in motivational biases at the behavioral level (de Boer et al. 2019; Guitart-Masip, Chowdhury, et al. 2012).

Accordingly, we recruited 61 healthy adult volunteers through public advertisement and randomly assigned them to perform one of two variants of the orthogonalized go/nogo task: one in which they learned from feedback presented immediately after their choice (*immediate feedback*; $n = 31$) and one from feedback that was delayed by several seconds relative to their choice (*delayed feedback*; $n = 30$). Note that five participants had to be excluded: Two participants (one immediate feedback and one delayed feedback) were excluded as they reported a history of psychiatric disease and/or were on psychotropic medication, two participants (one immediate feedback and one delayed feedback) were excluded after data-quality control (for details see Section 2.4), and one participant (immediate feedback) was excluded due to technical problems during data recording. Hence, the final sample consisted of 56 participants (28 immediate feedback and 28 delayed feedback; for an overview, see Table 1). Written informed consent was obtained from all participants prior to participation. The study was approved by the Ethical Committee of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University, Düsseldorf (Germany), and was in accordance with the Declaration of Helsinki. A monetary compensation of 20 Euros or course credit was provided for participation.

TABLE 1 | Sample characteristics after exclusions in the two groups of participants ($N = 56$).

	Immediate feedback ($n = 28$)	Delayed feedback ($n = 28$)[a]
Age (in years)	21.18 (3.94)	21.78 (3.42)
Sex (n; female/male)	24/4	22/5
Handedness (n; left/right)	23/5	26/1
Verbal IQ	105.46 (8.99)	108.33 (7.09)
BIS[b]	22.48 (3.59)	21.38 (3.14)
BAS[b]	38.78 (3.97)	41.42 (4.34)

Note: Data are presented as means with standard deviations (SDs) in parentheses (except for sex and handedness, where data represent the number of cases).
Abbreviations: BAS = behavioral activation system; BIS = behavioral inhibition system; IQ = intelligence quotient.
[a]Due to a technical error, demographic and questionnaire data of one participant were lost.
[b]Due to a technical error, BIS/BAS scores of two participants (one immediate feedback and one delayed feedback) were lost.

As motivational biases may partly depend on intelligence (Moutoussis et al. 2018), and to ensure comparable intelligence levels across experimental groups, intelligence was estimated based on a short German multiple-choice vocabulary test (Mehrfachwahl-Wortschatz-Test B, MWT-B; Lehrl et al. 1995; Merz et al. 1975). Similarly, to assess potential group differences in dispositional reward and punishment sensitivity, which may contribute to motivational biases, the German adaptation of the behavioral inhibition system/behavioral activation system scales (BIS/BAS; Carver and White 1994; Strobel et al. 2001) was employed. There were no significant between-group differences regarding age ($p = 0.371$), verbal IQ ($p = 0.110$), and BIS scores ($p = 0.202$), whereas BAS scores were slightly increased in the delayed ($M = 41.42$; $SD = 4.34$) compared with the immediate feedback group ($M = 38.78$; $SD = 3.97$; $p = 0.020$). Note, however, that neither BIS nor BAS scores covaried with motivational bias strength in a previous study (Vahedi et al. 2024).

2.2 | Experimental Task and Procedure

Participants completed a modified version of the orthogonalized go/nogo learning task, originally developed by Guitart-Masip et al. (2011). As illustrated in Figure 1, stimulus sequence and trial timing were structured as follows: Each trial began with one out of four distinct fractal cues (obtained from https://github.com/smathot/materials_for_P0010.5; Mathôt et al. 2015), presented for 1000 ms and followed by a fixation cross for 250–2000 ms. Each cue represented one of four experimental conditions: go to win (GW), go to avoid-losing (GAL), nogo to win (NGW), and nogo to avoid-losing (NGAL). After the

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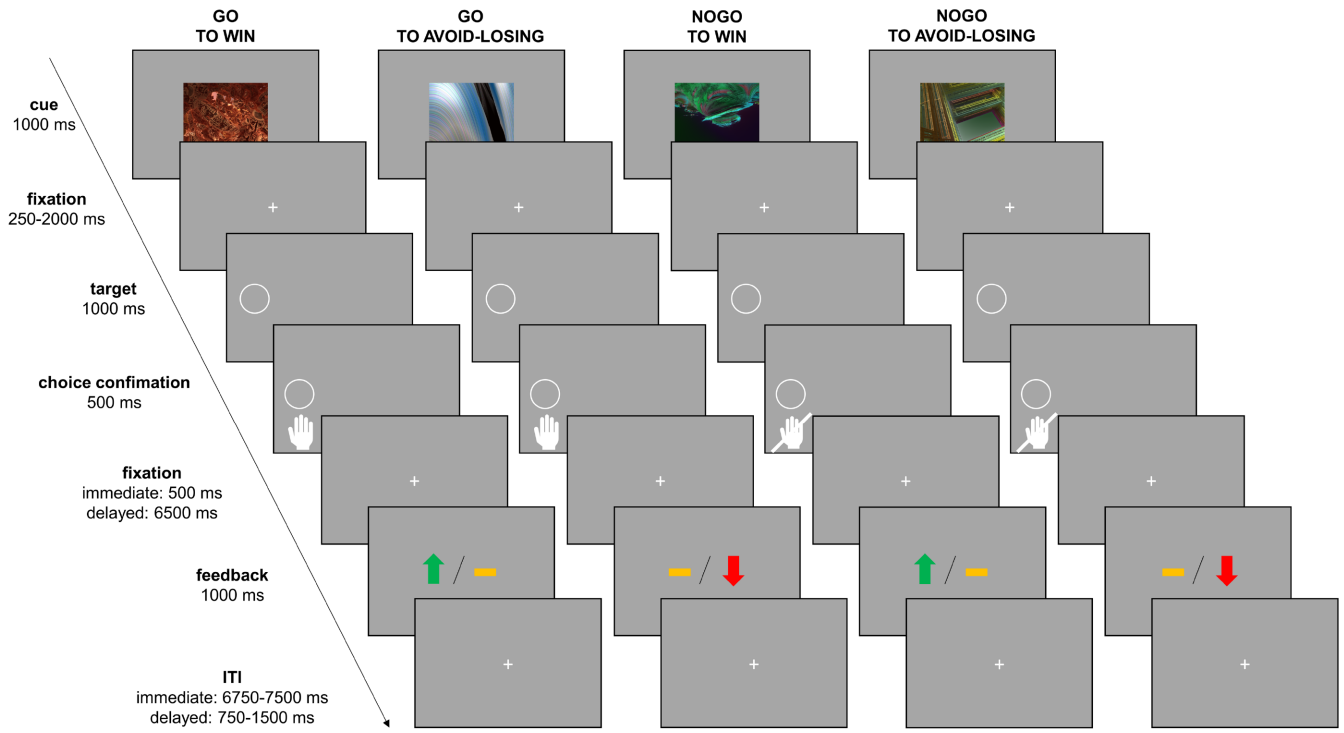


FIGURE 1 | Schematic illustration of the stimulus sequence and timing of an exemplary single trial for each cue condition. In each trial, participants had to either indicate the location of a target circle via pressing a button (go) or omit pressing a button by letting the 1000-ms response time period pass (nogo). Choices were confirmed by a hand symbol for go choices or a crossed-out hand symbol for nogo choices. Depending on the feedback timing condition, symbolic feedback was provided either immediately (after 500 ms) or with a slight delay (after 6500 ms) following choice confirmation. In win conditions, the favorable outcome was an upward-pointing green arrow indicating winning 10 points, while a yellow horizontal bar indicating neither winning nor losing points was the unfavorable outcome. Conversely, in avoid-losing conditions, the yellow horizontal bar was the favorable outcome indicating avoiding punishment, while a downward-pointing red arrow indicating losing 10 points was the unfavorable outcome. Feedback validity was 80%. Differences in trial duration for the immediate versus delayed feedback condition were balanced by adjusting the length of the intertrial interval (ITI).

cue, a white open circle appeared as a target stimulus on either the left or right side of the computer screen for 1000 ms, which served as the response time period. Within this period, participants had to decide whether to respond (*go*) or not respond (*nogo*). If participants chose to respond, they were required to indicate the location of the target stimulus by pressing the left or right Ctrl key on a standard USB keyboard. If participants decided not to respond, they had to simply wait and let the response period pass. The participant's choice was confirmed by presentation of a hand symbol underneath the target stimulus if participants pressed a valid key or a crossed-out hand symbol if no key was pressed, for 500 ms. Finally, a fixation cross was displayed before participants were shown the outcome of their choice via symbolic feedback. Crucially, experimental groups differed regarding the duration of the fixation cross, thus manipulating feedback timing; that is, the fixation cross was displayed for 500 ms in the immediate feedback variant and 6500 ms in the delayed feedback variant of the task.

Feedback was presented for 1000 ms as either a green upward-pointing arrow indicating a gain of 10 points (*win*), a red downward-pointing arrow indicating a loss of 10 points (*loss*), or a yellow horizontal bar indicating no change in the current score (*draw*). Importantly, for each experimental condition only two outcomes, one favorable and one unfavorable, were possible. In win conditions (GW and NGW), *win* was the favorable outcome whereas *draw* was the unfavorable outcome. By contrast, in avoid-losing conditions (GAL and NGAL), *draw* was the favorable outcome whereas *loss* was the unfavorable outcome. Therefore, *draw* feedback could be received in each of the four cue conditions, while *win* and *loss* feedback, respectively, could only be received in two of the four cue conditions while never co-occurring in the same cue condition (i.e., *win* only in GW/NGW and *loss* only in GAL/NGAL). Choices were classified as correct when they matched the *required response* for a given cue (i.e., *go* on GW/GAL and *nogo* on NGW/NGAL) and were hence associated with the best possible outcome. Crucially, feedback was probabilistic with a validity of 80%, such that correct responses were followed by favorable outcomes on 80% of trials, while incorrect responses resulted in favorable outcomes on 20% of trials. Participants were not explicitly informed about the probabilistic nature of the task. Notably, performance feedback was only presented when participants made a valid choice. Choices were considered invalid if participants pressed the key opposite the target location or responded outside the response period (> 1000 ms) during choice confirmation. In such cases, participants were reminded to carefully follow the task instructions. Participants were instructed to collect as many points as possible by maximizing favorable and minimizing unfavorable outcomes.

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To ensure comparable trial length in both feedback timing variants and prevent inequal task durations to confound the results, we adjusted the duration of the intertrial interval. Accordingly, a fixation cross with a jittered duration of 6750–7500 ms was presented in the immediate feedback group, whereas a jittered duration of 750–1500 ms was used in the delayed feedback group. Thus, task completion took about 35 min for both groups. The experiment consisted of four blocks of 40 trials, that is, a total of 160 trials. Presentation software (Version 20.1, Neurobehavioral Systems Inc., Albany, CA, USA) was used to control the experimental task and recording of behavioral responses.

2.3 | EEG Acquisition and Data Processing

2.3.1 | EEG Acquisition

EEG signals were acquired at a 1000-Hz sampling rate using a Brain Amp DC amplifier (Brain Products GmbH, Gilching, Germany) and BrainVision Recorder software (Version 1.20.0506, Brain Products GmbH, Gilching, Germany). Twenty-nine active silver/silver-chloride electrodes (Fz, F3, F4, F7, F8, FCz [=on-line reference], FC1, FC2, FC5, FC6, Cz, C3, C4, T7, T8, CP1, CP2, CP5, CP6, Pz, P3, P4, P7, P8, PO9, PO10, Oz, O1, and O2) were attached to an actiCAP elastic cap (Brain Products GmbH, Gilching, Germany) in accordance with the extended 10–20 system (Chatrian et al. 1985, 1988). Moreover, two electrodes were attached, one to each mastoid, for off-line re-referencing, and two additional electrodes were placed above the left eye and on the left outer canthus to record the vertical/horizontal electro-oculogram (vEOG/hEOG). The ground electrode was positioned at AFz. Impedances were kept below 20 kΩ.

2.3.2 | Preprocessing

EEG preprocessing was performed using BrainVision Analyzer software (v2.2.0; Brain Products GmbH, Gilching, Germany). In a first step, raw EEG recordings of each participant were visually inspected to identify defective or overly noisy channels. If present, any such channels were interpolated and the original signal removed (mean number of interpolated channels: 0.13, SD = 0.38, range = 0–2). Next, EEG data were re-referenced to the linked mastoids, thus allowing signal recovery of electrode site FCz. The re-referenced EEG data were then filtered using a 0.1- to 30-Hz bandpass and 50-Hz notch filter. To mitigate ocular artifacts, we used BrainVision Analyzer's built-in ocular correction independent component analysis (ICA) algorithm in semiautomatic mode (vEOG/hEOG against common average; Plank 2013).

The continuous EEG data were subsequently segmented into epochs of 800-ms length, spanning from 200 ms before to 600 ms after feedback onset. Because biased feedback processing should specifically occur for win and loss feedback, only segments corresponding to these non-neutral outcomes were considered in this study. Baseline correction was then applied by subtracting the mean voltage of the pre-feedback interval from each time point of the epoch. Ultimately, automatic artifact rejection excluded segments according to the following criteria: extreme amplitude fluctuations (exceeding ±100 μV), rapid voltage changes (> 200 μV within 200 ms), abrupt voltage steps (> 50 μV between consecutive data points), or low signal activity (< 0.5 μV within 100 ms). On average, applying these criteria led to the exclusion of 1.33% of segments (SD = 2.62). The remaining clean epochs were exported to MATLAB (Version 9.8, R2020a; The MathWorks Inc., Natick, Massachusetts, USA) for further data processing.

2.3.3 | ERP Component Scoring Procedure

The FRN/RewP was measured from electrodes within a frontocentral cluster (Fz, FC1, FC2, and FCz). For exploratory P3 analyses, the P3 was measured from electrodes within a centroparietal cluster (Cz, CP1, CP2, and Pz; see the Supporting Information for results on the P3 measured within a frontocentral cluster). Both the FRN/RewP and the P3 were scored separately for the immediate versus delayed feedback group, consistent with Weber and Bellebaum (2024). The scoring procedure was performed in accordance with Vahedi et al. (2025): For each electrode cluster (and feedback timing condition), we first created a composite waveform, calculated as the unweighted mean of the win- and loss-related grand average (GA) signal, pooled across electrodes within its cluster.

$$\text{COMP} = \frac{\text{pooled GA}_{\text{win}} + \text{pooled GA}_{\text{loss}}}{2}$$

Next, this composite waveform was used to identify the peak latency of each ERP component within a literature-backed a priori search window. Specifically, the FRN/RewP peak was searched as the local minimum in the time window 200- to 350-ms postfeedback (Faßbender et al. 2023). Conversely, the P3 peak was searched as the local maximum in the time window 250- to 500-ms postfeedback (Polich 2007). Each ERP component was eventually scored as the mean amplitude ±30 ms around the identified peak latency, for each individual electrode within its cluster, on each single trial. Details about empirical extraction time windows used for each ERP component are provided in Table 2.

2.4 | Data-Quality Control

Following Vahedi et al. (2024) and to prevent including participants with non-compliance and/or low motivation, we examined choice data based on three data-quality criteria for exclusion: First, we excluded participants with choice accuracy below-chance level (according to a one-tailed binomial test against chance, $\alpha = 0.05$) in GW, that is, the easiest learning condition (also see Albrecht et al. 2016; Weber et al. 2022). Second, we excluded participants with > 25% invalid key presses (i.e., key press on wrong side or late responding outside the response period) as in those trials no feedback was presented and participants could hence not learn the reward contingencies (Scholz et al. 2022). Last, we excluded participants who were overly biased by choosing the same response (go or nogo) in > 85% of trials (similar to Weber et al. 2022). Based on these criteria, two participants (one immediate feedback and one delayed feedback) with below-chance GW learning were excluded from further

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TABLE 2 | Scoring procedure.

ERP component	Cluster	Search window	Extraction time window
FRN/RewP	Fronto-central (Fz, FC1, FC2, and FCz)	200–350 ms[a]	Immediate feedback: 217–277 ms; delayed feedback: 242–302 ms
P3	Centro-parietal (Cz, CP1, CP2, and Pz)	250–500 ms[b]	Immediate feedback: 325–385 ms; delayed feedback: 335–395 ms

Abbreviations: ERP = event-related potential; FRN/RewP = feedback-related negativity/reward positivity.
[a]FRN/RewP search window was based on Faßbender et al. (2023).
[b]P3 search window was based on Polich (2007).

analyses. Furthermore, we removed invalid trials, with a total 3.40% of trials being removed.

2.5 | Computational Modeling of Behavioral Data

2.5.1 | Model Building

We fitted a series of Rescorla–Wagner-style reinforcement learning (RL) models (Sutton and Barto 2018) aiming to dissociate latent variables and test for the presence of an instrumental learning bias. In all models, state-action weights $W_t(a_t, s_t)$ were estimated for each choice a (*go* and *nogo*) and cue s (*GW*, *GAL*, *NGW*, and *NGAL*) on every trial t and converted into choice probabilities p using a softmax function. Choice probabilities $p(a_t|s_t)$ were calculated using an inverse temperature parameter $\beta \in (0, +\infty)$, capturing decision noise, where higher values of β reflected more deterministic and lower values of β led to more random decision-making, that is, exploitation and exploration, respectively:

$$p(a_t|s_t) = \frac{\exp(\beta * W_t(a_t, s_t))}{\sum_{a'} \exp(\beta * W_t(a', s_t))}$$

In the most parsimonious model M0, $W_t(a_t, s_t)$ equaled learned instrumental state-action values $Q_t(a_t, s_t)$, which reflected the anticipated reward associated with a given choice for a given cue. Q values were updated based on feedback $r \in \{-1, 0, 1\}$, indicating loss, draw, and win, respectively, and a learning rate parameter $\varepsilon \in [0, 1]$.

$$Q_t(a_t, s_t) = Q_{t-1}(a_t, s_t) + \varepsilon\,(r_t - Q_{t-1}(a_t, s_t))$$

In accordance with previous studies (e.g., Guitart-Masip, Chowdhury, et al. 2012; Raab and Hartley 2020; Swart et al. 2017), M0 was incrementally extended by adding additional model parameters. In M1, we first added a go bias parameter $b \in (-\infty, +\infty)$, with positive values of b indicating a bias toward go and negative values a bias toward nogo responding. Hence, in M1, $W_t(a_t, s_t)$ was calculated as

$$W_t(a_t, s_t) = \begin{cases} Q_t(a_t, s_t) + b & \text{if go} \\ Q_t(a_t, s_t) & \text{else} \end{cases}$$

In M2, we additionally implemented a Pavlovian bias parameter $\pi \in (-\infty, +\infty)$. This bias was added as a bonus term by scaling the Pavlovian state value $V_t(s_t)$, reflecting reward expectation associated with the cue, but independent of any choice:

$$W_t(a_t, s_t) = \begin{cases} Q_t(a_t, s_t) + b + \pi V_t(s_t) & \text{if go} \\ Q_t(a_t, s_t) & \text{else} \end{cases}$$

In analogy to $Q_t(a_t, s_t)$, V values were updated as follows:

$$V_t(s_t) = V_{t-1}(s_t) + \varepsilon(r_t - V_{t-1}(s_t))$$

Following recent studies suggesting a role of biased instrumental learning (e.g., Algermissen et al. 2024; de Boer et al. 2019; Swart et al. 2017), M3–M5 contained different parametrizations of an instrumental bias parameter $k \in (-\infty, +\infty)$. At the conceptual level, in all of these models, k modulated the learning rate ε by acting as a bonus weight for rewarded go choices and/or as a penalty weight for punished nogo choices, that is,

$$\varepsilon = \begin{cases} \varepsilon + k & \text{if } a = \text{go and } r = \text{win} \\ \varepsilon - k & \text{if } a = \text{nogo and } r = \text{loss} \\ \varepsilon & \text{else} \end{cases}$$

Because adding or subtracting k could push ε outside its mathematical bounds (i.e., [0, 1]), ε was therefore optimized in an unconstrained space, that is, $\varepsilon \in (-\infty, +\infty)$, but mapped onto [0, 1] via inverse logit transformation, that is, ε_0 (Algermissen et al. 2024; Swart et al. 2018; Swart et al. 2017). To ensure that k had a symmetric effect after this transformation, we first checked whether ε_0 was below or above 0.5. We then computed one part of the bias (i.e., $\varepsilon_{punishedNogo}$ if ε_0 was close to 0 or $\varepsilon_{rewardedGo}$ if ε_0 was close to 1) and applied the same-sized change in the opposite direction for the other part of the bias to keep it balanced, that is,

$$\varepsilon = \begin{cases} \varepsilon_0 = inv.logit(\varepsilon) & \\ \varepsilon_{punishedNogo} = inv.logit(\varepsilon - k) & \text{if } \varepsilon_0 < 0.5 \\ \varepsilon_{rewardedGo} = \varepsilon_0 + (\varepsilon_0 - \varepsilon_{punishedNogo}) & \text{if } \varepsilon_0 < 0.5 \end{cases}$$

$$\varepsilon = \begin{cases} \varepsilon_0 = inv.logit(\varepsilon) & \\ \varepsilon_{rewardedGo} = inv.logit(\varepsilon + k) & \text{if } \varepsilon_0 > 0.5 \\ \varepsilon_{punishedNogo} = \varepsilon_0 - (\varepsilon_{rewardedGo} - \varepsilon_0) & \text{if } \varepsilon_0 > 0.5 \end{cases}$$

Accordingly, in M3, the learning rate ε was modulated by both rewarded go and punished nogo choices by adding or subtracting the instrumental learning bias k, respectively. Moreover, and similar to de Boer et al. (2019), we also tested models that *only* added a bonus weight for rewarded go choices ($k_{rewardedGo}$ M4) or subtracted a penalty weight for punished nogo choices ($k_{punishedNogo}$; M5). Finally, in models M6–M8, we included both the Pavlovian bias parameter π and one of the three parametrizations of the instrumental bias parameter (i.e., k, $k_{rewardedGo}$, and

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$k_{punishedNogo}$) in the same model. For all models, Q and V values were initialized at the value of 0 (i.e., neither expecting reward nor loss; but see the Supporting Information for modeling with alternative initialization values).

2.5.2 | Model Fitting and Comparison

Models were fitted using a maximum a posteriori approach via the *fmincon* function (from the Optimization Toolbox) in MATLAB (see, e.g., Raab and Hartley 2020). Accordingly, we used minimally informative priors to regularize parameter ranges and to improve parameter identifiability (see Daw et al. 2011; Raab and Hartley 2020). A prior of *beta*(1.1, 1.1) was used for the ϵ parameter in models M0–M2 and a prior of *normal*(0, 1) for ϵ in models M3–M8. In addition to that, a prior of *normal*(0, 1) was also used for parameters b, π, k (including $k_{rewardedGo}$ and $k_{punishedNogo}$), whereas a prior of *gamma*(1.2, 5) was used for β. To reduce the risk of converging to local optima, optimization for each model and participant was initiated from 250 randomly chosen starting points. Models were compared to determine the winning model that best accounted for participants' observed behavior, based on the negative log likelihood (NLL), computed from choice probabilities $p(a_t|s_t)$, that is,

$$NLL = -\sum_t \log(p(a_t|s_t))$$

with the Bayesian information criterion (BIC) calculated as

$$BIC = 2NLL + n_{params}\ \log(N)$$

where n_{params} refer to the number of free model parameters and N to the number of observations. The winning model was considered the model with the lowest BIC value, that is, indicating the best model fit.

2.5.3 | Model Validation

Validation of the winning model included examining parameter identifiability and parameter recovery (Palminteri et al. 2017; Wilson and Collins 2019). Parameter identifiability was assessed via intercorrelations, where Pearson's correlation coefficients $|r| \leq 0.50$ were considered indicative of good identifiability. To evaluate parameter recovery, the winning model was re-fitted to 25 synthetic datasets per participant, generated from the parameter estimates obtained from the actual experimental data. Recovery success was quantified by computing Pearson's correlation coefficients between the true (empirical) and recovered (synthetic) parameter values, with $r \geq 0.70$ considered indicative of good recovery. To reduce variability, recovered parameters were averaged across simulations for each participant.

2.6 | Statistical Analysis

Behavioral and ERP data were analyzed at the single-trial level via (generalized) linear mixed-effects models ([G]LMMs), using the *lme4* package (Bates et al. 2015) in R (version 4.1.0; R Core Team 2021). In all models, (categorical) fixed effect predictors were coded using deviation contrasts (−0.5 vs. 0.5). To account for by-participant random variation, we implemented the maximal random-effects structure permitted by the data (Barr et al. 2013), determined via the *buildmer* function from the eponymous R package (Voeten 2020). ERP models additionally incorporated a random intercept by electrode. Full model formulae are provided in Wilkinson notation together with detailed modeling results in the Supporting Information. The *bobyqa* algorithm was used for parameter optimization with a limit of 1e6 function evaluations. For GLMMs, p-values were derived from Wald z-tests (but reported as equivalent χ^2-tests), and for LMMs based on Satterthwaite's approximation for degrees of freedom, as implemented in the *lmerTest* package (Kuznetsova et al. 2017). Effects with $p < 0.050$ were considered statistically significant. The *emmeans* package (Lenth 2022) was used to probe significant interactions, with p-values adjusted for multiple comparisons using the false discovery rate (FDR; Benjamini and Hochberg 1995).

In case of non-significant differences between conditions relevant to our hypotheses, we performed equivalence testing following the two one-sided tests (TOST) rule (Lakens 2017; Lakens et al. 2018), implemented in the *parameters* package (Lüdecke et al. 2020). This approach evaluates whether an observed effect is statistically distinguishable from effects larger than a predefined smallest effect size of interest (SESOI) by testing whether its 90% confidence interval (CI) lies entirely within a region of practical equivalence (i.e., ±SESOI). We chose a SESOI of ±0.18 log odds for choice behavior (Van der Biest et al. 2025; also see Maxwell et al. 2015) and ±0.50 μV for EEG measures, corresponding to a small but potentially meaningful effect in the ERP (see Jensen and MacDonald 2023). Crucially, equivalence testing was preferred over selective Bayes factor analyses for non-significant effects, which can be biased toward the null hypothesis (Schreiner and Kunde 2024) and is inconsistent with recent advice to maintain a single inferential framework (Dienes 2024).

2.6.1 | Behavioral Data

Motivational biases in decision-making were examined using GLMM analysis of choice accuracy. Fixed effects included the within-subject predictors cue valence (*win [=reference]* and *avoid-losing*) and required response (*go [=reference]* and *nogo*) as well as the between-subject predictor feedback timing (*immediate [=reference]* and *delayed*). Choice accuracy (0/1 = correct/incorrect) was set as a binary logistic dependent variable. The presence of motivational biases was operationalized as the effect of a cue valence × required response interaction.

In addition to RL modeling, biased learning was also exploratively investigated using a model-free approach. Therefore, a second GLMM assessed choice repetition behavior when encountering the same cue again (0/1 = switch/repeat), similar to win-stay/lose-shift behavior (Algermissen et al. 2024; also see Scholz et al. 2024). Because biased learning should primarily affect learning from *true* win and loss outcomes (Algermissen et al. 2024), we decided to omit trials with neutral outcomes for this analysis. Fixed effects included the within-subject predictors previous outcome valence (*win [=reference]* and *loss*) and response type (*go [=reference]* and *nogo*) as well as the between-subject predictor

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feedback timing (*immediate [=reference]* and *delayed*). Note that in contrast to the first GLMM, response type now reflects the *actual* choice made by the participant (on the previous trial of the same cue). Accordingly, an instrumental learning bias should manifest as the previous outcome valence × previous response type interaction, with a stronger effect of outcome valence for go compared with nogo choices.

2.6.2 | EEG Data

Feedback processing was assessed using LMMs, with FRN/RewP and the feedback-P3 amplitude as the dependent variable, respectively. Fixed effects included the categorical between-subject predictor feedback timing (*immediate [=reference]* and *delayed*), as well as the within-subject predictors outcome valence (*win [=reference]* and *loss*) and response type (*go [=reference]* and *nogo*). With these predictors, biased feedback processing, as predicted by an instrumental learning bias, should manifest as the response type × outcome valence interaction. Importantly, to fully disentangle effects of expectancy from those of outcome valence, we sought to investigate RPE coding. Trial-level RPEs were decomposed into its two constituents, that is, the expected state-action value (Q) and the received outcome (Burnside et al. 2019; Fischer and Ullsperger 2013; also see Caplin and Dean 2008). Single-trial Q values were obtained via latent variable inference from the winning RL model (Wilson and Collins 2019). Therefore, we included the absolute value of Q (i.e., $|Q|$) as an additional continuous predictor. Feedback following low $|Q|$ was weakly expected (i.e., unexpected), whereas feedback following high $|Q|$ was strongly expected, such that a main effect of $|Q|$ served as a proxy for the encoding of RPE magnitude, which has been linked to both the FRN/RewP (Ferdinand et al. 2012; Hauser et al. 2014; Talmi et al. 2013; Walentowska et al. 2019) and feedback-P3 (Kirsch et al. 2022; Philiastides et al. 2010). Encoding of signed RPEs was indicated by interaction of its constituents, that is, a significant outcome valence × $|Q|$ interaction. The higher order response type × outcome valence × $|Q|$ interaction would hence capture differences between RPE encoding for action versus inaction, although note that in case the winning RL model included an instrumental learning bias, RPEs itself would already be action biased. Trial-level $|Q|$ values were centered around 0.5 prior to model fitting.

We ensured to include a minimum of 10 trials (see Bellebaum and Daum 2008; Ichikawa et al. 2010) for each outcome valence × response type combination (4.48% of trials excluded, mean number of trials = 21.65, SD = 8.36, range = 10–40). Importantly, note that using LMMs improves parameter estimation even if including cases with limited data through partial pooling, which effectively reduces bias from low-trial observations (see, e.g., Gomes 2022).

3 | Results

3.1 | Computational Modeling

Model comparison revealed that M2 was the best fitting model as indicated by the lowest (mean) BIC (see Figure 2a). M2 included a learning rate ϵ, a go bias b, a Pavlovian bias parameter π, and an inverse temperature parameter β. Although mean BIC scores across models were relatively close (see Figure 2a), examining the sum of BICs across participants as an index of accumulated model evidence (Li et al. 2008) confirmed M2 as the best fitting model. Specifically, M2 was favored over the second-best model M3 that included an instrumental rather than Pavlovian bias parameter, with $\Delta BIC_{mean} = 2.55$ and $\Delta BIC_{sum} = 142.75$. Accordingly, choice behavior was overall better explained by a Pavlovian response bias rather than an instrumental learning bias. Still, note that there was some heterogeneity in individual model fits (see Table S1), suggesting that (latent) computational mechanisms may have slightly differed between participants.

Model validation of M2 revealed that all parameters were generally identifiable (all $|r| \leq 0.52$; see Figure 2c), and parameter recovery analysis further revealed excellent recoverability (all $r \geq 0.92$), with no spuriously high intercorrelations (all $|r| \leq 0.47$; see Figure 2d). Comparing parameter estimates between feedback timings did not show any significant differences (all $ps \geq 0.499$).

3.2 | Behavioral Data

A detailed summary of inferential statistics of behavioral GLMM analyses is provided in Tables S4 and S5.

3.2.1 | Choice Accuracy

GLMM analysis of choice accuracy yielded significant main effects of cue valence, $b = -0.37$ (SE = 0.15), $\chi^2(1) = 5.76$, $p = 0.016$, and required response, $b = -1.80$ (SE = 0.17), $\chi^2(1) = 109.16$, $p < 0.001$, suggesting overall better learning performance in the win versus the avoid-losing context and when the required response was go versus nogo. Crucially, motivational biases were evident as reflected in a significant cue valence × required response interaction effect, $b = 2.96$ (SE = 0.39), $\chi^2(1) = 57.25$, $p < 0.001$. Resolving this effect confirmed better learning in GW compared with GAL, $b = -1.85$ (SE = 0.23), $z = -7.87$, $p_{adj} < 0.001$, and NGAL compared with NGW, $b = 1.11$ (SE = 0.26), $z = 4.24$, $p_{adj} < 0.001$. Importantly, there were no significant main or interaction effects involving the predictor feedback timing ($p \geq 0.311$), providing no evidence that feedback timing modulated motivational biases (see Figure 3a) or choice behavior more generally. To formally assess whether motivational bias strength was practically equivalent across feedback timings, we performed equivalence testing on the originally non-significant feedback timing × cue valence × required response interaction. The effect (90% CI = [−1.55, 0.95]) overlapped with but did not lie entirely within the region of practical equivalence ([−0.18, 0.18]), $p = 0.825$; thus, we could not provide evidence for the practical absence of a feedback timing effect on motivational biases. Moreover, as this was central to our hypothesis, we conducted subordinate exploratory GLMM analyses separately for feedback timing, to examine whether motivational biases emerged independently across feedback timings (see Weber and Bellebaum 2024 for a similar approach). This was supported

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a. Model comparison

model	mean.BIC	std.BIC
M0: ε + β	172.56	44.56
M1: ε + b + β	165.01	43.69
M2: ε + b + π + β	**161.20**	**44.67**
M3: ε + b + k + β	163.75	46.44
M4: ε + b + k_{rewGo} + β	166.41	43.77
M5: ε + b + $k_{punNogo}$ + β	165.12	46.90
M6: ε + b + π + k + β	165.19	45.89
M7: ε + b + π + k_{rewGo} + β	167.06	45.11
M8: ε + b + π + $k_{punNogo}$ + β	166.52	45.65

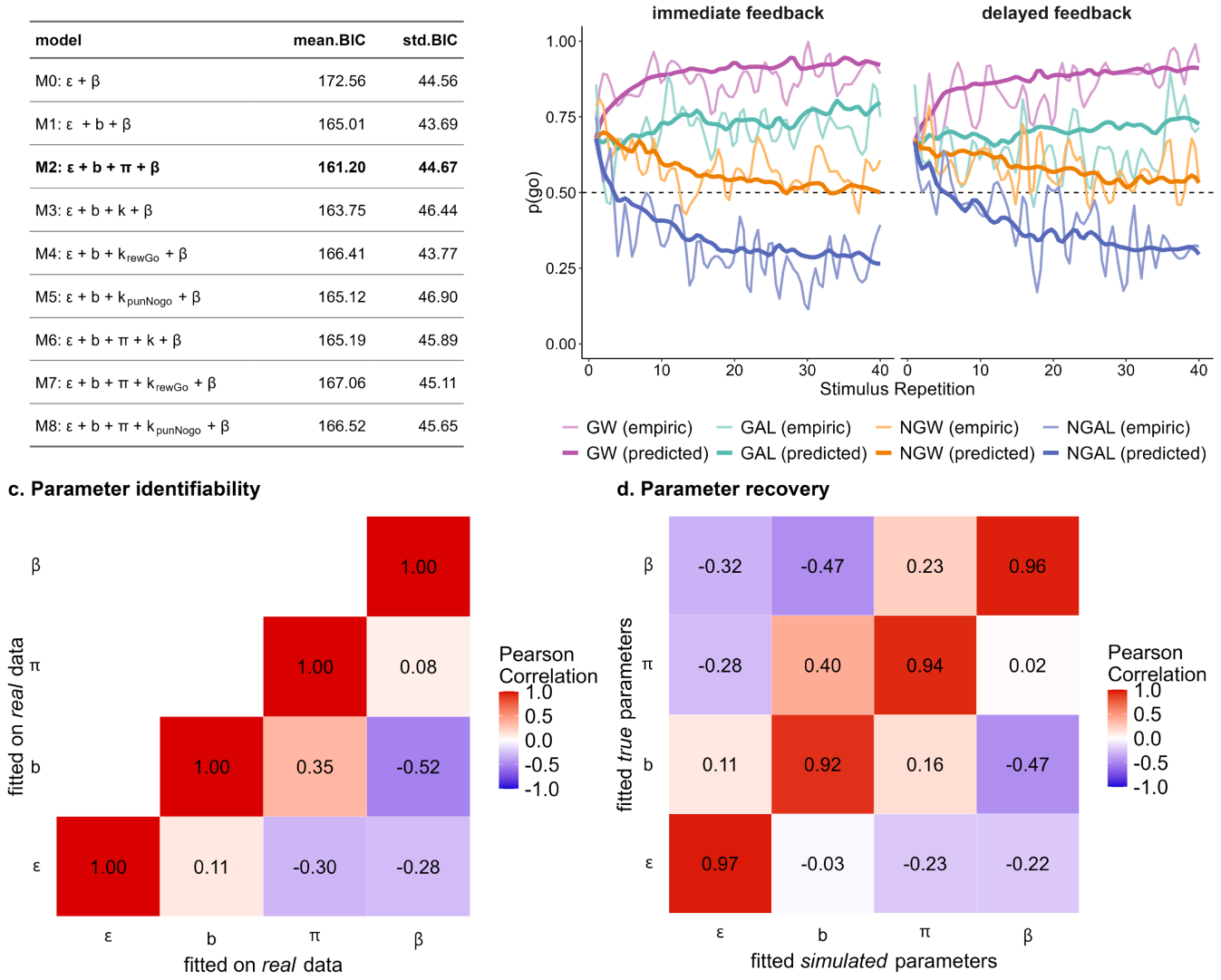


FIGURE 2 | Computational modeling results. (a) Model comparisons with the winning model highlighted in bold. (b) Posterior predictions for the winning model M2 with smoothed empirical data and (using locally estimated scatterplot smoothing) in lighter color intensity. (c,d) Results from validating the winning model M2, that is, parameter identifiability and parameter recovery. Model parameters: ε = learning rate; b = go bias parameter; π = Pavlovian bias parameter; k = instrumental learning bias parameter; β = inverse temperature parameter. BIC = Bayesian information criterion; GAL = go to avoid-losing; GW = go to win; NGAL = nogo to avoid-losing; NGW = nogo to win.

by significant cue valence × required response interactions for both immediate, $b = 3.09$ (SE = 0.57), $\chi^2(1) = 29.74$, $p < 0.001$, and delayed feedback, $b = 2.88$ (SE = 0.56), $\chi^2(1) = 26.08$, $p < 0.001$.

3.2.2 | Choice Repetition

The second, explorative GLMM for choice repetition behavior revealed significant main effects of previous outcome valence, $b = -2.17$ (SE = 0.23), $\chi^2(1) = 92.21$, $p < 0.001$, and previous response type, $b = -1.12$ (SE = 0.12), $\chi^2(1) = 88.84$, $p < 0.001$. Hence, participants were more likely to repeat their previous choice following wins than losses and following go than nogo choices. Moreover, the previous outcome valence × previous response type interaction proved to be significant, suggesting biased learning, with a larger effect of outcome valence on choice repetition behavior following go compared with nogo choices, $b = 1.42$ (SE = 0.19), $\chi^2(1) = 55.22$, $p < 0.001$ (see Figure 3b). Importantly, further resolving this effect showed that participants showed increased repetition of go versus nogo choices following wins, $b = 1.83$ (SE = 0.18), $z = 10.45$, $p_{adj} < 0.001$, in line with the assumed facilitation of learning from rewarded actions. Conversely, choice repetition was decreased for nogo versus go choices following losses, $b = 0.41$ (SE = 0.13), $z = 3.27$, $p_{adj} = 0.001$, contrary to the presumed impairment of learning from punished inactions. Again, there were no significant effects involving the predictor feedback timing ($p \geq 0.145$), providing no evidence that feedback timing modulated the instrumental learning bias or choice repetition behavior more generally. This was further confirmed by subordinate exploratory GLMM analyses separately for feedback timing, showing that the previous outcome valence × previous response type interaction emerged independently of learning from both immediate, $b = 1.59$ (SE = 0.29), $\chi^2(1) = 30.53$, $p < 0.001$, and delayed feedback, $b = 1.27$ (SE = 0.25), $\chi^2(1) = 25.21$, $p < 0.001$. Lastly, equivalence testing on the non-significant previous feedback

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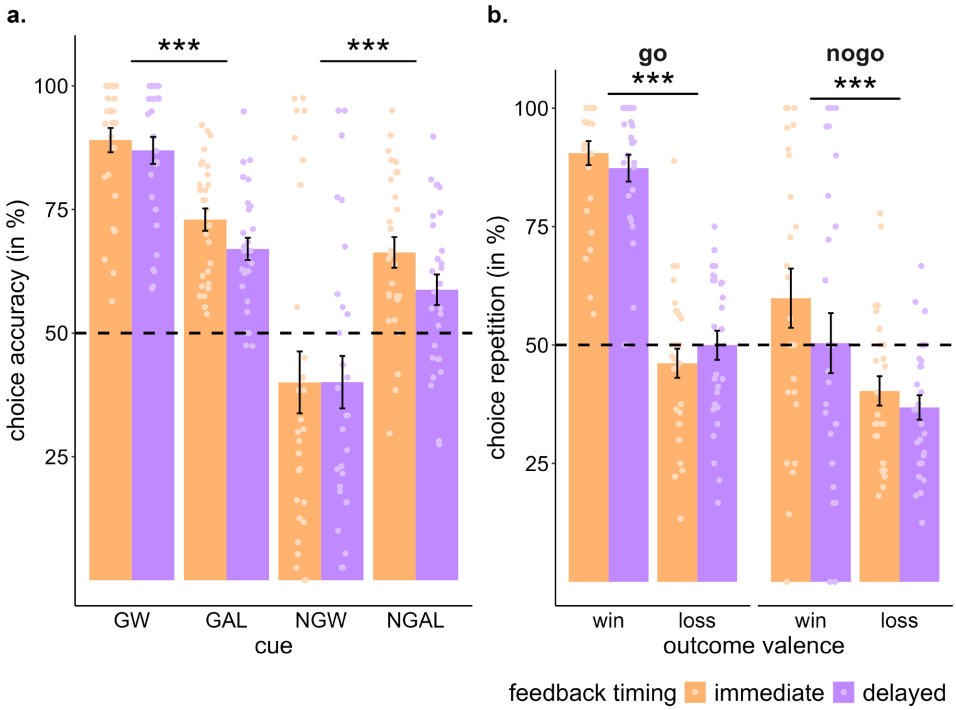


FIGURE 3 | (a) Task performance for all combinations of required response and cue valence (GW = go to win; GAL = go to avoid-losing; NGW = nogo to win; NGAL = nogo to avoid-losing), separately for each feedback timing group. (b) Choice repetition behavior for all combinations of previous outcome valence and previous response type, separately for each feedback timing group. Both plots are based on descriptive data. Lighter-shaded dots indicate mean choice accuracies at the subject level. Error bars represent the standard error of the mean. Asterisks indicate significant differences yielded from simple effects analyses. The dotted black line represents chance level performance and repetition behavior (= 50%), respectively. ·< 0.100, *p < 0.050, **p < 0.01, ***p < 0.001.

timing × outcome valence × previous response type interaction revealed that the effect (90% CI = [−0.91, 0.32]) overlapped with but did not lie entirely within the region of practical equivalence ([−0.18, 0.18]), p = 0.720; consequently, we could not provide evidence for the practical absence of this effect.

3.3 | EEG

Feedback-locked GA ERP waveforms are presented in Figure 4, with scalp topographies underlying the ERP results reported below shown in Figure S2. A detailed overview of inferential statistics for all LMM analyses is provided in Tables S6–S9.

3.3.1 | FRN/RewP

FRN/RewP results revealed a significant main effect of feedback timing, b = −5.00 (SE = 1.97), F(1, 38.95) = 6.48, p = 0.015, indicating that amplitudes were overall more negative for delayed versus immediate feedback. The effect of feedback timing was further qualified by a significant feedback timing × |Q| interaction effect, b = −7.28 (SE = 2.98), F(1, 28.27) = 5.97, p = 0.021, indicating that the FRN/RewP was more negative when feedback was more unexpected, for immediate feedback, b = 6.46 (SE = 2.13), t(28.90) = 3.04, p_{adj} = 0.010, but not for delayed feedback (p_{adj} = 0.696). Moreover, also, the outcome valence × |Q| interaction was significant, b = 7.46 (SE = 1.60), F(1, 31.26) = 21.79, p < 0.001, suggesting that, overall, the FRN/RewP reflected −RPEs, b = 6.54 (SE = 1.95), t(27.67) = 3.35, p_{adj} = 0.005, but no +RPEs (p_{adj} = 0.513). Further resolving this interaction using a spotlight approach indicated that the FRN/RewP was more negative for losses versus wins only when feedback was unexpected (|Q| = −0.25), b = −1.39 (SE = 0.61), t(39.27) = −2.27, p_{adj} = 0.038, whereas the opposite, that is, a more positive FRN/RewP for losses versus wins was observed when feedback was expected (|Q| = 0.25), b = 2.34 (SE = 1.08), t(31.00) = −2.17, p_{adj} = 0.038. Finally, the feedback timing × outcome valence × |Q| interaction reached significance, b = −11.22 (SE = 3.20), F(1, 31.26) = 12.34, p = 0.001 (see Figure 5a). Probing this interaction via simple slope analyses indicated that for immediate feedback the FRN/RewP encoded −RPEs, b = 12.99 (SE = 2.82), t(29.32) = 4.61, p_{adj} < 0.001, with no evidence for the encoding of +RPEs (p_{adj} = 0.971), whereas no RPE encoding was evident for delayed feedback, that is, neither for +RPEs nor for −RPEs (ps_{adj} ≥ 0.741).

Again, there were no significant effects involving the predictor response type (ps ≥ 0.071; see Table S6). Subordinate exploratory LMM analyses separately for response type replicated the effects reported above for both go (ps ≤ 0.014) and nogo choices (ps ≤ 0.037). To explore whether RPE encoding was practically equivalent regardless of response type, equivalence testing was performed on the non-significant response type × outcome valence × |Q| interaction effect. This revealed that the effect (90% CI = [−3.68, 7.07]) overlapped with but did not entirely lie within the region of practical equivalence ([−0.50, 0.50]), p = 0.894; thus, we could not provide evidence for the practical absence of such an effect.

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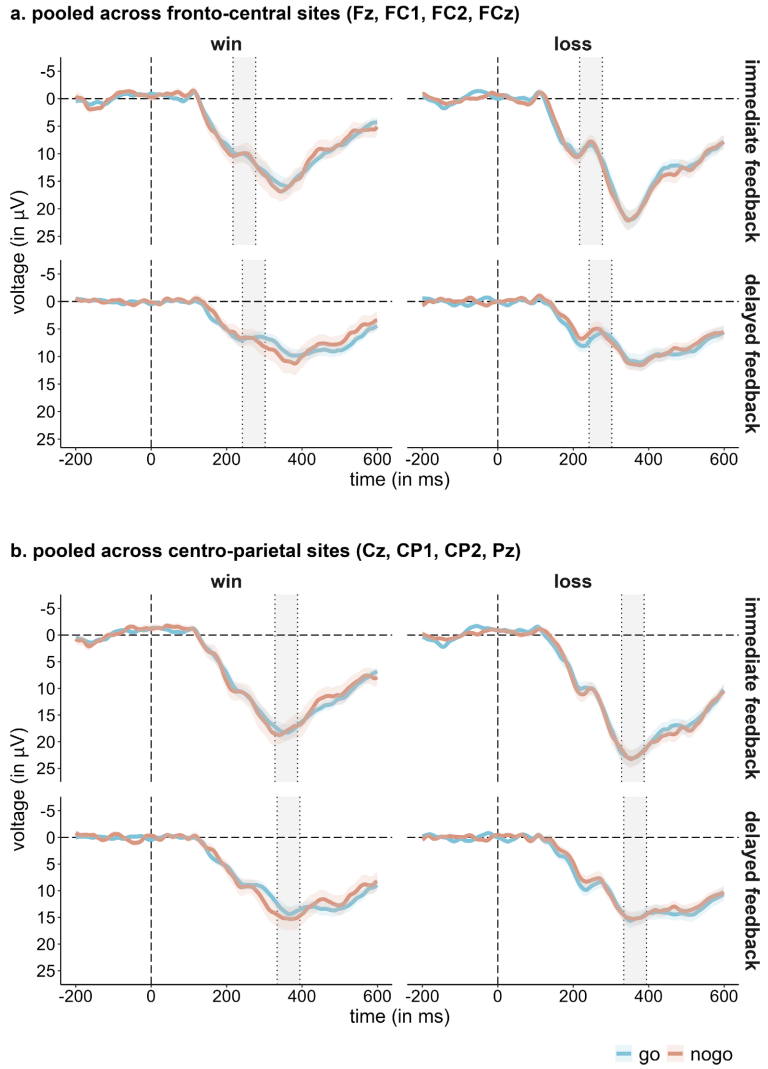


FIGURE 4 | Feedback-locked grand average ERP waveforms. Data are presented as mean ± standard error. Gray-shaded areas indicate the measurement windows used to score the feedback-related negativity/reward positivity (FRN/RewP) (shown in a) and the feedback-P3 (shown in b). ERP = event-related potential.

3.3.2 | Feedback-P3

Exploratory analyses for the feedback-P3 yielded significant main effects of feedback timing, $b = -6.14$ (SE = 2.08), $F(1, 44.07) = 8.69$, $p = 0.005$, and outcome valence, $b = 4.55$ (SE = 0.86), $F(1, 30.84) = 27.86$, $p < 0.001$, indicating generally more positive P3 amplitudes for immediate versus delayed feedback and for *loss* versus *win* feedback. In addition, the main effect of $|Q|$ was significant, $b = -3.64$ (SE = 1.59), $F(1, 29.71) = 5.22$, $p = 0.030$, suggesting that amplitudes of the P3 were more positive when feedback was more unexpected.

Moreover, results revealed a significant feedback timing × outcome valence interaction effect, $b = -4.05$ (SE = 1.72), $F(1, 30.84) = 5.51$, $p = 0.025$, with the effect of outcome valence being larger for immediate than delayed feedback. Finally, there was a significant outcome valence × $|Q|$ interaction, $b = -12.13$ (SE = 2.54), $F(1, 43.50) = 22.89$, $p < 0.001$, indicating that the P3 generally encoded a +RPE, $b = -9.70$ (SE = 2.07), $t(34.02) = -4.69$, $p_{adj} < 0.001$, with more positive amplitudes, the more unexpected *win* feedback was, but no evidence for −RPE encoding ($p_{adj} = 0.235$).

Importantly, RPE encoding depended on both the response type and feedback timing, as revealed by a significant response type × outcome valence × $|Q|$ interaction, $b = 6.68$ (SE = 2.17), $F(1, 1237.96) = 9.48$, $p = 0.002$, that was ultimately qualified by the higher-order feedback timing × response type × outcome valence × $|Q|$ interaction effect, $b = -9.58$ (SE = 4.34), $F(1, 1237.96) = 4.88$, $p = 0.027$. Resolving this effect showed that +RPEs were consistently encoded in the P3 across feedback timings and response type ($ps_{adj} \leq 0.026$, though note a non-significant trend for nogo with immediate feedback, $p_{adj} = 0.064$). By contrast, the P3 signaled a −RPE only for nogo with immediate feedback, $b = 11.16$ (SE = 4.28), $t(34.35) = 2.61$, $p_{adj} = 0.027$, whereas for all other conditions no such effect was detected ($ps_{adj} \geq 0.807$; see Figure 5b).

4 | Discussion

The present study aimed to examine whether feedback timing modulates motivational biases and to test the broader role of (biased) feedback processing in shaping them. To this end, two

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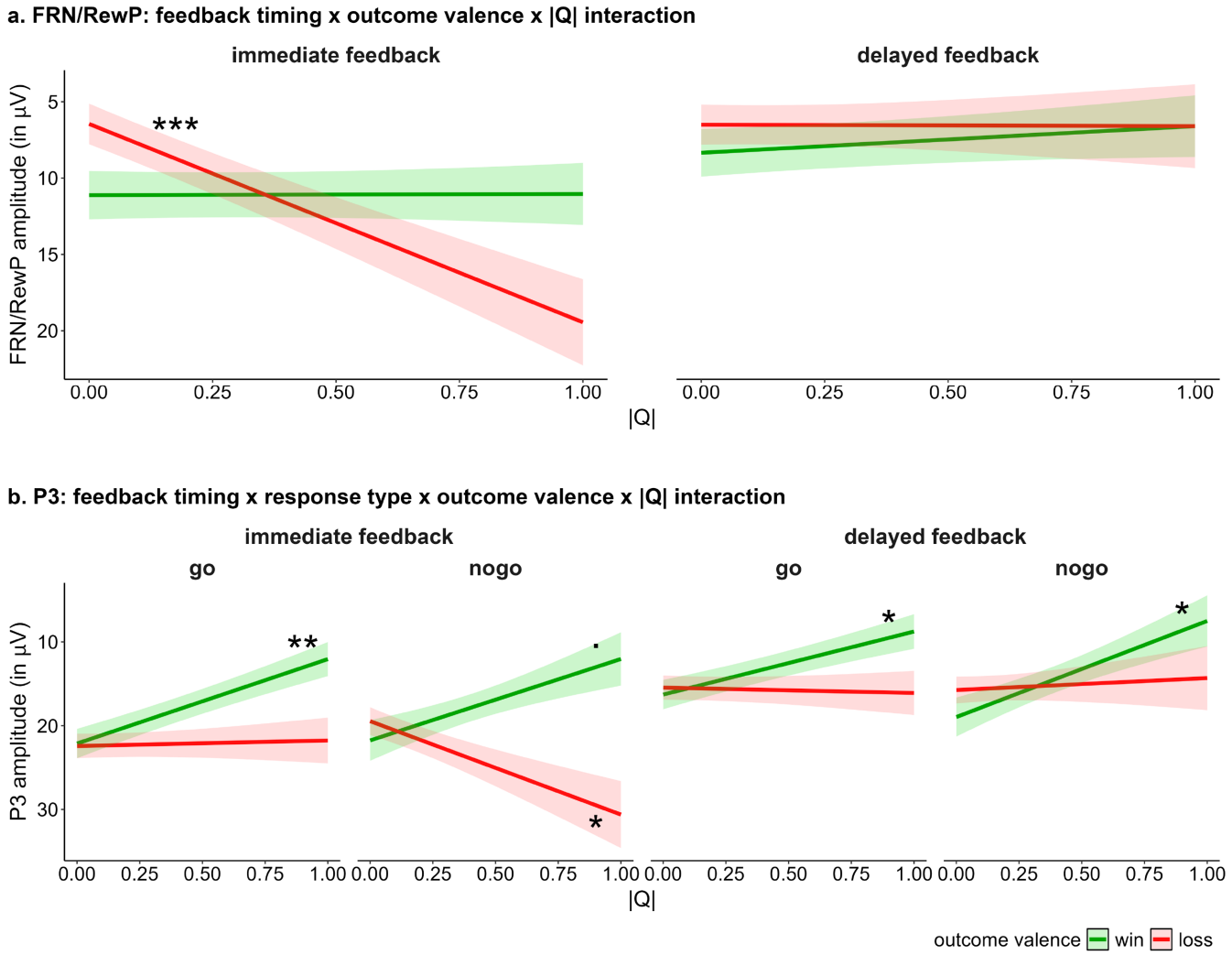


FIGURE 5 | EEG results. (a) Data underlying the significant feedback timing × outcome valence × |*Q*| interaction effect in the FRN/RewP analysis. (b) Descriptive data underlying the significant feedback timing × response type × outcome valence × |*Q*| interaction effect in the P3 analysis. With |*Q*| values close to zero, the presented feedback was unexpected, whereas with |*Q*| values close to one the presented feedback was expected. Data are presented as |*Q*| slopes, as predicted by linear mixed model analyses ± standard error of the mean. Asterisks indicate significant slopes yielded from simple slope analyses. ·< 0.100, *$p < 0.050$, **$p < 0.01$, ***$p < 0.001$.

groups of participants performed a modified orthogonalized go/nogo task, learning from either immediate or delayed feedback. Our results showed that motivational biases governed decision-making when learning from both immediate and delayed feedback. Yet, results from single-trial ERP analyses did not provide evidence for biased feedback processing of action over inaction, as predicted by an instrumental learning bias. Together with complementary evidence from computational modeling, our findings therefore do not support biased instrumental learning as a *substantial* mechanism underlying motivational biases.

4.1 | Motivational Biases in Learning From Immediate and Delayed Feedback

Our results replicate previous findings by showing that participants performed better when learning to execute a response to gain a reward than to avoid punishment, as well as when learning to withhold a response to avoid punishment than to gain a reward (Guitart-Masip et al. 2014; Guitart-Masip, Huys, et al. 2012). These motivational biases emerged across both learning from immediate and delayed feedback and were not found to be attenuated for learning from delayed feedback, thereby aligning with evidence showing the robustness of motivational biases to different learning contexts (Ereira et al. 2021; Peterburs et al. 2021; Vahedi et al. 2024). This finding is remarkable, given that motivational biases are argued to rely substantially on the striatum (e.g., de Boer et al. 2019; Guitart-Masip et al. 2014; Perosa et al. 2020; Richter et al. 2014), which appears to be less strongly involved in learning from delayed feedback (Foerde and Shohamy 2011; Hinneberg and Hegele 2022; Lighthall et al. 2018). Accordingly, motivational biases may be deeply ingrained, not *necessarily* depending on the striatum alone but on a broader network of brain regions. Specifically, previous studies have linked the prefrontal cortex with mediating motivational biases (Algermissen et al. 2024; Cavanagh et al. 2013; Kim et al. 2023; Ousdal et al. 2018).

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Moreover, the hippocampus, which may be increasingly involved in learning from delayed feedback (Foerde et al. 2013; Foerde and Shohamy 2011), was found to contribute to resolving approach-avoidance conflicts (Bach et al. 2014; Bryant and Barker 2020; Le Duc et al. 2025; for a review, see Ito and Lee 2016).

Importantly, although striatal recruitment may be reduced under learning from delayed feedback, it may still *contribute* to the emergence of motivational biases. This is further supported by evidence suggesting that processing of immediate and delayed feedback involve at least partially similar mechanisms (Weber and Bellebaum 2024; Weismüller et al. 2018; but also see corresponding evidence from this study, which is discussed below). Hence, our results suggest that motivational biases rely on such fundamental mechanisms that drive learning universally and independent of feedback timing. Taken together, our results therefore corroborate previous findings suggesting motivational biases to constitute a robust hallmark of decision-making that is only hardly modifiable (e.g., Ereira et al. 2021; Peterburs et al. 2021).

4.2 | Motivational Biases May Reflect a Pavlovian Response Bias

To gain deeper insight into the computational mechanisms underlying motivational biases, we fitted a series of RL models to the behavioral data (de Boer et al. 2019; Guitart-Masip, Chowdhury, et al. 2012; Raab and Hartley 2020). Previous work has demonstrated that motivational biases can be entirely (de Boer et al. 2019) or at least partly (Swart et al. 2017) explained by an instrumental learning bias, with facilitated learning from rewarded actions and impaired learning from punished inactions. Our results are not in line with these findings, as model comparison overall favored a model including a Pavlovian—but not instrumental—bias parameter (while all RL models were favored compared with simpler reference models suggesting random responding or a simple win-stay/lose-shift policy, see the Supporting Information). This result resonates well with our EEG findings, which did not yield stronger feedback valence coding for action versus inaction, which we had expected may underlie such an instrumental learning bias.

However, it must be acknowledged that most previous studies reporting biased instrumental learning typically employed a designated variant of the orthogonalized go/nogo task, teasing apart more general Pavlovian and action-selective instrumental effects by introducing separate cues for correct left and right go choices (Algermissen et al. 2024; Swart et al. 2018; Swart et al. 2017; but see de Boer et al. 2019 who employed the standard task). Yet, there still is reasonable cause to doubt biased instrumental learning as a *substantial* mechanism supporting motivational biases, as they have also been shown in observational learning (Peterburs et al. 2021). Specifically, for observational learning, biased instrumental learning—with boosted learning from rewarded actions and weakened learning from punished inactions—cannot be plausibly considered an underlying mechanism, as participants themselves do not engage in go/nogo choices during learning.

Still, this does not mean that biased learning does not contribute to motivational biases at all. Notably, there was a certain degree of heterogeneity in individual model fits, with choice behavior of some participants best explained by biased instrumental learning (see Table S1). Moreover, analysis of choice repetition behavior indicated biased adjustments to feedback. However, whereas this analysis confirmed facilitated learning from rewarded actions, results also suggested facilitated (rather than impaired) learning from punished inactions, thus only partially aligning with the predictions of an instrumental learning bias. Importantly though, it must be noted that such model-free analysis of biased learning does not allow to disentangle concurrent behavioral mechanisms. As such, increased overall choice repetition of go versus nogo choices likely reflects a general go bias. Moreover, although posterior predictions of the second-best fitting model, which included an instrumental learning bias, generally captured behavior relatively well (see Supporting Information), it must be emphasized that both average and accumulated model evidence favored a model including a Pavlovian bias and excluding an instrumental learning bias parameter. Taken together, our results therefore suggest that motivational biases were overall *better* explained by a Pavlovian response bias, as proposed in earlier studies (e.g., Guitart-Masip, Huys, et al. 2012).

4.3 | Similarities and Differences in Processing Immediate and Delayed Feedback

The FRN/RewP did not show general sensitivity to outcome valence. Note, however, that general encoding of outcome valence with more negative amplitudes for losses than wins was found in an exploratory model-free analysis, precluding the predictor $|Q|$ (see Supporting Information, also see Figure 4). Instead, amplitudes were more negative for losses versus wins only when feedback was unexpected (see, e.g., Weismüller and Bellebaum 2016), while the opposite pattern, that is, more positive amplitudes for losses versus wins, was found when feedback was expected. Such restricted coding of feedback valence may result from win and loss feedback arising through distinct learning contexts (win vs. avoid-losing), where altered value encoding may particularly affect avoid-losing contexts (e.g., see Glazer and Nusslock 2022; Kujawa et al. 2013; Novak and Foti 2015; Pfabigan et al. 2015).

More importantly, FRN/RewP results indicated that the FRN/RewP signaled a −RPE for immediate but not delayed feedback. While this finding generally aligns with the idea of a gradual shift away from the striatum with feedback delay (Foerde and Shohamy 2011; Hinneberg and Hegele 2022), it diverges from previous evidence by our group showing that the FRN/RewP reflects a +RPE, independently of feedback timing (Berlijn et al. 2025; Weber and Bellebaum 2024; but see Huvermann et al. 2025). Again, this discrepancy may partly reflect differences in task design, as −RPEs were derived from a loss-avoidance context and +RPEs from a reward-seeking context, such that wins and losses never occurred as alternative outcomes for the same cue. Beyond that, we found +RPE encoding across feedback timing conditions for the later P3, consistent with the P3 findings reported in Weber and Bellebaum (2024). Notably, this result pattern—with early sensitivity to −RPEs,

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and more slowly emerging sensitivity to +RPEs—generally aligns with evidence for a valence-dependent dissociation of RPE signals during feedback processing (Bai et al. 2015; Hoy et al. 2021). Given their close temporal proximity, these signals may sometimes overlap (Hoy et al. 2021), possibly accounting for the heterogeneity of findings either in favor of the FRN/RewP reflecting a −RPE (e.g., Bai et al. 2015) or +RPE (e.g., Weber and Bellebaum 2024). Ultimately, combined evidence from the present study and earlier work from our group (e.g., Weber and Bellebaum 2024) suggests that particularly +RPE processing may be universally involved in the processing of immediate and delayed feedback, whereas early (-)RPE processing may be more sensitive to feedback timing and preserved only for processing of immediate feedback. Note, however, that also the P3 encoded a −RPE, that is, selectively for immediate feedback following nogo choices.

4.4 | Feedback Processing Underlying Motivational Biases

Most importantly, and contrary to our hypotheses, feedback valence coding in the FRN/RewP did not depend on the response type nor did we find any other processing differences in the FRN/RewP for action versus inaction. These findings contrast with prior work reporting stronger feedback valence effects for action than for inaction (Bikute et al. 2022; Di Bernardi Luft et al. 2024; Yeung et al. 2005). Note, however, that in these studies, participants were explicitly instructed to act or not to act, effectively rendering their responses forced. Notably, reduced FRN/RewP valence coding has been typically observed under conditions of reduced agency, such as observational learning (Bellebaum and Colosio 2014; Bellebaum et al. 2010), or with reduced personal responsibility (Li et al. 2010). As individuals typically favor action over inaction (e.g., Sunderrajan and Albarracin 2021; also reflected in a general go bias in this study), instructed actions may naturally carry stronger agency than inactions, potentially explaining the larger feedback valence effects reported in prior studies.

Also, P3 results did not provide evidence for action-biased feedback processing as predicted by an instrumental learning bias, therefore contrasting with results by Schevernels et al. (2016) (but note that only positive feedback was analyzed in that study). Instead, stronger RPE effects were found following inaction, reflected in selective −RPE coding following nogo choices for immediate feedback. This pattern may indicate that punishments following inaction are processed as more salient, particularly when unexpected, potentially due to difficulties in attributing punishment to inaction (e.g., Swart et al. 2017). Consistent with the role of the P3 in reflecting motivational significance (e.g., San Martín 2012), such increased salience could hence contribute to the finding of stronger −RPE effects for nogo versus go choices. Note, however, that the LMM yielding this result did not support a maximal random-effects structure (critically lacking the outcome valence × response type × $|Q|$), which may increase the risk of Type I error for this effect and therefore warrants cautious interpretation (see Matuschek et al. 2017). Overall, our results suggest feedback processing to be largely unaffected by the response type, providing no evidence for biased feedback processing for action over inaction.

4.5 | Limitations and Future Directions

A few limitations must be acknowledged. First, a disadvantage of the task used is that it naturally leads to unequal and, in some cases, limited numbers of trials per condition (e.g., particularly for rewarded nogo choices). Although LMMs are generally robust to imbalanced datasets (Volpert-Esmond et al. 2018), and examining RPEs may partly mitigate misinterpretation of, in truth, frequency-induced expectancy effects, future studies should include a larger number of trials for more stable results. Still, it should be noted that unequal trial counts may introduce more general frequency-related effects on feedback processing (e.g., Krigolson 2018) that may not fully be accounted for by modeling RPEs. Moreover, while both the FRN/RewP and P3 have proven to be well-established markers of feedback processing (San Martín 2012) shown to reflect RPE-related activity (Sambrook and Goslin 2015), it may be possible that those measures failed to capture relevant activity underlying biased learning. For instance, biased learning has recently been interpreted in terms of biased credit assignment (Algermissen et al. 2024), which may rely more strongly on brain regions typically not associated with contributing to the FRN/RewP-P3 complex (see, e.g., Koutsoumpari et al. 2026). Accordingly, studying motivational biases using other ERP components may be worthwhile, with the N170, which is associated with representational reactivation, a potential candidate (see Röhlinger, Albrecht, and Bellebaum 2025; Röhlinger, Albrecht, Ghio, and Bellebaum 2025). Interpreting biased learning as biased credit assignment may have broader implications for studying feedback timing effects, as credit assignment becomes increasingly difficult with temporal delays (Stolyarova 2018). In addition to that, more elaborated and spatially refined imaging techniques may be needed to unveil the neural signatures of biased learning. Note, however, that even our behavioral data did not provide convincing evidence for biased instrumental learning as a substantial mechanism behind motivational biases. Future work is thus needed to clarify its role in motivational biases. Finally, while aiming to control for overall task duration, learning in the immediate feedback group involved an unusually long ITI. Although choice accuracies descriptively matched those from our previous study using short ITIs (Vahedi et al. 2024), we cannot completely rule out that this manipulation induced unintended effects on learning.

5 | Conclusion

In conclusion, our results replicate robust motivational biases in feedback-based learning, while showing that the emergence of these biases does not depend on feedback timing. Moreover, results from computational modeling and single-trial ERP analyses provided no evidence for biased instrumental learning or feedback processing as substantial mechanisms shaping motivational biases. Instead, motivational biases were overall better accounted for by a Pavlovian response bias. Future research is needed to validate these findings and further clarify the neurocognitive mechanisms underlying motivational biases.

Author Contributions

Julian Vahedi: project administration, methodology, formal analysis, data curation, software, visualization, writing – original draft, writing – review and editing, conceptualization. **Sandra Schneider:**

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investigation, formal analysis, writing – review and editing. **Livia Swiatek:** investigation, writing – review and editing, formal analysis. **Jutta Peterburs:** project administration, methodology, validation, supervision, writing – review and editing. **Christian Bellebaum:** project administration, conceptualization, methodology, validation, resources, supervision, writing – review and editing.

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Ethics Statement

All procedures performed in this study were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Consent

Informed consent was obtained from all individual participants included in the present study. All individual participants signed informed consent regarding publishing their (anonymized) data.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code to reproduce all analyses in this manuscript can be found on the Open Science Framework (https://osf.io/27gjw/overview?view_only=1556006846ad42f3bdc326c81f5fd53f). The study was not preregistered.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ejn.70717.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Comparison of posterior predictions from the best fitting model M2 and the second-best model M3. **Figure S2:** Descriptive scalp topographies underlying the ERP results. **Table S1:** Participant-wise model fits according to the Bayesian information criterion (BIC) with the best fitting model for each participant marked in bold. **Table S2:** Results from alternative modeling using fixed values of *V*. **Table S3:** Consistency of modeling results across models using different baseline parameters. **Table S4:** Generalized linear mixed-effects model (GLMM) results on choice accuracy. **Table S5:** Generalized linear mixed-effects model (GLMM) results on choice repetition. **Table S6:** Model-based linear mixed-effects model (LMM) results on FRN/RewP data. **Table S7:** Model-based linear mixed-effects model (LMM) results on P3 data. **Table S8:** Model-free linear mixed-effects model (LMM) results on FRN/RewP data. **Table S9:** Model-free linear mixed-effects model (LMM) results on P3 data. **Table S10:** Generalized linear mixed-effects model (GLMM) results on brain–behavior relationships. **Table S11:** Generalized linear mixed-effects model (GLMM) results on brain–behavior relationships.

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Altered Reward Processing in Obsessive–Compulsive Disorder: Insights From Active and Observational Learning

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ABSTRACT

Obsessive–compulsive disorder (OCD) has been associated with altered performance monitoring, reflected in enhanced amplitudes of the error-related negativity in the event-related potential. However, this is not specific to OCD, as overactive error processing is also evident in anxiety. Although similar neural mechanisms have been proposed for error and feedback processing, it remains unclear whether the processing of errors as indexed by external feedback, reflected in the feedback-related negativity (FRN), is altered in OCD. Likewise, it is currently unknown whether performance monitoring in OCD differs between learning from self-performed and observed outcomes. The present study compared OCD patients ($n = 27$) with healthy controls (HCs; $n = 27$) and patients with social anxiety disorder (SAD; $n = 29$) in an active and observational variant of a probabilistic feedback learning task while EEG was recorded. Compared to HCs, OCD patients showed generally impaired task performance across both active and observational learning, as well as more indecisive choice behavior. This was accompanied by generally more positive amplitudes of the FRN, with enhanced valence coding for active compared to observational learning, driven by more positive FRN amplitudes for wins. However, no differences were found for losses. Overall, these results suggest deficient reward—rather than punishment—processing in OCD. Similar performance monitoring alterations in OCD and SAD imply reliance on shared, disorder-general mechanisms. Possible candidates for these mechanisms, such as intolerance of uncertainty, pessimism, and depressiveness are discussed.

Obsessive–compulsive disorder (OCD) is a disabling mental disorder characterized by intrusive thoughts (*obsessions*) and/or repetitive behaviors (*compulsions*; American Psychiatric Association 2013). Neurobiological models suggest that dysregulated cortico-striato-thalamo-cortical (CSTC) circuits play a pivotal role in the pathophysiology of OCD (Aouizerate et al. 2004; Milad and Rauch 2012; Saxena et al. 1998; Saxena and Rauch 2000), while these circuits also underlie performance monitoring and adaptive behavior (Ullsperger, Danielmeier, et al. 2014; Ullsperger and von Cramon 2006). Consistent with this, OCD patients often exhibit deficits in action monitoring and impulse control, with feelings of discomfort and incompleteness persisting until completing a compulsive or mental ritual (Coles et al. 2003, 2005; Wahl et al. 2008). Accordingly, obsessive–compulsive (OC) symptoms have been linked to persistent hyperactive error signals in the brain (Pitman 1987), suggesting impairments in the integration of action-related feedback to flexibly guide behavior (Olley et al. 2007).

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In support of this notion, neuroimaging studies have shown that activity within the posterior medial frontal cortex (pMFC), including the midcingulate cortex (MCC), is abnormally increased in OCD patients when committing an error (e.g., Fitzgerald et al. 2005; Grützmann et al. 2016; for an overview see Norman et al. 2019). An entire line of research has focused on error processing via the error-related negativity (ERN), a component of the event-related potential (ERP), characterized by a negative deflection peaking within 100 ms after error commission at fronto-central electrode sites (Falkenstein et al. 1991; Gehring et al. 1993; for a review see Gehring et al. 2012). A similar, albeit markedly reduced, negative deflection is also seen for correct responses and is referred to as the correct-related negativity (CRN).

Crucially, the MCC has been identified as the primary neural generator of the ERN (Debener et al. 2005; Dehaene et al. 1994; Fu et al. 2022). Not surprisingly, OCD has been associated with ERN enhancement (Endrass et al. 2008; Ruchsow et al. 2005; for a review see Riesel 2019). Although the ERN is not affected by OCD symptom severity (Nawani et al. 2018) or expression (Riesel et al. 2014), ERN hyperactivity in OCD appears context dependent. For instance, Riesel (2019) found ERN enhancement only during action monitoring under response conflict, but not during other tasks, including feedback learning.

While during error monitoring the correctness of specific behavior is known to the agent already during action execution based on *internal* information, feedback learning requires *external* feedback to signal whether current behavior is (un)favorable and should be (dis)continued. Feedback learning has been primarily linked to the mesencephalic dopamine (DA) system (Arias-Carrión et al. 2010) and reward-related frontostriatal circuits (Balleine et al. 2007; Cox and Witten 2019; Samejima et al. 2005). In ERP research, feedback processing has been most extensively studied through the feedback-related negativity (FRN), a fronto-central negative deflection peaking approximately 200–350 ms after feedback presentation that is typically more pronounced for negative compared to positive feedback (Gehring and Willoughby 2002; Miltner et al. 1997; Nieuwenhuis et al. 2004; Yeung and Sanfey 2004; but also see Faßbender et al. 2023). As for the ERN, source localization suggests that the FRN is primarily generated in the MCC (Hauser et al. 2014; Luu et al. 2003; Oerlemans et al. 2024), though the FRN has also been linked to striatal processing (Becker et al. 2014; Carlson et al. 2011; Foti et al. 2011).

An influential framework posits that both ERN and FRN reflect prediction error (PE) signals, mediated by phasic activity of mesencephalic DA neurons: Specifically, negative PE signals—marked by dips in DA firing for events worse than expected—have been assumed to enlarge the ERN/FRN (Holroyd and Coles 2002). The functional difference between the ERN and FRN has thus mainly been explained in terms of the ERN reflecting *predictive* error processing based on internal information, while the FRN may reflect *postdictive* error processing based on external information (Holroyd and Coles 2002; Maurer et al. 2021; Walsh and Anderson 2012). However, a purely dopaminergic mechanism in generating ERN/FRN amplitudes is controversial and has been repeatedly questioned, given the rapid changes in post-synaptic potentials required (e.g., Jocham and Ullsperger 2009; Ullsperger, Fischer, et al. 2014).

No matter the neural mechanism, the FRN has been repeatedly shown to reflect reward expectancy (Bellebaum and Daum 2008; Holroyd et al. 2004; Pfabigan et al. 2011) and PEs (Burnside et al. 2019; Fischer and Ullsperger 2013; Hoy et al. 2021; Sambrook and Goslin 2015). Still, there is an ongoing debate about whether the difference waveform signal in the time window of the FRN—with more negative amplitudes for negative than positive feedback—is in fact evoked by an increased negativity to unfavorable events, thus reflecting external error processing, or rather by a reward-related positivity (RewP) to favorable outcomes, thus reflecting reward processing (Holroyd et al. 2008; Proudfit 2015). Indeed, the FRN is not only modulated by negative (Huvermann et al. 2025; Ichikawa et al. 2010) but also positive PEs, indicating events better than expected (Berlijn et al. 2025; Kirsch et al. 2022; Weber and Bellebaum 2024), suggesting it to be involved more generally in feedback processing by reflecting both punishment and reward processing (but see Hoy et al. 2021). While the terms FRN and RewP are often used interchangeably, we use the term FRN throughout this work, in accordance with Faßbender et al. (2023). Notably, other studies reported that the FRN may not reflect a *signed* but rather an *unsigned* PE, i.e., general unexpectedness or salience (e.g., Hauser et al. 2014; Oliveira et al. 2007; Pfabigan et al. 2015; Sallet et al. 2013; Talmi et al. 2013).

While error monitoring and the ERN have been extensively studied in OCD patients (e.g., see Norman et al. 2019; Riesel 2019), relatively few studies have addressed feedback monitoring and the FRN in OCD. Endrass and Ullsperger (2014) suggested a functional dissociation between error and feedback monitoring in OCD, with hyperactive error processing but hypoactive processing of external feedback. However, previous work is rather inconsistent, with some studies reporting an attenuated FRN in OCD patients (Endrass et al. 2013) and subclinical OCD (Gründler et al. 2009; O'Toole et al. 2012; Simons 2010), while others found increased FRN amplitudes in OCD patients (Luo et al. 2020) and subclinical OCD (Zhu et al. 2014). Yet other studies found no differences in FRN amplitudes between OCD patients and healthy controls (Nieuwenhuis et al. 2005; Schüller et al. 2015). Therefore, whether monitoring of errors as indicated by external (negative) performance feedback, reflected in the FRN, is altered in OCD remains unclear. Moreover, to our best knowledge, no previous study has investigated the relationship between the FRN and coding of PEs in OCD. Previous neuroimaging studies in OCD patients suggested enhanced PE coding in the anterior cingulate cortex (ACC) and putamen (Hauser et al. 2017; Murray et al. 2019), whereas Suzuki et al. (2023) reported attenuated PE coding. Given the shared neural basis for error and feedback processing, as well as the close link between overactive error monitoring and OCD, investigating feedback monitoring in OCD constitutes an important step toward a deeper understanding of OCD psychopathology.

Aside from monitoring one's own behavior and consequences, observing others provides valuable information to

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the performance monitoring system, particularly in social contexts. OCD has been linked to impaired social cognitive functioning, including increased affective responsiveness and empathic distress during social observation (Jansen et al. 2020). Altered social cognition may contribute to how OCD patients perceive and process information related to themselves or others, for example, how they process feedback related to other people's actions. However, to our best knowledge, there are no studies yet that explicitly examine observational performance monitoring in OCD.

Interestingly, observing others' errors or action–outcomes elicits activation of brain areas resembling those involved in the processing of one's own, including the (p)MFC, and extending from the ACC to the MCC (de Bruijn et al. 2009; Hill et al. 2016; Mobbs et al. 2009; Newman-Norlund et al. 2009; Shane et al. 2008; but also see Morelli et al. 2015). Observed outcomes also evoke FRN-like (e.g., Bellebaum et al. 2010; Yu and Zhou 2006) deflections in the ERP with comparable topography and shared neural origin in the MCC (Koban et al. 2012). However, amplitudes of the observer FRN are typically reduced (Koban et al. 2012) and less distinctive for positive versus negative feedback (Bellebaum and Colosio 2014; Bellebaum et al. 2010). Importantly, PE coding in the FRN appears agency-dependent, with Burnside et al. (2019) showing that the FRN reflected PEs only for own but not observed outcomes. These results generally corroborate findings by Kobza et al. (2012) which suggest a less prominent role of the striatum in observational relative to active learning. Although many mental disorders have been linked to altered performance monitoring, no previous clinical studies have investigated feedback processing in an observational learning context. However, results by de la Asuncion et al. (2015) on error observation indicate that performance monitoring systems dissociate depending on agency in schizophrenic patients. It is thus conceivable that similar dissociations may also occur during feedback processing in OCD.

Recent developments in precision medicine and psychiatry have led to a rethinking of rigid categorical symptom-based diagnostic classification, moving toward an integrative, transdiagnostic-dimensional model of psychiatric nosology (Insel et al. 2010; Morris and Cuthbert 2012). The research domain criteria (RDoC) framework therefore aims to identify fundamental neurocognitive features underlying multiple phenotypically heterogeneous disorders (Morris and Cuthbert 2012). In line with that, overactive error monitoring as indexed by enhanced ERN amplitudes is not exclusive to OCD but has also been observed in various anxiety disorders (e.g., Carrasco et al. 2013; Endrass et al. 2014; Riesel et al. 2017; Weinberg et al. 2010). As a consequence, a better understanding of OCD requires identifying both disorder-general, i.e., transdiagnostic, and disorder-specific mechanisms, emphasizing the need for comparing OCD with nosologically distinct disorders, most promisingly within the anxiety spectrum. Here, social anxiety disorder (SAD) seems to be a reasonable candidate. SAD is among the most frequent co-occurring disorders in OCD (Assuncao et al. 2012; Lochner et al. 2014; Ruscio et al. 2010) while sharing several overlapping symptoms, including doubt (Carpita et al. 2020), intolerance of uncertainty (Boelen and Reijntjes 2009), perfectionism, and fear of negative evaluation (Rudy et al. 2014). Both OCD and SAD have been linked to overactive monitoring of self-committed errors (Endrass et al. 2014). However, no previous studies have directly compared OCD and SAD regarding feedback monitoring and the FRN.

The present study thus aimed to examine performance monitoring during active and observational learning in OCD. Following recent calls for transdiagnostic research, we additionally sought to identify disorder-general and/or disorder-specific alterations in OCD in comparison to SAD. To this end, patients with OCD, SAD, and healthy individuals completed an active and an observational variant of a probabilistic learning task. While our primary focus was on feedback processing, reflected in the FRN, we also examined action monitoring in active learning, through the ERN/CRN given their assumed conceptual and mechanistic overlap. This aligns with the broader OCD literature, which has predominantly focused on the ERN/CRN. Beyond that, as alterations in feedback processing in OCD have often been interpreted in terms of altered reward expectations (e.g., O'Toole et al. 2012), we additionally explored PE coding via model-based analyses.

Given the importance of the striatum in outcome processing (e.g., Balleine et al. 2007; Samejima et al. 2005), we expected aberrant striatal functioning in OCD (e.g., Burguiere et al. 2015) to interfere with learning and feedback processing, particularly for active learning, thus possibly leading to a dissociation between performance monitoring in active and observational learning. Specifically, we expected impaired task performance in OCD to manifest in rigid, perseverative decision-making (e.g., Moritz et al. 2009). At the neural level, this may be reflected in aberrant processing of negative feedback; although, due to inconsistent findings in previous FRN studies, the anticipated direction of this effect remained more speculative. If overactive error processing extends to the monitoring of external feedback, this should be expressed in enhanced, i.e., more negative FRN amplitudes to punishment feedback, whereas reduced striatal involvement in observational learning (e.g., Kobza et al. 2012) may lead to preserved, i.e., comparable FRN amplitudes between OCD patients and healthy controls. On the other hand, if the performance monitoring system in OCD is generally disrupted, patients should show similarly altered FRN amplitudes both during active and observational learning. Regarding response evaluation in active learning and consistent with findings by Riesel (2019) showing ERN enhancement only during tasks involving response conflict, we hypothesized that OCD patients would show comparable ERN/CRN amplitudes relative to healthy controls.

Given shared neural mechanisms in OCD and SAD, we hypothesized task performance to be similarly impaired in SAD and OCD patients. Moreover, as both disorders have been linked to overactive error processing (Endrass et al. 2014), we expected comparable amplitudes of the ERN/CRN. Accordingly, non-differences between groups may also be plausible for the FRN. Alternatively, OCD and SAD patients may be differently sensitive to positive and negative feedback. Thus, while SAD patients may be particularly impaired in reward processing, possibly reflected in enhanced FRN amplitudes to positive feedback (e.g., Cao et al. 2015), OCD patients may rather show alterations in punishment processing.

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TABLE 1 | Demographic and clinical characteristics of study participants after exclusions ($N = 83$).

	HC ($n = 27$)	OCD ($n = 27$)	SAD ($n = 29$)
Demographics			
Age (in years)	32.93 (12.40)	32.37 (9.88)	31.55 (11.34)
Sex (*n* female:male)	15:12	16:11	23:6
Handedness (*n* right:left:ambidextrous)	23:3:1	24:2:1	27:1:0[a]
Clinical features			
Verbal IQ[b]	110.52 (14.92)	114.52 (12.04)	113.62 (17.19)
Comorbidities (*n* with:without a history of comorbid disorders)[c]	—	20:7	21:8
Medication status (*n* medicated:unmedicated)[d]	—	18:9	14:15
BDI-II	3.00 (4.54)	17.52 (9.68)	16.52 (10.59)
OCI-R	7.67 (6.58)	28.37 (14.50)	13.24 (9.85)
OBQ-D	2.93 (0.87)	4.38 (1.16)	3.87 (1.10)
Y-BOCS	—	21.15 (7.65)	—
LSAS	—	—	83.66 (21.44)

Note: Data are presented as means with standard deviations (SD) in parentheses (except for sex, handedness, comorbidities and medication status, which are presented as count data). All data were obtained from self-report.
Abbreviations: BDI-II=Beck Depression Inventory-II; HC=healthy controls; LSAS=Liebowitz Social Anxiety Scale; OBQ-D=Obsessive-Beliefs Questionnaire; OCD=obsessive–compulsive disorder; OCI-R=Obsessive–Compulsive Inventory-Revised; SAD=social anxiety disorder; Y-BOCS=Yale-Brown Obsessive–Compulsive Scale.
[a]Missing data on handedness for one patient in the SAD group.
[b]Verbal IQ was estimated using the Mehrfachwahl-Wortschatz-Test B (MWT-B).
[c]Detailed overview about the history of comorbid disorders can be obtained from Table S1 in the Supplement.
[d]Detailed overview about the current use of psychotropic medication can be obtained from Table S2 in the Supplement.

1 | Materials and Methods

1.1 | Participants

The required sample size was estimated based on previous studies that tested a group of OCD patients together with a clinical as well as a healthy control group (e.g., Endrass et al. 2014 with 24 participants per group). Accordingly, we aimed to test a sample of approximately 30 participants per group, which we assumed to have sufficient statistical power even in case of drop-outs or exclusions. In total, we recruited 90 volunteers between 18 and 65 years of age. OCD and SAD patients were recruited from the Psychotherapeutic Institute Outpatient Clinic at the Heinrich Heine University Düsseldorf, Germany, the Outpatient and Day Clinic at the Department of General Psychiatry 2 at the University Hospital Düsseldorf, Germany, and an independent collaborating psychotherapy practice in Krefeld, Germany. Further patients were recruited through regional self-help groups and through disorder-specific online forums and counseling platforms. Data exclusion (for details, see Supplement) left a sample of 83 participants including 27 HCs, 27 OCD patients and 29 SAD patients (see Table 1).

Patients had either a primary diagnosis of OCD or SAD, according to self and clinical judgment, as assessed with the Structured Clinical Interview for DSM-5—Clinician Version SCID-5-CV; First et al. 2016, German Version: (Beesdo-Baum et al. 2019). Accordingly, patients with comorbid OCD and SAD were not included in the present study. Further exclusion criteria for clinical groups were a lifetime history of substance use or bipolar disorder as well as psychotic symptoms. Twenty OCD patients and 21 SAD patients reported a history of at least one comorbid mental disorder. Moreover, 18 OCD and 14 SAD patients were receiving current psychopharmacological treatment. Details on comorbid diagnoses and prescribed (psychotropic) medications are provided in Tables S1 and S2. HCs were only eligible to participate if they were not taking any psychotropic medication and did not report a history of any mental or neurological disorders (including OC or social anxiety symptoms) as assessed by a customized abbreviated version of the SCID-5. Furthermore, as previous studies showed altered performance monitoring in asymptomatic first-degree relatives of OCD patients (e.g., Cavedini et al. 2010; Chamberlain et al. 2007; Riesel et al. 2011), only individuals with no family history of OCD were included in the HC group.

All participants had normal or corrected-to-normal vision and were naïve to the study's intent. The study procedures conformed to the Declaration of Helsinki and received ethical approval by the Ethics Board of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University Düsseldorf, Germany. Written informed consent was obtained from all participants prior to participation. Participants were paid monetary compensation (50€).

1.2 | Self-Report Questionnaires

All participants completed a short multiple-choice German vocabulary test (Mehrfachwahl-Wortschatz-Test B, MWT-B;

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Merz et al. 1975) that allowed estimating (verbal) intelligence (Lehrl et al. 1995). Furthermore, the Beck Depression Inventory II (BDI-II; Beck et al. 1996; German Version: Hautzinger et al. 2006) was administered to assess depressive symptoms. Obsessive–compulsive symptoms and beliefs were assessed in all participants using the Obsessive–Compulsive Inventory Revised (OCI-R; Foa et al. 2002; German Version: Gönner et al. 2008) and the abbreviated German version of the Obsessive-Beliefs Questionnaire (OBQ-D; Ertle et al. 2008; original version: Obsessive Compulsive Cognitions Working Group 2001). Symptom severity in OCD patients was assessed using a self-report version of the Yale-Brown Obsessive Compulsive Scale (Y-BOCS; Goodman et al. 1989; German Version: Hand and Büttner-Westphal 1991). In SAD patients, symptom severity was assessed using the self-report version of the Liebowitz Social Anxiety Scale (LSAS; Liebowitz 1987; German Version: Stangier and Heidenreich 2003).

1.3 | Experimental Task and Procedure

Participants completed two versions of a probabilistic feedback learning task (Frank et al. 2004; see Bellebaum, Rustemeier, et al. 2012 for the extended version used in this study): an active task, where they learned from feedback on their own choices, as well as an observational task, where they learned from vicarious feedback on another participant's choices. Both tasks were as closely matched as possible (see Figure 1) and comprised 400 trials, including four learning blocks of 60 trials, alternating with four test blocks of 30 trials, plus a 40-trial transfer phase. Crucially, the observational task differed from the active task only during learning. Thus, during test blocks and the transfer phase, the active and observational tasks were fully identical. Note that this study primarily focused on performance in learning and test blocks, with details on the transfer phase provided in the Supplement.

In learning blocks, on each trial, participants were presented with one of three stimulus pairs (A/B, C/D, E/F) consisting of modified Japanese characters, shown on the left and right sides of a computer screen. Each stimulus was associated with a unique reward probability, while within stimulus pairs, reward probabilities were kept opposing and reciprocal (i.e., A/B = 80%/20%, C/D = 70%/30%; E/F = 60%/40%). In the active task version, participants had to actively choose one character by pressing the left or right Ctrl key on a standard USB keyboard, whereas in the observational task version, they had to observe choices made by a previous participant. The task was fully computerized so that observers did not observe another participant's task performance in their physical presence. Instead, a previous active learner's choices were presented virtually, indicated by the picture of a hand in a yoked design. Once active or observed learners indicated their decision, the chosen character was shortly highlighted by a surrounding red circle. After a short delay, participants were provided with performance feedback indicating that they had either gained 20 points (*win*) or lost 10 points (*loss*). Test blocks required active responding from both active and observational learners. Trial structure in test blocks closely resembled that of learning blocks, although trials ended after choice selection, without feedback being presented. Still, participants were encouraged to continue choosing the characters they predicted would lead to reward and avoid those they expected would lead to punishment, as their current score would still be updated and revealed at the end of each test block. Finally, in the transfer phase, both active and observational learners had to choose between novel stimulus pairs combining stimulus A and B with all other stimuli they had not previously been paired with (Figure 1d; but see Supplement for details).

Participants were instructed to learn the relationship between stimulus selection and feedback by evaluating feedback related to their own or observed choices. Since in learning trials during observational learning participants did not actively choose stimuli, they were instructed that the observed participant collected points for both themselves and the observing participant, thus in a cooperative manner. Conversely, for the test (and transfer phase) participants collected points only for themselves. To keep participants motivated during learning, they were instructed that they would need to use the knowledge gained during learning to guide decision-making in subsequent test blocks. To specifically ensure attentiveness during observational learning, we implemented catch trials after randomly selected trials, requiring observers to indicate which stimulus the observed participant had chosen or whether they had gained or lost points in the immediately preceding trial.

Task versions were held in separate experimental sessions approximately 1 week apart, and participants were randomly assigned to start as an active or observational learner. To preclude stimulus–outcome associations from the first session to bias task performance in the second session, a different stimulus set was introduced in the second session. Participants were tested in the Department of Biological Psychology at Heinrich Heine University Düsseldorf, Germany. However, note that two OCD patients of the final sample were tested at a collaborating psychotherapeutic practice in Krefeld, Germany. The completion of each task took approximately 30 min, including 10 practice trials at the beginning of each task. Stimulus presentation was controlled using Presentation software (Version 20.1, Neurobehavioral Systems Inc., Albany, CA, USA).

1.4 | EEG Acquisition and Data Processing

1.4.1 | EEG Acquisition

EEG data were acquired from 29 scalp sites, i.e., FCz (used as online reference), F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, PO10, O1, Oz, and O2, via active silver/silver-chloride electrodes that were attached to an elastic textile electrode cap (actiCAP; Brain Products GmbH, Gilching, Germany) according to the extended 10–20 system (Chatrian et al. 1985, 1988). The ground electrode was placed at electrode site AFz, and two additional electrodes were attached, one to each mastoid. Horizontal and vertical electro-oculograms (EOGs) were recorded with one electrode attached lateral to the left outer canthus (hEOG), and one electrode placed above the left eye (vEOG), respectively. Impedances were kept below 20 kΩ. EEG data were amplified using a Brain Amp DC amplifier (Brain Products GmbH, Gilching, Germany) and recorded via BrainVision Recorder software (version 1.20.0506, Brain Products GmbH, Gilching, Germany) with a sampling rate

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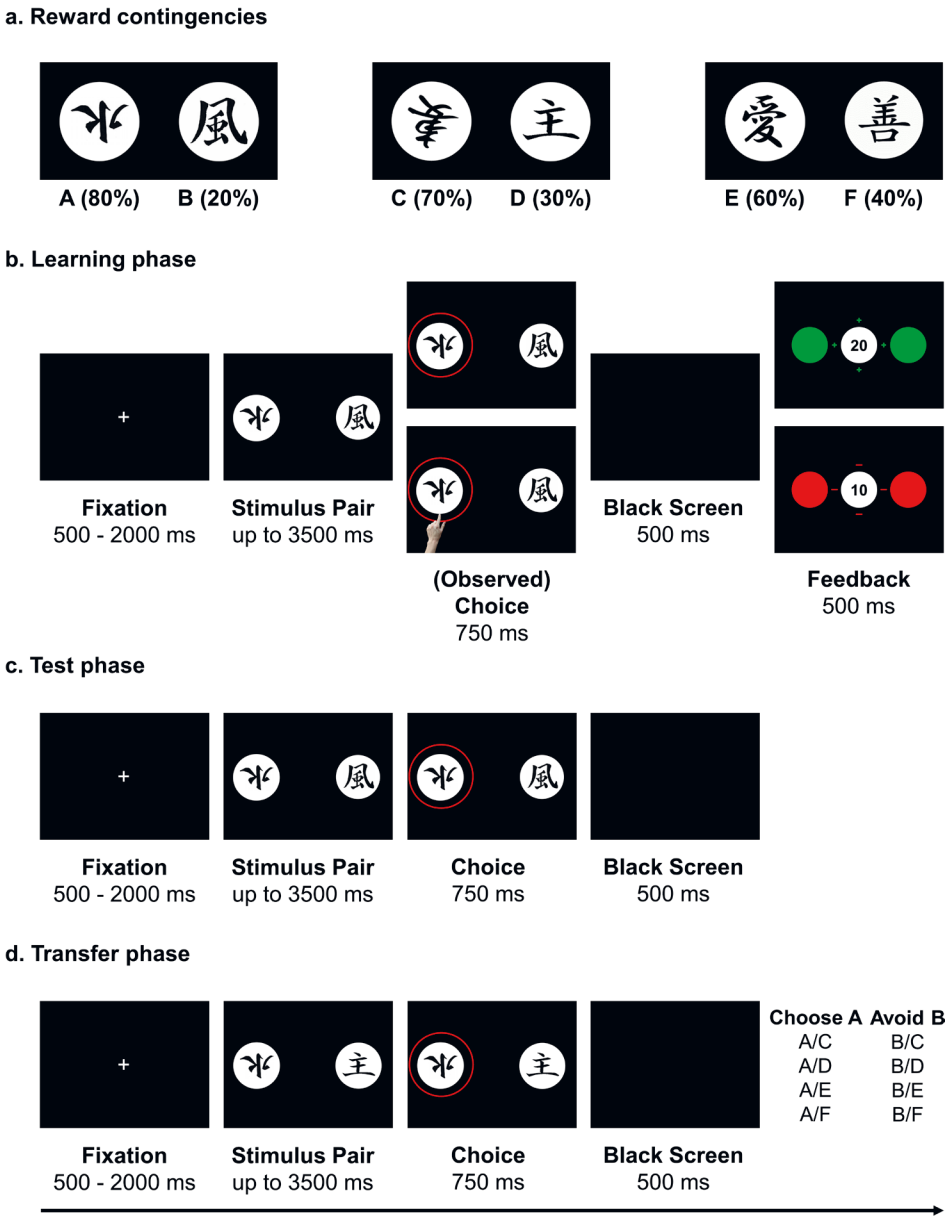


FIGURE 1 | Probabilistic learning task. (a) Reward contingencies for each stimulus in the probabilistic learning task. On each trial, selecting the stimulus with the higher reward contingency, i.e., higher probability to receive positive feedback, was considered the correct response. (b) Trial sequence in the learning phase. In the active learning condition, participants had to choose stimuli and received performance feedback for self-performed choices. In the observational learning condition, participants observed choices made by another participant, as indicated by a hand symbol, and the corresponding feedback for the observed choices. (c) Trial sequence in the test phase. In the test phase both participants in the active and observational learning condition had to actively choose between stimuli, based on the knowledge gained from the preceding learning phase. However, no feedback was shown for the choices made during the test phase. (d) Trial sequence in the transfer phase. The transfer phase was nearly identical to the test phase; however, new stimulus pairs were presented. Specifically, stimulus A (with the highest reward probability) and stimulus B (with the lowest reward probability) were combined with all remaining stimuli to assess the propensity to seek reward (by choosing A) and to avoid punishment (by avoiding B).

of 1000 Hz and an online low-pass filter of 100 Hz on a Windows workstation.

1.4.2 | Preprocessing

EEG data were preprocessed offline using BrainVision Analyzer software (version 2.2.0, Brain Products GmbH, Gilching, Germany). First, for each participant, the raw EEG data were visually inspected to identify electrodes with excessive noise or flat lines. If present, the signal of these channels was interpolated (active task: mean number of channels interpolated = 0.31, SD = 0.68, range = 0–3; observational task: mean number of channels interpolated = 0.30, SD = 0.66, range = 0–3). Next, to restore the signal from electrode FCz, EEG data were re-referenced to the average signal of the mastoid channels. Data were then filtered for frequencies below 0.1 Hz and above 30 Hz. Additionally, we applied a 50 Hz notch filter. Signal portions

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contaminated by ocular artifacts were corrected using an independent component analysis (ICA) based ocular correction approach implemented in the BrainVision Analyzer software (Plank 2013). Subsequently, the continuous EEG data were segmented into epochs spanning the time from 200 ms before to 600 ms after feedback (win or loss) onset. Similarly, we additionally extracted response-locked (correct or incorrect) epochs for active learning data with a duration of 800 ms (including a 200-ms pre-response interval). For both feedback and response-locked epochs, baseline correction was applied based on the pre-stimulus or pre-response period.

Epochs in which sampling points exceeded the minimal or maximal allowed amplitude of ±100 μV or exhibited activity below 0.5 μV (within 100 ms), a voltage difference of 200 μV (within 200 ms), or voltage steps > 50 μV between consecutive sampling points were removed during artifact rejection (for details on mean percentage of removed segments, see Table S3). The remaining, artifact-free segments of electrodes Fz, FCz, FC1, FC2, and Cz were exported for further processing in MATLAB (version R2020a; The MathWorks Inc., Natick, Massachusetts, USA).

1.4.3 | Scoring Procedure

For the ERP analyses, we opted for a trial-level approach (see e.g., Volpert-Esmond et al. 2018). In line with our research question, we therefore focused on the feedback-locked FRN in active and observational learning, whereas the response-locked ERN/CRN was explored in active learning only. Both FRN and ERN/CRN were scored in a predefined fronto-central electrode cluster (Fz, FCz, FC1, FC2, Cz). The scoring procedure was based on a hierarchical data-driven approach (for a similar procedure, see, e.g., Rodrigues et al. 2024). Importantly, visual inspection of the feedback-locked grand average (GA) waveforms indicated that the observer FRN was slightly delayed. Hence, in order to allow for adequate assessment of the FRN, this procedure was applied separately for active and observational learning data.

For both response- and feedback-locked ERPs, we first computed a composite waveform (COMP) by calculating the mean of the condition-wise GAs of the pooled signal from the predefined (fronto-central) electrode cluster, for example:

$$\mathrm{COMP}_{\mathrm{feedback-locked}} = \frac{\text{pooled GA}_{\mathrm{win}} + \text{pooled GA}_{\mathrm{loss}}}{2}$$

Thus, this composite waveform represented the *condition-unweighted average signal*, ensuring that conditions were weighted equally. Next, the composite waveform was used to determine each component's peak latency—i.e., the local minimum (due to the negative polarity of both FRN and ERN/CRN)—within a predefined, literature-backed a priori search window. These windows were 200–350 ms post-feedback for the FRN (Faßbender et al. 2023), and 0–100-ms post-response for the ERN/CRN (Gehring et al. 2018). ERP components were then scored as the mean amplitude in an extraction time window ±30 ms around the identified peak for each electrode within its (fronto-central) cluster in each trial. Accordingly, the FRN was scored as the mean amplitude within 231–291 ms following feedback for active learning, and 241–301 ms for observational learning. The ERN/CRN was scored as the mean amplitude within −11-49 ms relative to response onset.

1.5 | Statistical Analyses

All statistical analyses were performed using R statistical software (version 4.1.0; R Core Team 2021). We opted for a trial-level approach using (generalized) linear mixed-effects models ([G]LMMs). Binary choice behavior was analyzed using GLMMs implemented in the R package *afex* (Singmann et al. 2022). LMMs as implemented in the *lme4* package (Bates et al. 2015) were used for the analysis of single-trial ERP data. Contrast weights for all categorical predictors were deviation coded (e.g., −0.5, 0.5) and all continuous predictors were centered around zero such that the intercept represented the grand mean. Importantly, when using (G)LMMs for categorical factors with more than two levels (e.g., diagnostic group), main and interaction effect terms are calculated as *n-1* comparisons (where *n* is the number of factor levels), dependent on a predefined reference level (Clopper 2013). These planned contrasts are preferable to traditional omnibus tests as they directly incorporate the hypotheses of interest into the statistical model (Hays 1978; Schad et al. 2020). Given our focus on OCD-related alterations in performance monitoring, all group-related main and interaction effects were therefore estimated in reference to OCD (i.e., in comparison to HCs and SAD).

For all models, we attempted to incorporate the maximum possible random-effects structure, including random intercepts and slopes for all within-participant main and interaction effects as well as their correlation (Barr et al. 2013). For EEG analyses, a random intercept by electrode site was also included. In case of non-convergence or singular fit, we used the *buildmer* package (Voeten 2020) to find the maximal model that still converged. The threshold for defining statistically significant results was set to $p < 0.050$. *P*-values for GLMMs were calculated via likelihood ratio tests (LRT) based on type III sums of squares, and for LMMs they were based on Satterthwaite approximated degrees of freedom implemented in the *lmerTest* package (Kuznetsova et al. 2017). Significant interaction effects were resolved using the *emmeans* package (Lenth 2022). Adjusted *p*-values for multiple comparisons were obtained by controlling the false-discovery rate (FDR; Benjamini and Hochberg 1995). Prior to model fitting, we removed invalid trials, including no-response trials as well as trials with rushed responses (< 200 ms) resulting in the exclusion of 1.91% of trials.

1.5.1 | Choice Behavior

1.5.1.1 | Task Performance in Test Trials. To examine learning performance in the experimental task, we conducted GLMM analysis on binary single-trial choice accuracy data (0 = incorrect, 1 = correct). Choice accuracy was defined as selecting the stimulus with the higher reward probability. Given that choices were merely observed but not performed in learning blocks during observational learning, this analysis was restricted to test trials. Categorical fixed-effect predictors included the between-subjects factor group (*OCD [=reference], HC, SAD*) and the within-subjects factor agency (*active [=reference], observational*). Reward contingency for each stimulus pair (A/B: 80%,

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C/D: 70%, E/F: 60%, coded as −1, 0, 1) was implemented as a continuous predictor. Furthermore, to assess learning-related effects of task duration, we included block (1–4) as an additional continuous predictor, centered around 2.5 (corresponding to the midpoint of the total number of test blocks). The GLMM was specified according to the following Wilkinson notation formula:

$$\text{Choice Accuracy} \sim \text{Group} * \text{Agency} * \text{Contingency} * \text{Block} + (1 + \text{Agency} * \text{Contingency} * \text{Block} | \text{Participant})$$

1.5.1.2 | Win-Stay/Lose-Shift Behavior in Learning Trials.

Choice shift (0 = stay, 1 = shift) was set as the dependent variable in the GLMM analysis of win-stay/lose-shift behavior. Since feedback was only presented during learning trials, and active responding was only required in active learning, this analysis was restricted to active learning trials. Here, choice shifting reflected whether participants maintained (*stay*) or switched (*shift*) their choice compared to their previous choice when encountering the same stimulus pair again. To this end, we included the between-subjects factor group (*OCD [=reference], HC, SAD*) and the within-subjects factor previous feedback valence (*win [=reference], loss*) as categorical fixed-effect predictors. Due to the probabilistic nature of the task, changing the response strategy following loss feedback and maintaining the response strategy following win feedback was not always adaptive. Therefore, and motivated by Kirschner et al. (2024), we additionally included the categorical fixed-effect predictor previous feedback authenticity (*authentic [=reference]*, *misleading*), allowing us to distinguish between authentic (i.e., feedback that aligns with the choice accuracy) and misleading feedback (i.e., probabilistic deviations in feedback, thus not in alignment with the choice accuracy), which, depending on feedback valence, required opposite adjustments (i.e., shifting following authentic loss or misleading win feedback as well as staying following authentic win or misleading loss feedback). Again, block (1–4) was included as a continuous predictor, centered around 2.5. The GLMM was specified as the following Wilkinson notation formula:

$$\text{Choice Shift} \sim \text{Group} * \text{Previous Feedback Valence} * \text{Previous Feedback Authenticity} * \text{Block} + (1 + \text{Previous Feedback Valence} * \text{Block} | \text{Participant})$$

1.5.2 | EEG

1.5.2.1 | Feedback-Related Negativity (FRN).

LMM analysis on the feedback-locked FRN component used single-trial FRN amplitudes as the dependent variable. Categorical fixed-effect predictors included the between-subjects factor group (*OCD [=reference], HC, SAD*), and the within-subjects factors agency (*active [=reference], observational*) and feedback valence (*win [=reference], loss*). The model formula in Wilkinson notation was:

$$\text{FRN}_{\text{amp}} \sim \text{Group} * \text{Agency} * \text{Feedback Valence} + (1 + \text{Agency} * \text{Feedback Valence} | \text{Participant}) + (1 | \text{Electrode})$$

1.5.2.2 | Error- and Correct-Related Negativity (ERN/CRN).

LMM analysis for the response-locked ERN/CRN in active learning was conducted with single-trial ERN/CRN amplitudes set as the dependent variable. Categorical fixed-effect predictors included the between-subjects factor group (*OCD [=reference], HC, SAD*) and the within-subjects factor choice accuracy (*correct [=reference], incorrect*). Additionally, on each trial and for each participant and stimulus pattern, we examined the current learning status, i.e., whether the participant had sufficiently learned the reward contingency. To this end, we first determined when participants first exceeded a mean choice accuracy of 90% in the preceding 10 trials for each stimulus pair separately, using a sliding window approach. Once this initial criterion was met, we then ensured that learning was stable by checking whether the mean choice accuracy for the remaining trials remained above 65%. Crucially, we assumed that participants had sufficiently learned the reward contingency for that stimulus pair only if learning was stable for the remainder of the task. If learning was not stable, we searched for the next potential breakpoint. Once a valid breakpoint was identified, trials were divided into a pre- and post-learning phase. Note, however, that by applying these criteria, some participants did not sufficiently learn the contingencies for all stimulus pairs. For these instances, all trials of these specific pairs were assumed to persist in the pre-learning phase. Learning status (*pre-learning [=reference]*, *post-learning*) was finally entered as an additional categorical predictor in the LMM analysis. The LMM was specified according to the following Wilkinson notation formula:

$$\text{ERN/CRN}_{\text{amp}} \sim \text{Group} * \text{Choice Accuracy} * \text{Learning Status} + (1 + \text{Choice Accuracy} * \text{Learning Status} | \text{Participant}) + (1 | \text{Electrode})$$

1.5.3 | Exploratory Analyses

1.5.3.1 | Model-Based ERP Analyses

1.5.3.1.1 | Computational Modeling of Behavioral Data.

To ensure that potential processing differences were not solely driven by differences in learning performance, we aimed to explore the relationship between participants' underlying reward expectations and the FRN and ERN/CRN. To obtain single-trial estimates of participants' reward expectations and PEs, we fitted different reinforcement learning (RL) models to each participant's choice sequence and reinforcement history (Sutton and Barto 2018; Watkins and Dayan 1992). Models were fitted using the *fmincon* function implemented in the Optimization Toolbox in MATLAB (see, e.g., Raab and Hartley 2020) and compared using the Bayesian information criterion (BIC).

For a comparable fitting procedure and assessment of reward expectancy in both active and observational learning, BIC scores were based on the negative loglikelihood (NLL) to identify the model that best predicted actual choice behavior in the test and transfer phases (as motivated by Schultner et al. 2024), from which we eventually extracted latent reward expectancies (*Q*-values) and PE estimates. Models were fitted separately to active and observational learning data, though the winning model for both active and observational learning included separate learning rates for positive (α^+) and negative feedback (α^-) as well as an inverse temperature parameter (β). Additionally, the winning model contained a choice-induced preference change (CIPC)

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parameter (ε) used to update Q-values even in the absence of external feedback in test trials, consistent with recent findings suggesting internal value updating when feedback is not available (e.g., Ptasczynski et al. 2022). Note that this model outperformed models which assumed static or decaying action values in the absence of feedback. For further details including model validation with parameter identifiability and recovery, see the Supplement.

1.5.3.1.2 | Exploratory EEG Analyses. For the model-based FRN analysis, we extended the LMM formula reported for the model-free analysis by including the absolute value of the PE as a continuous within-subjects predictor. This unsigned PE hence indexes the general unexpectedness or surprise of the obtained performance feedback, and has thereby also been referred to as a salience PE (SPE; Heydari and Holroyd 2016; Talmi et al. 2013). Thus, including both the SPE and feedback valence allowed us to disentangle whether the FRN signaled general unexpectedness (in this case to be reflected in a main effect of SPE) or a signed, i.e., positive and/or negative, PE (in this case to be reflected in an SPE × feedback valence interaction effect). SPE values were centered around zero, with negative values indicating expected and positive values indicating unexpected feedback. The LMM was specified using the following Wilkinson notation formula:

$$\mathrm{FRN}_{\mathrm{amp}} \sim \mathrm{Group} * \mathrm{Agency} \times \mathrm{Feedback\ Valence} * \mathrm{SPE} + (1 + \mathrm{Agency} * \mathrm{Feedback\ Valence} * \mathrm{SPE} | \ \mathrm{Participant}) + (1 | \mathrm{Electrode})$$

Model-based ERN/CRN analysis was based on the difference in Q-values for the chosen and unchosen option ($\Delta Q = Q_c - Q_{\bar{c}}$). Accordingly, ΔQ indexes *predictive accuracy* where positive values indicate internally anticipated correct choices (i.e., choosing the option with the higher reward expectation) and negative values indicate internally anticipated incorrect choices (i.e., choosing the option with the lower reward expectation). Thus, continuous ΔQ replaced the categorical predictor *objective* choice accuracy, but should predict ERN/CRN amplitude regardless of the current learning status. As ΔQ was already meaningfully centered around zero (0 = equal reward expectations for both options), we did not need to further transform ΔQ before model fitting. The model formula in Wilkinson notation was:

$$\mathrm{ERN\,/\,CRN}_{\mathrm{amp}} \sim \mathrm{Group} * \Delta Q * \mathrm{Learning\ Status} + (1 + \Delta Q * \mathrm{Learning\ Status} | \ \mathrm{Participant}) + (1 \mid \mathrm{Electrode})$$

1.5.3.2 | Transdiagnostic-Dimensional Analyses. We further explored OCD specificity by conducting transdiagnostic-dimensional (G)LMM analyses based on OCD symptom severity. Specifically, all (G)LMMs that showed significant group effects were re-fitted, replacing the categorical predictor group with the continuous predictor OCI-R. The OCI-R was chosen because it measures OC symptoms relatively independently from symptoms of depression, anxiety, worry, and perfectionism (Gönner et al. 2008). Transformed scores were then centered around the sample mean prior to model fitting. Comparable analyses using the BDI-II as an alternative dimensional predictor are reported in the Supplement.

2 | Results

2.1 | Choice Behavior

Detailed results of all GLMM analyses as well as all parameter estimates and inferential statistics are provided in Tables S4–S6. Exploratory results on transfer phase performance as well as on the modulating role of depressive symptoms on choice behavior can be found in the Supplement.

2.1.1 | Task Performance in Test Trials

Task performance was assessed by analyzing choice accuracy in test trials. Results revealed significant main effects of block, $z = 5.19$, $p < 0.001$, $b = 0.24$ (95% CI = 0.15 to 0.33), and contingency, $z = -7.66$, $p < 0.001$, $b = -0.71$ (95% CI = −0.89 to −0.53), indicating that choice accuracy linearly increased across blocks and across reward contingencies. Planned contrasts suggested task performance was generally impaired in OCD patients relative to HCs, $z = 2.47$, $p = 0.014$, $b = 0.73$ (95% CI = 0.15 to 1.31), whereas no difference was found in learning performance between OCD and SAD patients ($p = 0.734$; see Figure 2a). Moreover, planned contrasts for the group × contingency interaction effect showed a larger contingency effect in HCs compared to OCD, $z = 2.46$, $p = 0.014$, $b = -0.56$ (95% CI = −1.01 to −0.11; see Figure 2b). Specifically, while both OCD patients and HCs performed similarly when reward contingency was low (E/F), $z = 0.60$, $p_{\mathrm{adj}} = 0.549$, $b = 0.17$ (95% CI = −0.39 to 0.73), there were increasing differences for medium (C/D), $z = 2.47$, $p_{\mathrm{adj}} = 0.021$, $b = 0.73$ (95% CI = 0.15 to 1.31), and high (A/B) reward contingency, $z = 2.90$, $p_{\mathrm{adj}} = 0.011$, $b = 1.29$ (95% CI = 0.42 to 2.17). Again, for the comparison of OCD and SAD patients, planned interaction contrasts did not yield significant results ($p = 0.227$).

Transdiagnostic-dimensional GLMM analysis mirrored the results reported above. Interestingly, there was a significant OCI-R × contingency interaction effect, $z = 2.09$, $p = 0.037$, $b = 0.01$ (95% CI = 0.00 to 0.03), suggesting that the higher the reward contingency, the more strongly OCI-R scores affected learning performance by (descriptively) predicting lower choice accuracy.

2.1.2 | Win-Stay/Lose-Shift Behavior in Learning Trials

To test whether impaired task performance was due to maladaptive choice perseveration, we analyzed win-stay/lose-shift behavior in active learning trials. Results yielded significant main effects of block, $z = -3.49$, $p < 0.001$, $b = -0.13$ (95% CI = −0.20 to −0.06) and previous feedback valence, $z = 10.30$,

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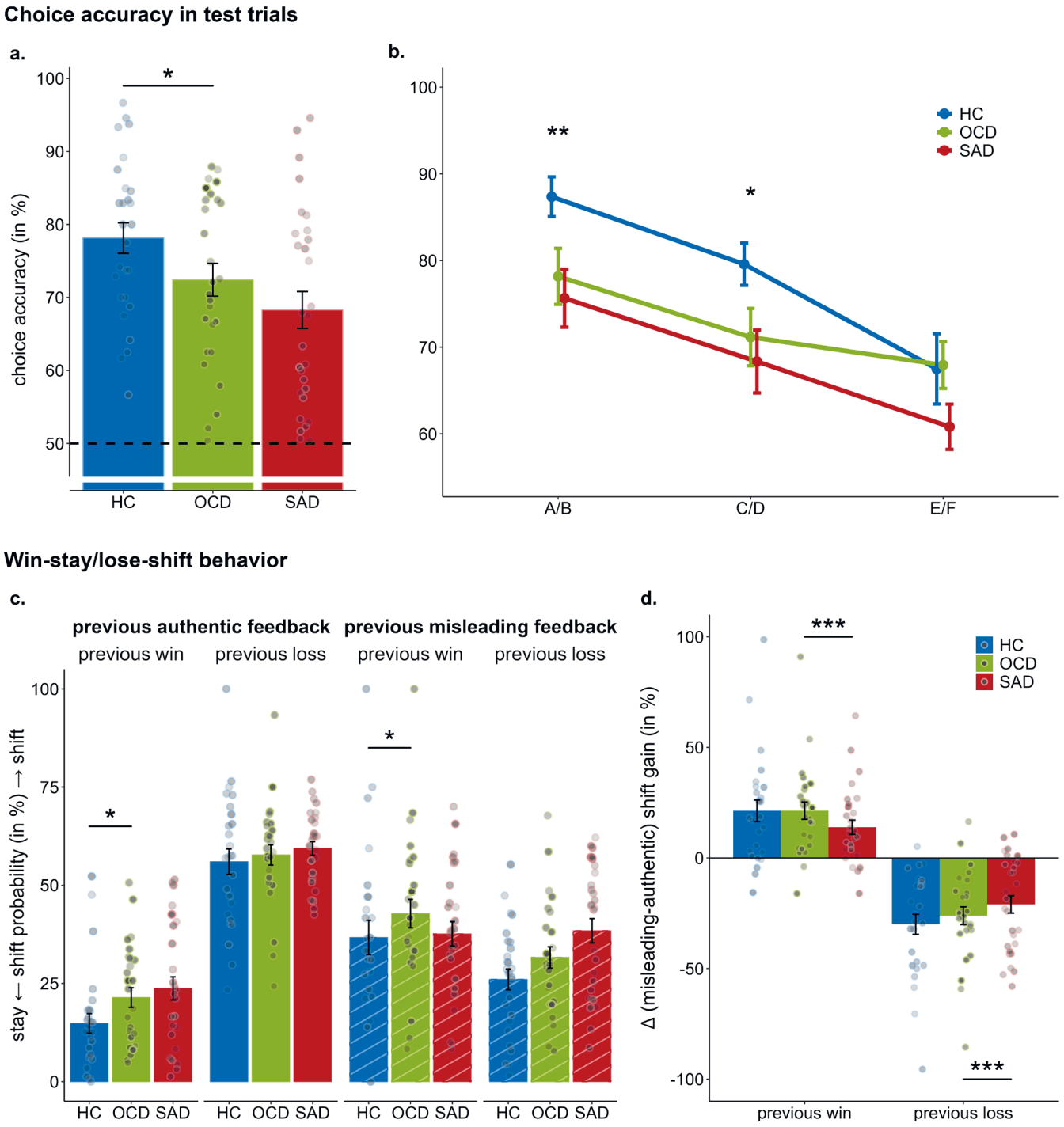


FIGURE 2 | Choice behavior. (a) and (b) Show learning performance in test blocks. Plots (c) and (d) show win-stay/lose-shift behavior in learning blocks. Plots show aggregated empirical means and individual data points, and are therefore presented on the response scale. Darker shaded individual data points indicate higher OCD symptom severity, that is, higher OCI-R scores. Asterisks indicate significant group differences as revealed by planned group contrasts (OCD vs. HC; OCD vs. SAD) in generalized linear mixed-effects model analyses. Error bars represent the standard error of the mean. Abbreviations: HC=healthy controls; OCD=obsessive–compulsive disorder; SAD=social anxiety disorder. *$p<0.050$, **$p<0.010$, ***$p<0.001$.

$p<0.001$, $b=0.86$ (95% CI = 0.70 to 1.02), suggesting generally decreased shifting with task progression and overall increased shifting behavior following losses compared to wins, thus confirming win-stay/lose-shift behavior. Furthermore, results revealed a previous feedback valence × previous feedback authenticity interaction effect, $z=21.57$, $p<0.001$, $b=-1.75$ (95% CI = −1.91 to −1.59). Shifting was increased following authentic compared to misleading losses, $z=-18.10$, $p_{adj}<0.001$, $b=-0.93$ (95% CI = −1.03 to −0.83), but decreased following authentic compared to misleading wins, $z=13.08$, $p_{adj}<0.001$, $b=0.82$ (95% CI = 0.70 to 0.94). Further comparisons showed no differences in choice shifting when feedback was misleading

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($p_{adj} = 0.865$). However, increased shifting was observed for losses versus wins when feedback was authentic, $z = 20.19$, $p_{adj} < 0.001$, $b = 1.74$ (95% CI = 1.57 to 1.90). Furthermore, there was a significant previous feedback valence × previous feedback authenticity × block interaction effect, $z = -3.11$, $p = 0.002$, $b = -0.22$ (95% CI = −0.37 to −0.08). Shifting behavior progressively decreased for authentic, $z = -4.08$, $p_{adj} < 0.001$, $b = -0.19$ (95% CI = −0.28 to −0.10), but not misleading wins ($p_{adj} = 0.651$), suggesting overall successful learning to adapt to positive feedback. Decreased learning-related shifting was also found for misleading losses, $z = -4.03$, $p_{adj} < 0.001$, $b = -0.18$ (95% CI = −0.27 to −0.09), as well as decreased maladaptive shifting for authentic losses, $z = -2.72$, $p_{adj} = 0.009$, $b = -0.12$ (95% CI = −0.20 to −0.03).

Most importantly, choice shifting differed between groups, with planned contrasts showing generally increased shifting—not perseveration—in OCD compared to HCs, $z = -2.48$, $p = 0.013$, $b = -0.47$ (95% CI = −0.85 to −0.10), but not SAD ($p = 0.813$). Furthermore, while planned contrasts for the group × previous feedback valence × previous feedback authenticity interaction did not reveal significant differences between OCD and HCs ($p = 0.500$), the interaction coefficient for the feedback valence × previous feedback authenticity effect was increased for OCD compared to SAD, $z = 3.07$, $p = 0.002$, $b = 0.58$ (95% CI = 0.21 to 0.94). To unravel the underlying result pattern, we examined the patients' sensitivity to misleading feedback, calculated as Δ (misleading-authentic), reflecting how effectively patients adapted to feedback by distinguishing between misleading and authentic feedback. If adjusting effectively, Δ-scores should be positive for wins and negative for losses where higher absolute values indicate better differentiation between misleading and authentic feedback. Comparing Δ-scores for wins and losses between patients indicated that SAD patients were more insensitive to misleading feedback. Accordingly, the (absolute) Δ value was decreased in SAD compared to OCD for both previous wins, $z = -2.21$, $p_{adj} = 0.031$, $b = -0.32$ (95% CI = −0.60 to −0.04), and losses, $z = 2.16$, $p_{adj} = 0.031$, $b = 0.26$ (95% CI = 0.23 to 0.49; see Figure 2c,d).

Transdiagnostic-dimensional GLMM analysis suggested that OCD symptom severity predicted the overall tendency to shift, $z = 2.14$, $p = 0.032$, $b = 0.01$ (95% CI = 0.00 to 0.02). A significant OCI-R × previous feedback valence interaction effect, $z = -2.07$, $p = 0.038$, $b = -0.01$ (95% CI = −0.02 to −0.00), further revealed that higher OCI-R scores predicted increased choice shifting only following wins, $z = 2.34$, $p_{adj} = 0.039$, $b = 0.02$ (95% CI = 0.00 to 0.03), but not losses ($p_{adj} = 0.171$).

2.2 | EEG

Feedback- and response-locked GA ERPs are provided in Figure 3. Detailed LMM results, including all parameter estimates and inferential statistics, are provided in the supplementary Tables S7–S10. Exploratory results on the modulating role of depressive symptoms on feedback processing are provided in the Supplement.

2.3 | Model-Free ERP Analyses

2.3.1 | Feedback-Related Negativity (FRN)

Results yielded significant main effects of feedback valence, $t(77.78) = -6.95$, $p < 0.001$, $b = -1.62$ (95% CI = −2.09 to −1.16), and agency, $t(75.21) = -9.05$, $p < 0.001$, $b = -3.81$ (95% CI = −4.64 to −2.97), indicating more negative FRN amplitudes for losses than wins and in observational compared to active learning. Importantly, the significant agency × feedback valence interaction indicated enhanced valence coding (loss-win) for active compared to observational learning, $t(77.43) = 5.70$, $p < 0.001$, $b = 1.86$ (95% CI = 1.21 to 2.51).

Planned contrasts showed that FRN amplitudes were generally attenuated in OCD patients relative to HCs, $t(51.48) = -4.60$, $p = 0.012$, $b = -2.87$ (95% CI = −5.11 to −0.64), but not relative to SAD patients ($p = 0.109$). Moreover, planned interaction contrasts suggested that the agency × feedback valence interaction (i.e., larger loss–win difference for active vs. observational learning) was stronger in OCD patients relative to HCs, $t(78.10) = 2.61$, $p = 0.011$, $b = 2.10$ (95% CI = 0.50 to 3.70), whereas, although descriptively enhanced in OCD compared to SAD, this difference did not reach statistical significance ($p = 0.059$). To further elucidate the effect for the OCD versus HC subsample, we examined simple effects of feedback valence, separately by agency. For active learning, we found larger FRN amplitudes for losses compared to wins in both OCD patients, $t(78.00) = -6.32$, $p_{adj} < 0.001$, $b = -3.83$ (95% CI = −5.04 to −2.63), and HCs, $t(78.04) = -2.61$, $p_{adj} = 0.011$, $b = -1.59$ (95% CI = −2.79 to −0.38), but with enhanced valence coding in OCD patients, $t(78.02) = 2.62$, $p = 0.011$, $b = 2.25$ (95% CI = 0.54 to 3.96; see Figure 4a). Crucially, this was driven by more positive FRN amplitudes in OCD patients relative to HCs for wins, $t(78.03) = -3.23$, $p_{adj} = 0.004$, $b = -4.55$ (95% CI = −7.36 to −1.74; see Figure 4b), while no group differences emerged for losses ($p_{adj} = 0.107$). Conversely, for observational learning, the FRN did not differentiate between wins and losses in either OCD patients or HCs (both $p_{adj} \geq 0.061$), and valence coding did not significantly differ between groups ($p = 0.762$). Transdiagnostic-dimensional analysis showed that these FRN modulations were not predicted by OCI-R scores ($ps \geq 0.085$).

2.3.2 | Error- and Correct-Related Negativity (ERN/CRN)

To investigate response evaluation in active learning, analysis of trial-level ERN/CRN amplitudes yielded a significant main effect of learning status, $t(60.34) = -2.03$, $p = 0.047$, $b = -0.27$ (95% CI = −0.53 to −0.00), indicating generally more negative ERN/CRN amplitudes post- compared to pre-learning. More interestingly, there was a significant accuracy × learning status interaction effect, suggesting increased differentiation between incorrect and correct choices post- versus pre-learning, $t(64.13) = -2.01$, $p = 0.049$, $b = -0.59$ (95% CI = −1.17 to −0.00). Post-hoc comparisons with FDR-correction, conducted separately for pre- and post-learning trials, indicated comparable ERN/CRN amplitudes for incorrect and correct choices pre-learning ($p_{adj} = 0.834$).

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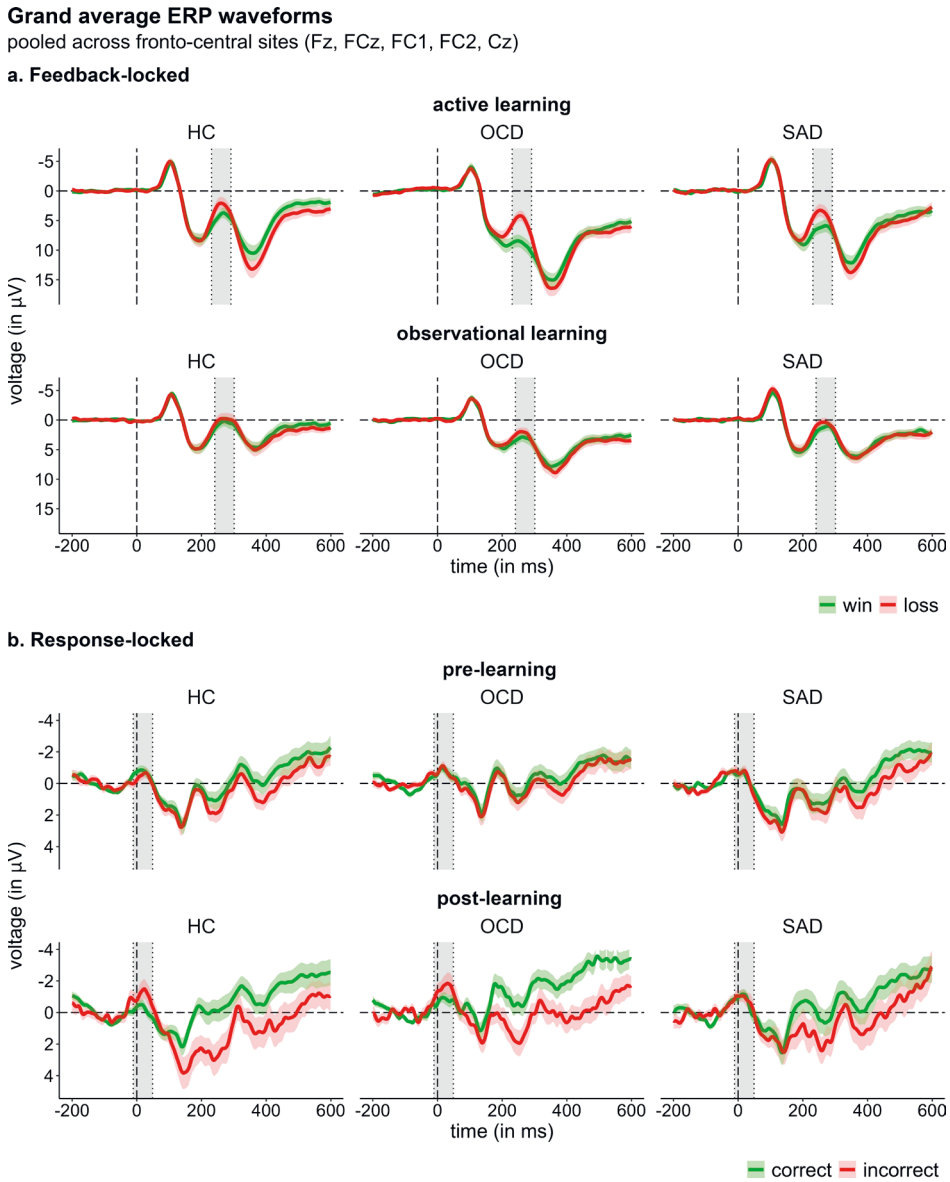


FIGURE 3 | Grand average ERP waveforms pooled across fronto-central sites. (a) Shows feedback-locked ERP waveforms separately for active and observational learning. (b) Shows response-locked ERP waveforms in the pre- and post-learning stage for active learning data. Data represent the mean ± standard error. Zero points on the *x*-axis refer to feedback or response onset, respectively. Gray-shaded areas indicate the measurement windows used for scoring the feedback-related negativity (FRN) as well as the error- and correct-related negativity (ERN/CRN). Abbreviations: ERP=event-related potential; HC=healthy controls; OCD=obsessive–compulsive disorder; SAD=social anxiety disorder.

However, also post-learning incorrect choices elicited only marginally larger—though non-significant—ERN amplitudes compared to correct choices ($p_{adj} = 0.098$). There were no significant group effects ($ps \geq 0.211$).

2.4 | Model-Based ERP Analyses

2.4.1 | Feedback-Related Negativity (FRN)

To examine whether abnormally positive FRN amplitudes for win feedback were driven by impaired learning and correspondingly reduced reward expectations, model-based FRN analysis was conducted. Adding the SPE as an additional predictor led to an increase in the proportion of variance explained, as indicated by the conditional R^2 statistic (from 0.225 to 0.280, $\Delta BIC = 1520$). Results showed a significant feedback valence × SPE interaction effect, $t(67.29) = -2.91$, $p = 0.005$, $b = -3.73$ (95% CI = −6.29 to −1.17). Resolving this effect revealed that the FRN signaled a positive, $t(66.53) = 2.74$, $p_{adj} = 0.011$, $b = 2.24$ (95% CI = 0.36 to 4.12) and negative PE, $t(62.29) = -2.63$, $p_{adj} = 0.011$, $b = -1.49$ (95% CI = −2.79 to −0.19) with more positive FRN amplitudes for feedback better than expected and more negative FRN amplitudes for feedback worse than expected. PE coding was modulated by agency, reflected in an agency × feedback valence × SPE interaction effect, $t(67.22) = 3.13$, $p = 0.003$, $b = 7.52$ (95% CI = 2.73 to 12.31). Resolving this effect showed that while for active learning, the FRN coded both a positive, $t(61.43) = 3.14$, $p_{adj} = 0.003$,

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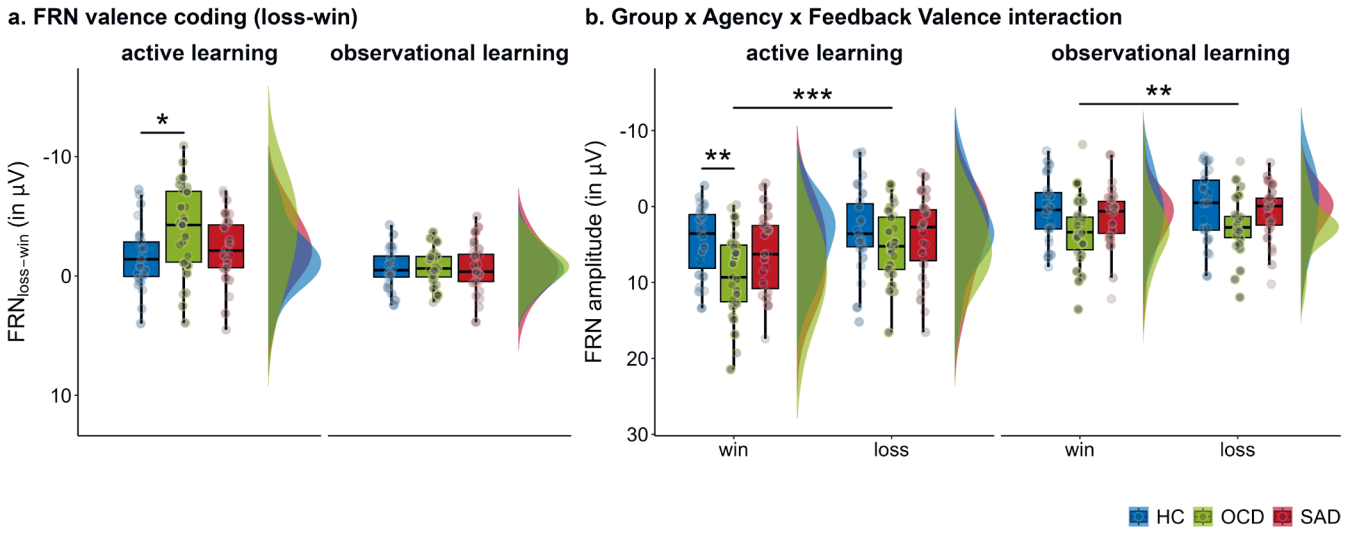


FIGURE 4 | FRN amplitudes. (a) Depicts FRN valence coding. (b) Shows FRN amplitudes separately for win and loss feedback. Plots show aggregated empirical means and individual data points, and are therefore presented on the response scale. Darker shaded individual data points indicate higher OCD symptom severity, i.e., higher OCI-R scores. Asterisks indicate significant (group) differences as revealed by planned (group) contrasts (i.e., OCD vs. HC; OCD vs. SAD) in model-free linear mixed-effects model analysis. Abbreviations: HC=healthy controls; OCD=obsessive–compulsive disorder; SAD=social anxiety disorder. *$p<0.050$, **$p<0.010$, ***$p<0.001$.

$b=4.33$ (95% CI = 1.17 to 7.50), and negative PE, $t(58.33)=-3.43$, $p_{adj}=0.002$, $b=-3.16$ (95% CI = −5.27 to −1.04), no PE coding was found for observational learning ($ps_{adj}\geq 0.847$).

As for the model-free analysis, planned a priori contrasts revealed generally more positive FRN amplitudes in OCD patients compared to HCs, $t(77.69)=-2.27$, $p=0.026$, $b=-2.74$ (95% CI = −5.14 to −0.34), whereas no differences emerged between OCD and SAD patients ($p=0.117$). In addition, planned interaction contrasts showed enhanced valence coding in OCD compared with HCs, $t(69.64)=2.13$, $p=0.037$, $b=1.28$ (95% CI = 0.08–2.48), with abnormally positive FRN amplitudes for win, $t(78.64)=-2.70$, $p_{adj}=0.017$, $b=-3.38$ (95% CI = −5.87 to −0.88), but no difference for loss feedback ($p_{adj}=0.093$). Interestingly, when controlling for the SPE, planned interaction contrasts additionally indicated enhanced valence coding in OCD relative to SAD, $t(69.05)=2.23$, $p=0.029$, $b=1.34$ (95% CI = 0.14 to 2.53), again driven by more positive FRN amplitudes for win, $t(77.85)=-2.06$, $p_{adj}=0.085$, $b=-2.58$ (95% CI = −5.07 to −0.09), though FDR-correction prevented this effect from reaching statistical significance.

When substituting the categorical predictor group by the continuous predictor OCI-R, results revealed a significant OCI-R × feedback valence interaction effect, $t(71.20)=-2.03$, $p=0.046$, $b=-0.04$ (95% CI = −0.07 to −0.00). This interaction suggested that the positive relationship between OCI-R and FRN amplitude was stronger for wins compared to losses; however, note that individual tests for each outcome type did not show a significant relationship between OCI-R for neither wins nor losses ($p_{adj}\geq 0.198$).

2.4.2 | Error- and Correct-Related Negativity (ERN/CRN)

To better account for *internal* response valuation, model-based ERN/CRN analysis was conducted. Model-based ERN/CRN analysis showed an increased proportion of variance explained compared to the model-free LMM, as indicated by the conditional R^2 statistic (from 0.043 to 0.068, ΔBIC = 178). Results revealed a significant main effect of ΔQ, $t(29.13)=2.22$, $p=0.034$, $b=0.63$ (95% CI = 0.05 to 1.22), suggesting that ERN amplitudes increased with lower predictive accuracy (ΔQ). Thus, choosing a stimulus with lower subjective reward expectancy compared to the alternative stimulus predicted more pronounced ERN amplitudes, whereas choosing a stimulus with a larger subjective reward expectancy compared to the alternative stimulus predicted less pronounced ERN amplitudes. Importantly, there were no effects of learning status or group ($ps\geq 0.171$).

3 | Discussion

In the present study, we investigated performance monitoring in active and observational learning in OCD. Results showed widespread alterations in feedback learning and outcome processing in OCD patients compared to HCs, but only minor differences compared to SAD patients. Overall, we found that OCD patients showed equally impaired task performance when learning from their own versus observed actions and their outcomes. Notably, this was accompanied by abnormally positive FRN amplitudes following wins, especially during active learning.

3.1 | Impaired Feedback Learning in OCD

Results on choice behavior were only partially in line with our hypotheses. As expected, task performance was impaired in OCD patients relative to HCs, reflected in reduced learning and lower overall choice accuracy. However, while learning impairments in OCD were observed in various experimental paradigms (e.g., Endrass et al. 2013; Luo et al. 2020; Nielen et al. 2009),

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these deficits were often rather nuanced. For instance, Endrass et al. (2013) found that OCD patients performing in a reversal learning task were impaired only after reversals. Moreover, learning in OCD was particularly impaired for negative feedback compared to positive feedback (Endrass et al. 2013; Nielen et al. 2009). However, in studies using probabilistic selection tasks similar to the one used in this study, previous studies did not indicate any impairments (Endrass et al. 2011; Nieuwenhuis et al. 2005). Notably, in the study by Endrass et al. (2011), participants did not collect points (or money); thus, increased motivational significance of feedback in our study may partly explain the diverging results.

Another key distinction is that the present study assessed both active and observational learning; therefore, it included test blocks with no external feedback. This required additional flexibility in recalling and maintaining knowledge about action–outcome associations gained during earlier learning blocks and may have added an additional layer of complexity and uncertainty. However, exploratory analysis of learning trial data similarly indicated impaired learning in OCD (for details see Supporting Information S1). Moreover, task performance in OCD patients was especially impaired when the reward contingency was high, as evidenced by the significant group-by-contingency interaction contrast. This may be explained by patients' unrealistic pessimism about obtaining rewards (Niemeyer et al. 2013; Zetsche et al. 2015), which may reduce the motivational impact of positive feedback, thereby particularly interfering with learning high-contingency pairs.

Crucially, given the null effect of agency, our results expand previous findings by showing that OCD-related deficits in feedback learning are evident across both active and observational learning contexts. This suggests that performance monitoring in OCD may not dissociate between active and observational learning. Although at least partially distinct neural systems have been discussed to underlie active and observational learning (Morelli et al. 2015), previous research has shown that overall learning performance is typically unaffected by agency in healthy individuals (Bellebaum and Colosio 2014; Bellebaum, Jokisch, et al. 2012; Peterburs et al. 2021; Rak et al. 2013). Comparable performance for active and observational learning in OCD therefore suggests neural systems supporting both forms of learning to be equally disrupted in OCD.

Impaired learning performance reflects only the surface level of aberrant choice behavior, and hence may be driven by distinct and potentially opposing maladaptive mechanisms. We hypothesized that deteriorated learning performance in OCD may arise from an increased tendency toward choice perseveration (Moritz et al. 2009). However, results on win-stay/lose-shift behavior demonstrated overall choice vacillation with overall *increased* shifting in OCD compared to HCs. What seems counterintuitive at first may relate to heightened intolerance of uncertainty in OCD (Hauser et al. 2017; Stern et al. 2013). Fradkin et al. (2020) recently proposed that both perseverative and shifting behavior can be observed in OCD but that they rely on the degree of perceived certainty in a given situational context. Thus, they predicted choice perseveration in well-established and predictable situations, while under more ambiguous conditions with high uncertainty, OCD patients should rather tend to response shifting. In fact, Apergis-Schoute et al. (2024) recently confirmed these predictions by showing more perseverative behavior in OCD patients than in controls in a deterministic reversal task, i.e., when outcomes were highly predictable. However, when the same patients were engaged in a probabilistic reversal task, thus inducing outcome uncertainty, OCD patients showed more indecisive behavior. This observation is also in line with various other studies reporting generally less perseveration but more choice shifting under uncertainty in OCD (e.g., Hauser et al. 2017; Kanen et al. 2019; Pushkarskaya et al. 2015). The probabilistic design in our study may likewise have induced uncertainty in OCD patients, thus promoting more indecisive, over-exploratory behavior. This behavioral strategy closely resembles random exploration (e.g., Wilson et al. 2014), a low computational decision heuristic which may serve as a compensatory mechanism under uncertainty when inferring action–outcome relationships is hard to achieve. On the other hand, increased shifting may be a form of evidence gathering aimed at reducing uncertainty (Stern et al. 2013).

3.2 | Altered Reward Processing in OCD

FRN amplitudes were generally attenuated in OCD patients relative to HCs, aligning with evidence suggesting a functional dissociation between error and feedback monitoring (see Endrass and Ullsperger 2014). Still, FRN studies in OCD are sparse and reveal rather inconsistent results, which may be at least partly due to differences in how the FRN was quantified. For instance, studies reporting FRN enhancement in OCD often rely on the FRN difference signal (loss-win), therefore isolating valence coding (e.g., Luo et al. 2020; also see Bellato et al. 2021). Importantly, enhanced valence coding can in theory result from an enhanced FRN for negative feedback, a more positive FRN for positive feedback, or both. Therefore, enhanced valence coding and (general) FRN reduction may not necessarily be mutually exclusive. Indeed, our results show that the FRN distinguishes more strongly between loss and win feedback during active (but not observational) learning in OCD patients compared to HCs, as reflected in the significant group-by-agency-by-feedback-valence interaction contrast. To our surprise, this effect was selectively driven by abnormally positive FRN amplitudes for positive feedback, especially for active learning, suggesting that reward—rather than punishment processing—may be disrupted in OCD.

This finding sharply contrasts with the widely held notion of hyperactive error monitoring in OCD (e.g., Pitman 1987). Instead, this result aligns with increasing evidence suggesting aberrant functioning of the reward system in OCD (Alves-Pinto et al. 2019; Ferreira et al. 2017; Figee et al. 2011; Kaufmann et al. 2013; Koch et al. 2018; Marsh et al. 2015). Reward processing has been shown to mainly rely on the striatum (e.g., Balleine et al. 2007; Delgado et al. 2000, 2003; O'Doherty et al. 2004), which is substantially implicated in OCD pathophysiology (Burguiere et al. 2015). For instance, ventral striatal hypoactivation in OCD has been shown during reward anticipation (Figee et al. 2011), whereas other studies reported decreased activation in various brain areas including the striatum also during

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reward receipt (Koch et al. 2018; Remijnse et al. 2006), though the exact role of the reward system in OCD is still being explored (Bragdon et al. 2023).

Reduced FRN amplitudes in OCD have mainly been interpreted in terms of aberrant outcome expectations (e.g., O'Toole et al. 2012). Specifically, the FRN has previously been explained in terms of an over-optimistic bias, i.e., the tendency toward anticipating positive outcomes (Oliveira et al. 2007). This bias is thought to be reduced in OCD, such that patients rather overestimate the occurrence of negative events (Moritz and Pohl 2009; Zetsche et al. 2015), which therefore has been assumed to contribute to the FRN reduction in OCD (O'Toole et al. 2012). Generally reduced FRN amplitudes in OCD may therefore reflect uncertainty and pessimistic reward expectations during learning. Notably, results from exploratory model-based FRN analysis suggest that PE-encoding was unaffected in OCD. This contrasts with previous studies showing enhanced (Hauser et al. 2017; Murray et al. 2019) or attenuated (Suzuki et al. 2023) PE signaling in OCD. However, these studies were based on estimates of the *signed* PE only and hence were unable to fully orthogonalize effects of general expectancy violations (i.e., SPE) from common feedback valence effects. Thus, when disentangling SPE and feedback valence in this study, our results do not support altered sensitivity for unexpected events in OCD per se, but suggest that dysfunctional reward anticipation in OCD may rather reflect impaired learning. Specifically, with successful learning, reward expectations for correct choices increase, while PE signals monotonically decrease. However, when learning is impaired, PE signals do not (or only slowly) decrease. Accordingly, when being rewarded, persistently high positive PE signals may lead to FRN attenuation (see Eppinger et al. 2008). This provides a reasonable explanation for why OCD patients show generally more positive FRN amplitudes, particularly following positive feedback, while FRN amplitudes for negative feedback were less affected. On the other hand, due to impaired learning in OCD, positive outcomes may not only be perceived as more unexpected but were in fact experienced less frequently, possibly further contributing to the observed processing differences.

Importantly, when expectancy violations were held constant in model-based FRN analyses, planned contrasts still showed enhanced valence coding in OCD when compared to HCs, due to more positive FRN amplitudes for positive feedback. However, model-based analysis indicated that this effect was agency-invariant. This suggests that besides altered reward anticipation, aberrant reward evaluation and integration may also contribute to differential sensitivity to positive feedback. Thus, besides hyperactive error monitoring (Pitman 1987), hypoactive reward processing in OCD appears to be a reasonable explanation for the phenotypic expression of the disease. Accordingly, a reward can be understood as an indicator that an action has been successfully completed, thus serving as a stop signal. Notably, OCD patients typically report feelings of incompleteness including not-just-right experiences (Coles et al. 2003, 2005), and difficulties in stopping behaviors (Hinds et al. 2012; Wahl et al. 2008). Szechtman and Woody (2004) suggested that these difficulties may be due to a reduced signal of satiety and goal attainment, such that OCD patients seek continuous reaffirmation (but also see Stern and Taylor 2014). Reduced FRN amplitudes may reflect such attenuated feedback evaluation.

However, it has to be noted that FRN amplitudes to positive feedback have been interpreted differently in the context of depression: Here, enhanced as opposed to reduced FRN amplitudes for positive feedback have been suggested to indicate reward hyposensitivity in depression (e.g., Nelson et al. 2016; Proudfit 2015). Following this interpretation, FRN attenuation for positive feedback would rather indicate reward hypersensitivity, i.e., an enhanced reward signal in OCD. Indeed, it has also been argued that OC symptoms such as repetitive behaviors and mental acts may actually arise from being excessively rewarding (see Bragdon et al. 2023). Still, enhanced reward signals can result in maladaptive behaviors when they cannot be properly translated into adaptive adjustment strategies, perhaps related to cognitive inflexibility. Alternatively, biased attentional processing of threat-related stimuli (Moritz and Pohl 2009) possibly makes rewards more salient. This would also be supported by increased P3 amplitudes for positive feedback in OCD (see the Supplement). Either way, altered reward processing in OCD aligns well with our behavioral results, such as impaired learning when reward contingency is high or maladaptive choice shifting following (authentic) wins, suggesting dysfunctional integration of positive outcomes in OCD.

3.3 | Processing of Vicarious Feedback in OCD

While FRN amplitudes were generally attenuated in OCD patients compared to HCs across both active and observational learning conditions, greater differentiation between positive and negative feedback in the FRN was observed in OCD patients only during active, but not observational learning. This finding aligns with prior evidence of striatal dysfunction in OCD (Burguiere et al. 2015) and the notion that active and observational learning rely on similar yet distinct neural mechanisms, particularly suggesting a minor role of the striatum for processing of vicarious feedback (Kobza and Bellebaum 2015; Kobza et al. 2012). However, note that even though the striatum may be less involved in observational learning, it does not appear to operate according to an all-or-nothing principle, but still contributes to the processing of observed outcomes (e.g., see Bellebaum, Jokisch, et al. 2012; Burke et al. 2010; Cooper et al. 2012).

Importantly, the FRN has been shown to reflect striatal (Becker et al. 2014; Carlson et al. 2011; Foti et al. 2011) and/or midcingulate processing (Hauser et al. 2014; Oerlemans et al. 2024). In line with decreased striatal involvement in observational learning, FRN studies typically report reduced FRN valence coding for observational versus active learning (Bellebaum and Colosio 2014; Bellebaum et al. 2010), which we could replicate in the present study. Moreover, the FRN has recently been shown to reflect a (signed) PE signal only in active but not observational learning (Burnside et al. 2019), consistent with our findings from exploratory model-based FRN analysis.

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Crucially, as OCD patients were similarly impaired in active and observational learning, greater differentiation of the FRN for win and loss feedback in active but not observational learning further suggests differential contributions of the striatum to the learning from self- versus other-related feedback. Hence, the FRN appears to reflect impaired learning, i.e., attenuated choice valuation and thus persistently enhanced (positive) PEs only for active but not (or to a lesser extent) for observational learning. This suggests further reliance on other brain areas *not* captured by the FRN that may contribute to impaired learning also in observational contexts. For instance, activation of the ventromedial prefrontal cortex (vmPFC) has been reported similarly for both processing personal and observed performance feedback (Morelli et al. 2015) and has been linked to the computation of subjective value during feedback-based learning (Bartra et al. 2013; Gläscher et al. 2009). However, unlike the striatum, the vmPFC tracks subjective values agency-invariantly, i.e., similarly for both active and observational learning (Zaki et al. 2014). OCD has additionally been associated with vmPFC hyperactivation (e.g., Apergis-Schoute et al. 2017; Fitzgerald et al. 2005; Stern et al. 2011; also see Robbins et al. 2019). Given its ubiquitous role in the computation of subjective value, alterations in vmPFC functioning in OCD may contribute to deficient action–outcome learning and encoding of expected reward both during active and observational learning. However, this assumption remains highly speculative, as the role of the vmPFC in value encoding and feedback learning could not be tested in this study. However, model-based FRN analysis indicated that altered reward processing in OCD does not depend on agency when controlling for reward expectancy. Therefore, processing differences between active and observational learning in model-free analyses may instead reflect (subtle) differences in learning performance and reward anticipation.

3.4 | Normalized Action Monitoring for Decision-Making Under Uncertainty in OCD

Although we did not find the ERN/CRN to be more negative for incorrect (ERN) compared to correct choices (CRN) post-learning, the significant accuracy-by-learning-stage interaction showed that the ERN/CRN distinction was stronger post-learning, generally in line with our hypothesis. This finding is consistent with prior evidence showing learning-related increases in ERN amplitude (e.g., Bellebaum and Colosio 2014; Gawlowska et al. 2018), thus supporting the notion that the ERN reflects predictive action evaluation (Holroyd and Coles 2002; Maurer et al. 2021; Walsh and Anderson 2012). Results from our model-based ERN/CRN analysis provide further evidence for this idea by showing that lower individual predictive accuracy (ΔQ) successfully predicted higher ERN amplitudes, regardless of the current learning status.

Moreover, ERN amplitudes did not differ between OCD patients and HCs. Although this finding contradicts prior evidence showing overactive error monitoring in OCD, this result aligns with meta-analytical evidence suggesting ERN enhancement in OCD only under conditions involving response conflict (Riesel 2019). Moreover, this suggests distinct underlying mechanisms when monitoring simple motor errors during response conflict and more complex decision-making during feedback-based learning (Gründler et al. 2009). Importantly, it has been suggested that action monitoring demands in OCD may decrease when external feedback is available by reducing anxiety at the time of action execution, as there is no need for internal response evaluation (Nieuwenhuis et al. 2005). Alternatively, the results may again be explained in terms of uncertainty in outcome prediction. Thus, when actions are unmistakably incorrect, such as in simple response time tasks, action monitoring may become hyperactive in OCD. However, when associations between actions and outcomes are more ambiguous, such as in probabilistic learning, increased uncertainty about the response outcome may mask otherwise overactive error monitoring, and hence normalize action monitoring. Thus, deficits in outcome prediction under uncertainty would interfere with the implementation of adaptive, goal-directed behavior, and could therefore explain impaired task performance in OCD. However, note that compared to other tasks showing ERN enhancement in OCD, ERN amplitudes in the present task were generally rather small ($<2\,\mu V$). Accordingly, low amplitudes combined with the relatively high variance in the data may also have contributed to the lack of significant group effects in our data.

3.5 | Role of Transdiagnostic Mechanisms

Comparisons between OCD and SAD patients revealed that performance monitoring alterations were generally similar in both disorders, suggesting shared, disorder-general mechanisms. This is not surprising given the shared pathophysiology including abnormal cingulate (Brennan et al. 2015; Nutt et al. 1998; Phan et al. 2005) and striatal (Burguiere et al. 2015; Manning et al. 2015) functioning as well as the involvement of the dopaminergic and serotonergic neurotransmitter system in both disorders (Denys et al. 2004; Hesse et al. 2005; Stein et al. 2002).

Shared pathophysiology is also reflected at the phenomenological level by numerous overlapping features (Carpita et al. 2020). Our results suggest that deficient value assignment and uncertainty in outcome prediction may constitute potential transdiagnostic mechanisms (e.g., Cavanagh and Shackman 2015; but also see Rosser 2019). Moreover, abnormal predictive processing under uncertainty in clinical anxiety has been implicated in an integrative neurobiological model, relying on the MCC (Grupe and Nitschke 2013). Accordingly, we argue that specifically outcome uncertainty may have hindered learning and may therefore account for similar performance monitoring alterations in OCD and SAD in the present study. In support of this assumption, intolerance of uncertainty has not only been linked to OCD but also to SAD (Boelen and Reijntjes 2009; Carleton et al. 2010). Beyond that, both OCD and SAD patients have been linked to biased attentional processing of threat-related stimuli (Mathews and Mackintosh 1998; Moritz and Pohl 2009). Supplementary analyses examining modulation by depressive symptoms showed that impaired task performance and indecisiveness, as well as altered feedback processing—specifically, disrupted PE coding in the FRN during active learning—were associated with higher BDI-II scores (for details, see Supplement). Note, however, that OCI-R and BDI-II scores were moderately positively correlated, suggesting that the symptom scores used in this study may have been influenced by shared, transdiagnostic

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mechanisms, making it difficult to clearly disentangle OC- and depression-related contributions.

Despite extensive similarities in performance monitoring between OCD and SAD, some minor OCD-specific effects were observed. This particularly concerns choice behavior and adaptations to feedback. However, these effects likely represent rather nuanced expressions of the same transdiagnostic mechanisms. Interestingly, controlling for expectancy in model-based FRN analyses showed valence coding in OCD not only to be enhanced relative to HCs but also to SAD patients, suggesting early processing differences in stimulus valuation. Processing differences between OCD and SAD were also found for supplementary model-free P3 analysis, though group differences were absent in our exploratory model-based P3 analysis, therefore suggesting that this effect was entirely driven by expectancy (see Supplement). Collectively, however, while there may be processing differences between OCD and SAD, these effects appear to be rather subtle and not action-relevant. Still, OC symptoms also modulated performance monitoring, both at the behavioral and neural level. However, there were no clear relationships that could fully account for the OCD group effects reported for the categorical analyses, again highlighting the role of transdiagnostic mechanisms.

3.6 | Strength, Limitations and Future Directions

We observed widespread alterations in feedback monitoring in OCD patients compared to neurotypical controls. This evidence stems from comprehensive data analyses using single-trial (G)LMMs, which have been proposed to be the preferred analysis method compared to traditional averaging approaches (such as ANOVAs; Quené and Van den Bergh 2004; Volpert-Esmond et al. 2018, 2021). A major strength of the present study was the recruitment of a transdiagnostic sample, including OCD and SAD patients, which allowed us to additionally examine disorder-general or -specific mechanisms that may contribute to the psychopathology of OCD.

Nevertheless, several limitations must be acknowledged. First, patients with comorbid disorders were included in this study. While this may not compromise the generalizability and external validity of our results, it introduces the possibility that the observed effects were neither driven solely by OCD nor SAD psychopathology (including shared pathophysiological mechanisms). Due to high rates of comorbidity in both patient groups, we were not able to further explore disorder-unique contributions to feedback monitoring. Anxiety has also been shown to account for variations in (overactive) error processing (Meyer 2016), and may therefore explain alterations in feedback processing. Unfortunately, we did not collect estimates of trait anxiety across the whole sample. Moreover, most patients were on medication at the time of testing. Dopamine and serotonin have been implicated in the etiology of both OCD (Denys et al. 2004; Hesse et al. 2005; Pauls et al. 2014) and SAD (Nutt et al. 1998; Stein et al. 2002), and have been thought to substantially contribute to performance monitoring (Jocham and Ullsperger 2009). Crucially, Murray et al. (2019) showed that increased cingulate PE signaling was reduced under acute dopaminergic drug therapy using both the DA-receptor agonist pramipexole and DA-receptor antagonist amisulpride, while no modulatory effect on choice behavior was observed. On the other hand, the ERN in OCD has been shown to be insensitive to medication (Riesel 2019), suggesting that at least certain neurocognitive markers may be unaffected by medication use. However, potential modulatory effects of psychotropic drug intake can only be ruled out when testing medication-free, ideally drug-naïve patient populations. Again, as most of our patients were receiving medication, we were not able to conduct such subgroup analyses.

Despite these limitations, our results may have important implications. More research is needed on feedback and especially reward processing in OCD. Impaired value computation and reward expectation in OCD, as suggested by our data, need further validation and should be explicitly addressed in future work by using dedicated task designs which allow PE modeling for both active and observational learning. Moreover, our results strongly highlight the importance of extending research on performance monitoring to observational learning, especially in clinical populations (see Musco et al. 2023). Due to widespread impairments in social functioning in many mental disorders, it has been recently proposed to re-conceptualize them as disorders of social interaction (Schilbach 2016; Schilbach et al. 2013). This view allows for a further breakdown of relevant (sub-)processes of social interactions that may be impaired in mental disorders. Along these lines, future research in clinical populations should not be limited to (passive) observation but should be extended to more fine-grained social interactions such as cooperation or competition. Last, our study highlights the importance of transdiagnostic research, encouraging direct comparison of more patient groups and/or dimensional approaches to further unveil disorder-specific or -general mechanisms underlying psychopathology.

4 | Conclusion

The present results suggest deficient feedback learning in OCD in active *and* observational learning, as reflected in overall impaired task performance and indecisive decision-making compared to neurotypical individuals. At the neural level, impaired learning in OCD patients was reflected in abnormally reduced, i.e., more positive FRN amplitudes, most particularly for positive feedback during active learning, with enhanced valence coding for active but not observational learning. Conversely, there were no significant group differences in action monitoring reflected in the ERN/CRN. Similar results for SAD patients portend reliance on transdiagnostic mechanisms. Overall, our results suggest altered reward processing—not punishment processing—in OCD. As this conflicts with the prevailing notion of overactive error monitoring in OCD, future research is needed to clarify the significance of our results.

Author Contributions

Julian Vahedi: investigation, methodology, formal analysis, data curation, visualization, writing – original draft, writing – review and editing. **Armin Bahic:** resources, writing – review and editing. **Irini Chaliani:** resources, writing – review and editing. **Leonhard Schilbach:**

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resources, writing – review and editing. **Burkhard Ciupka-Schön:** resources, writing – review and editing. **Christian Bellebaum:** project administration, conceptualization, methodology, resources, supervision, writing – review and editing. **Reinhard Pietrowsky:** funding acquisition, project administration, conceptualization, methodology, resources, supervision, writing – review and editing. **Jutta Peterburs:** funding acquisition, project administration, conceptualization, methodology, supervision, writing – review and editing.

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Disclosure

AI-assisted writing tools were occasionally used during internal revision of the original draft to proof the document for language errors and improve readability. AI-generated rewording was carefully reviewed and adopted only if it contributed significantly to a better understanding of the content.

Ethics Statement

All procedures performed in this study were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Consent

Informed consent was obtained from all individual participants included in the present study.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code to reproduce all analyses in this manuscript can be found on the Open Science Framework (https://osf.io/a6uzm/?view_only=aeaca475dcfb4465bff8c9f4071dd350).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.**

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Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder

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Abstract

Humans are more likely to perform an action to obtain a reward, and to withhold action to avoid punishment, which is a robust pattern in both active and observational learning. The neurophysiological substrate of such motivational biases may arise from the striatum and be regulated by the frontal cortex, although whether they reflect biased action selection and/or learning and outcome processing remains debated. While altered motivational biases are observed across mental disorders, evidence in obsessive-compulsive disorder (OCD), which has been linked to fronto-striatal dysfunction, is limited. The present study examined whether motivational biases are altered in OCD, and whether such alterations depend on agency, given allegedly reduced striatal involvement in observational learning. We used an active and observational variant of an orthogonalized go/nogo task, comparing OCD patients (n=26) with healthy controls (HCs; n=28) and a clinical control group of patients with social anxiety disorder (SAD; n=27). Outcome processing was assessed via electroencephalography, focusing on the feedback-related negativity/reward positivity (FRN/RewP) and the P3 component. Motivational biases were generally attenuated in observational compared to active learning, but there was no evidence that they were altered in OCD. Still, in OCD patients, FRN/RewP alterations suggested disrupted distinction of self- and other-related outcomes. No group differences were found for the P3. Although motivational biases were unaltered in OCD, our findings suggest aberrant self-other distinction during outcome processing. Comparison with SAD patients indicated that these alterations were particularly characteristic of OCD, highlighting the potential of extending research to observational learning to better understand OCD psychopathology.

Keywords: obsessive-compulsive disorder, social anxiety disorder, reinforcement learning, performance monitoring, agency

Unaltered motivational biases but disrupted self-other monitoring during active and observational learning in obsessive-compulsive disorder

Decision-making is rigidly shaped by *motivational biases*, i.e., we are more likely to act to obtain a reward and to withhold action to avoid punishment (Cavanagh et al., 2013; Guitart-Masip, Duzel, et al., 2014; Guitart-Masip et al., 2012). This phenomenon has been mainly explained as a bias in action selection and referred to as the *Pavlovian bias* (see Guitart-Masip et al., 2012), while recent evidence suggests that it can also arise through *biased instrumental learning*, with facilitated learning from rewarded action and impaired learning from punished inaction (Swart et al., 2017). Both motivated action selection and learning rely on dopaminergic modulation of the striatum (Collins & Frank, 2014; Frank, 2005; Frank et al., 2004). Midbrain dopamine neurons encode reward prediction errors (RPEs; Bayer & Glimcher, 2005; Glimcher, 2011; Schultz et al., 1997), with increased firing to better-than-expected outcomes (+RPEs) invigorating actions via the striatal *direct pathway* and reduced firing to worse-than-expected outcomes (-RPEs) inhibiting actions via the *indirect pathway* (Collins & Frank, 2014). Striatal contribution to motivational biases is well supported (de Boer et al., 2019; Perosa et al., 2020; Richter et al., 2021; Richter et al., 2014), while the prefrontal cortex (PFC) may be involved in top-down regulation of these biases (Cavanagh et al., 2013; Guitart-Masip, Economides, et al., 2014; Kim et al., 2023; Richter et al., 2021; Swart et al., 2018).

Regulating motivational biases is essential as they can be maladaptive when interfering with our goals. Unsurprisingly, altered motivational biases have been observed across various mental disorders including schizophrenia, anxiety, and substance dependence (e.g., Albrecht et al., 2016; Chen et al., 2023; Garbusow et al., 2016; Mkrtchian et al., 2017; Ousdal et al., 2018). Beyond these disorders, obsessive-compulsive disorder (OCD) is characterized by impaired

decision-making (Cavedini et al., 2006; Nistico et al., 2021; Sachdev & Malhi, 2005), alongside deficits in action control (e.g., Bannon et al., 2002; Morein-Zamir et al., 2010; Penadés et al., 2007) and (instrumental) learning (e.g., Palminteri et al., 2012; Remijnse et al., 2006; Vahedi et al., 2025). Altered motivational biases in OCD would be plausible, given that the neural mechanisms underlying motivational biases overlap with those implicated in OCD pathophysiology. Specifically, OCD has been linked to fronto-striatal circuit dysregulation, with altered RPE signaling (Hauser et al., 2017; Murray et al., 2019; Suzuki et al., 2023) and excessive reliance on the direct "go" pathway (Milad & Rauch, 2012; Pauls et al., 2014; Saxena & Rauch, 2000).

Results from Pavlovian-to-instrumental transfer studies have suggested attenuated motivational biases in (sub)clinical OCD (Krypotos & Engelhard, 2020; Peng et al., 2022; but see Marzuki et al., 2024). A major shortcoming of this paradigm is, however, that it examines motivational biases after, but not *during*, learning. Another paradigm to study motivational biases is the *orthogonalized go/nogo task* (Guitart-Masip et al., 2011), which allows incidental Pavlovian and instrumental learning by decoupling action (go vs. nogo) and valence (win vs. loss) within the same task. Although recent evidence using this task indicated that *compulsions and intrusive thoughts* may not predict motivational biases in a non-clinical sample (Scholz et al., 2026), it remains to be clarified whether motivational biases are altered in clinical OCD.

In healthy individuals, motivational biases were generally found to be robust against contextual manipulation (Ereira et al., 2021; Peterburs et al., 2021; Vahedi et al., 2024). For instance, Peterburs et al. (2021) showed that motivational biases emerged not only in active learning but also, to a similar extent, in observational learning. This may not necessarily be the case for OCD as the striatum, which motivational biases seem to rely on (e.g., de Boer et al.,

2019; Perosa et al., 2020), appears less strongly involved in observational compared to active learning (Bellebaum et al., 2016; Kobza & Bellebaum, 2015; Kobza et al., 2012). Striatal circuit dysfunction in OCD (Pauls et al., 2014) could hence differentially impact motivational biases that emerge through active or observational learning. On the other hand, using an instrumental learning task, we recently demonstrated that behavioral performance in OCD was altered across both active and observational learning (Vahedi et al., 2025), thus consistent with findings linking OCD to an altered sense of agency (Borrelli et al., 2024; Gentsch et al., 2012; Grossmann et al., 2025; Szalai, 2019), including inflated responsibility beliefs (Salkovskis et al., 1999) and heightened affective responses to others (Jansen et al., 2020). Determining whether motivational biases are altered in OCD, and differentially modulated by agency, would hence provide important insights into the neurocognitive mechanisms of both OCD and motivational decision-making.

Although rarely studied, current theoretical frameworks of motivational biases (e.g., see Collins & Frank, 2014; Guitart-Masip, Duzel, et al., 2014; Swart et al., 2017) hint at a putative role of outcome processing. Using electroencephalography (EEG), outcome processing is most commonly studied through a fronto-central event-related potential (ERP) component that emerges within 200-350 ms after outcome presentation and is more negative for aversive compared to appetitive outcomes (Faßbender et al., 2023; San Martín, 2012; Walsh & Anderson, 2012). Often labelled the feedback-related negativity (FRN) or reward positivity (RewP), accumulating evidence suggests that the observed signal difference constitutes a compound component, with FRN and RewP reflecting dissociable processes (see Cavanagh & Holroyd, 2026). Specifically, while the FRN was traditionally linked to processing aversive outcomes (Holroyd & Coles, 2002; Miltner et al., 1997), it may largely reflect a baseline N2 that is overlaid

by the RewP, reflecting appetitive outcomes (Holroyd et al., 2008; Krigolson, 2018; Proudfit, 2015). Given their spatiotemporal overlap and unclear mechanistic interpretation, we use the term *FRN/R*ewP in this work. The FRN/RewP originates from the midcingulate cortex (Hauser et al., 2014; Luu et al., 2003; Oerlemans et al., 2025) while also reflecting striatal processing (Becker et al., 2014; Carlson et al., 2011; Foti et al., 2011). Importantly, beyond valence, the FRN/RewP has been shown to reflect +/-RPEs (Fischer & Ullsperger, 2013; Hauser et al., 2014; Sambrook & Goslin, 2015; Vahedi et al., 2025). Furthermore, the FRN/RewP is modulated by agency, typically expressed in attenuated outcome valence (Bellebaum & Colosio, 2014; Bellebaum et al., 2010) and lacking RPE coding for observational learning (Burnside et al., 2019; Vahedi et al., 2025).

The P3 represents another marker of outcome processing, emerging as a (centro-parietal) positive deflection 250-500 ms after outcome presentation and reflecting contextual updating and motivational significance, that scales with outcome magnitude (Polich, 2007; San Martín, 2012; Ullsperger, Danielmeier, et al., 2014; Wu & Zhou, 2009; Yeung & Sanfey, 2004). Unsurprisingly, the P3 is modulated by agency, being generally reduced and less distinctive for outcome valence during observational learning (Bellebaum & Colosio, 2014; Bellebaum et al., 2010). Notably, the neural origin of the P3 remains unclear, but likely involves distributed fronto-parietal sources (Ullsperger, 2024).

Previous studies on outcome processing in OCD, almost exclusively focusing on the FRN/RewP, yielded inconclusive evidence regarding alterations relative to healthy controls (e.g., Endrass et al., 2013; Luo et al., 2020; Nieuwenhuis et al., 2005). Yet, we recently showed enhanced outcome valence coding in the FRN/RewP in OCD patients, selectively for active but not observational learning, using a modified probabilistic selection task (Vahedi et al., 2025).

However, studies directly linking outcome processing to motivational biases are very rare (see Albrecht et al., 2016; Csifcsák & Mittner, 2026 for rare exceptions), and they did not test whether outcome processing differs following action versus inaction, as predicted by biased instrumental learning. Although evidence from other paradigms supports action-biased outcome processing in both the FRN/RewP and P3 (Bikute et al., 2022; Di Bernardi Luft et al., 2024; Schevernels et al., 2016; Yeung et al., 2005), its direct contribution to motivational biases and possible interaction with OCD remains unclear.

In the present study, we aimed to examine whether motivational biases are altered in OCD, and whether they are differently modulated depending on agency. To this end, participants completed a modified orthogonalized go/nogo task in an active and observational task variant (Peterburs et al., 2021) while EEG was recorded. To disentangle disorder-general from OCD-specific effects, OCD patients were compared not only to healthy controls (HCs), but also to a clinical control group of patients with social anxiety disorder (SAD), because SAD shares key clinical features and neural mechanisms with OCD (Carpita et al., 2020; Freitas-Ferrari et al., 2010; Weidt et al., 2016).

While we generally hypothesized motivational biases to be present across active and observational learning (see Peterburs et al., 2021), reduced striatal engagement during observational learning may lead to OCD-related alterations that are more strongly pronounced during active compared to observational learning. Specifically, it would be conceivable that fronto-striatal imbalances, with hyperactivity of the direct “go” pathway (e.g., Pauls et al., 2014), exaggerate motivational biases in OCD. On the other hand, motivational biases in OCD may be attenuated (Peng et al., 2022), or unchanged (Scholz et al., 2026). Finally, depending on whether OCD patients show altered motivational biases, action-biased outcome processing in the

FRN/RewP and/or P3, i.e., enhanced outcome valence coding for action versus inaction, may be correspondingly exaggerated or attenuated compared to HCs, with effects particularly pronounced for active learning (cf. Vahedi et al., 2025). Comparisons between OCD and SAD patients were exploratory.

Materials and methods

Participants

Sample size estimation was based on previous studies examining motivational biases with a clinical focus, which typically tested approximately 30 participants per experimental group (e.g., Montagnese et al., 2020; Ousdal et al., 2018). Comparable group sizes have also been successfully employed to detect group differences in outcome processing (Bellebaum & Colosio, 2014; Weismüller & Bellebaum, 2016). Accordingly, we recruited 90 adult volunteers in three groups (OCD, SAD, and HCs; age range 18-65 years), which we deemed sufficient to ensure adequate statistical power (even after exclusions). The recruited sample was the same as described in Vahedi et al. (2025).

Patients were primarily recruited from collaborating mental health care facilities and local self-help groups and had a primary diagnosis of either OCD or SAD, confirmed using the *Structured Clinical Interview for DSM-5 – Clinician Version* (SCID-5-CV; First et al., 2016, German Version: Beesdo-Baum, Zaudig, & Wittchen, 2019). Note that some patients took (prescribed) psychopharmacological medication or had comorbid disorders other than OCD and SAD, except psychotic symptoms or a lifetime history of substance use or bipolar disorder (for details, see Tables S1 and S2 in the Supplement). HC participants were recruited from the general population via public advertising. HCs did not take any psychotropic medication and did not present with a lifetime diagnosis for any mental or neurological disorder, as assessed via a

customized, abbreviated version of the SCID-5. Importantly, given previous findings of altered performance monitoring in asymptomatic first-degree relatives of OCD patients (e.g., Cavedini et al., 2010; Chamberlain et al., 2007; Riesel et al., 2011), only individuals without a family history of OCD were considered in the HC group. All participants had normal or corrected-to normal vision and were naïve to the study's intent. After data exclusions (see Data quality control), the final sample consisted of 81 participants, including 28 HCs, 26 OCD patients and 27 SAD patients (see Table 1). Participants were relatively young on average (M_{age} = 32.51, *SD* = 11.42), with no significant age differences between groups (p = .820; see Supplement), and were predominantly female and right-handed.

The study procedures conformed with the Declaration of Helsinki and received ethical approval by the Ethics Board of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University Düsseldorf, Germany. All participants gave written informed consent and received a monetary compensation of 50€.

[insert Table 1 here]

Psychometric measurement

Intelligence was estimated in all participants using a multiple-choice German vocabulary test (Mehrfachwahl-Wortschatz-Test B, MWT-B; Lehrl et al., 1995; Merz et al., 1975). Moreover, all participants completed the Beck Depression Inventory II (BDI-II; Beck et al., 1996; German Version: Hautzinger et al., 2006), the Obsessive-Compulsive Inventory Revised (OCI-R; Foa et al., 2002; German Version: Gönner et al., 2008), and the abbreviated German version of the Obsessive Beliefs Questionnaire (OBQ-D; Ertle et al., 2008; original version: Obsessive Compulsive Cognitions Working Group, 2001) to assess depressive and obsessive-compulsive symptoms and beliefs. Within OCD patients, symptom severity was further assessed

using the self-report version of the Yale-Brown Obsessive Compulsive Scale (Y-BOCS; Goodman et al., 1989; German Version: Hand & Büttner-Westphal, 1991). Symptom severity in SAD patients was assessed using a self-report version of the Liebowitz Social Anxiety Scale (LSAS; Liebowitz, 1987; German Version: Stangier & Heidenreich, 2003).

Groups did not differ in (verbal) intelligence ($p = .401$). However, BDI-II scores were higher in both OCD and SAD patients than in HCs (both $p_{adj} < .001$), with no differences between patient groups ($p_{adj} = .989$). OCD patients further scored higher than both HCs and SAD patients (both $p_{adj} < .001$) on the OCI-R, and than HCs ($p_{adj} < .001$) but not SAD patients ($p_{adj} = .235$) on the OBQ-D (also see Supplement). Collectively, these results support SAD as an appropriate clinical control group.

Experimental task and procedure

All participants completed an active and observational variant of the orthogonalized go/nogo task, first described by Guitart-Masip et al. (2011), extended for observational learning as described in Peterburs et al. (2021). In this task, participants are presented with cues and must choose between action (*go*) and inaction (*nogo*) to *win* or *avoid losing* points. By orthogonalizing the required response (*go*, *nogo*) and cue valence (*win*, *avoid-losing*), this task thus yields four cued conditions in a balanced two-by-two design: go to win (GW), go to avoid-losing (GAL), nogo to win (NGW), and nogo to avoid-losing (NGAL). The active and observational task variants were designed to be as similar as possible, each comprising 320 trials, divided into four learning blocks with feedback, alternating with four test blocks without feedback (i.e., 40 trials per block). Stimulus presentation and timing were controlled using Presentation software (version 20.1, Neurobehavioral Systems, Inc., Albany, CA, USA). Task structure and the trial sequence are illustrated in Figure 1.

Each trial began with the presentation of one distinctive, abstract cue (Mathôt et al., 2015; obtained from https://github.com/smathot/materials_for_P0010.5) representing one of the four experimental conditions (GW, GAL, NGW, NGAL). After a fixation cross was displayed, an open white circle appeared on the left or right side of the screen. In learning blocks of the active learning task, participants then had to choose either to press—depending on the location of the target—the left or right Ctrl-key on a standard USB-keyboard (*go*), or to not press any key (*nogo*). Go choices had to be made within 1000 ms as later key presses or pressing the key opposite to the location of the target stimulus were classified as invalid. Participants were explicitly informed when their response was *too slow* or indicated the *wrong side* via visual feedback. Conversely, in learning blocks of the observational learning task, participants did not choose between action and inaction themselves but observed the recorded choices made by a previous participant, i.e., in a yoked design (see Peterburs et al., 2021). For this purpose, observed go choices were indicated by a hand symbol, whereas nogo choices were indicated by non-appearance of the hand symbol.

In learning blocks and when participants made or observed a valid choice, another fixation cross was displayed, followed by symbolic performance feedback. Feedback either indicated that participants had gained 10 points (*win*; green upward-pointing arrow), lost 10 points (*loss*; red downward-pointing arrow), or that the current score remained unchanged (*draw*; yellow horizontal bar). Importantly, for each cue, there was always one favorable and one unfavorable outcome. In GW and NGW, *win* was the favorable and *draw* the unfavorable outcome, whereas in GAL and NGAL *draw* was the favorable and *loss* was the unfavorable outcome. While *win* and *loss* thus unequivocally indicated positive and negative feedback, *draw* feedback could either be favorable (i.e., when avoiding loss of points) *or* unfavorable (i.e., when

not winning points). Stimulus-response-outcome associations were probabilistic, such that correct choices were rewarded with the favorable outcome in 80% of cases and punished with the unfavorable outcome in the remaining 20% (analogously, incorrect choices were punished in 80% of cases, and rewarded in 20%). Importantly, during observational learning performance feedback was vicarious, i.e., related to the observed—rather than own—choice. To ensure vigilance and attentiveness during observational learning, we included catch trials that required observers to indicate the previously observed choice or feedback, after randomly selected trials.

Test blocks in which there was no trial-by-trial feedback and which followed after each learning block were included so that task performance and motivational biases could be directly compared between active and observational learning. Crucially, test blocks required own decision-making both in the active *and* observational learning task. Participants were thus instructed to transfer the knowledge about the stimulus-response-outcome contingencies gained during preceding learning blocks to effectively guide decision-making in test blocks. Moreover, although trial-by-trial feedback was not provided in test blocks, participants were told that points were still awarded, with the total score revealed at the end of each block.

All participants completed the active and observational task variant in separate sessions scheduled about one week apart. To prevent stimulus-response-outcome associations of the first session from biasing learning in the second session, a different set of fractal images was used as cues for the second session. Moreover, to avoid sequence effects, task order was balanced across the sample, such that participants were randomly assigned to start the task as an active or observational learner. Demographic and psychometric data were obtained in the first session. Testing took place at the Department of Biological Psychology at Heinrich Heine University Düsseldorf, Germany, except for two OCD patients who were tested at a collaborating

psychotherapeutic practice in Krefeld, Germany. Trial order was randomized within each block. Each task lasted about 35 minutes and included 10 practice trials.

Data quality control

To prevent including participants with low task motivation and/or compliance, behavioral data were assessed for quality control following the criteria reported in Vahedi et al. (2024). Specifically, participants were excluded if (1) performing below chance level in GW, the easiest learning condition, based on a one-tailed binomial test against chance (also see Albrecht et al., 2016; Weber et al., 2022); (2) showing >25% invalid responses (i.e., wrong side or late responding), or (3) selectively choosing either go or nogo in >85% of trials (similar to Weber et al., 2022). Criteria were applied separately to active and observational learning data, such that participants' data were excluded only for the task version for which the quality control criteria were not met. Applying these criteria to the recruited sample of 90 participants left a final sample of 81 participants (28 HC, 26 OCD, 27 SAD). However, for six participants (2 HC, 2 OCD, 2 SAD) only data from either active or observational learning were included in the analyses.

EEG recording and data processing

EEG Recording

EEG data were recorded from 29 active silver/silver-chloride electrodes (Fz, F3, F4, F7, F8, FCz, FC1, FC2, FC5, FC6, Cz, C3, C4, T7, T8, CP1, CP2, CP5, CP6, Pz, P3, P4, P7, P8, PO9, PO10, Oz, O1, O2), mounted on an actiCAP EEG cap (Easycap GmbH, Wörthsee, Germany) according to the extended 10-20 system (Chatrian et al., 1985, 1988). Electrode FCz served as the on-line reference, and the ground electrode was positioned at AFz. Two additional electrodes were attached—one at each mastoid—for later off-line re-referencing. Last, vertical and horizontal electrooculograms (vEOG/hEOG) were recorded using one electrode placed

above the left eye (vEOG) and another at the left outer canthus (hEOG). EEG signals were amplified using a BrainAmp DC amplifier (Brain Products GmbH, Gilching, Germany) and recorded at a 1000 Hz sampling rate using BrainVision Recorder software (version 1.20.0506, Brain Products GmbH, Gilching, Germany). Impedances were kept below 20kΩ.

Preprocessing

EEG preprocessing was performed offline using BrainVision Analyzer software (version 2.2.0, Brain Products GmbH, Gilching, Germany). First, during visual inspection of the raw EEG data, channels identified as corrupted or overly artifactual were topographically interpolated (active learning: $M = 0.20$ interpolated channels, $SD = 0.57$, range = 0-2; observational learning: $M = 0.33$ interpolated channels, $SD = 0.71$, range = 0-3). Next, we restored the signal of the on-line reference channel FCz by re-referencing the EEG data to the averaged mastoid signal. The EEG was then filtered using a 0.1-30 Hz bandpass and 50 Hz notch filter. To attenuate eye-movement-related artifacts, we applied BrainVision Analyzer's built-in independent component analysis (ICA)-based ocular correction (Plank, 2013).

Next, the continuous EEG was segmented from 200 ms before to 600 ms after outcome onset. In accordance with previous studies on outcome processing in this paradigm, we here focused on the neural responses to win and loss outcomes (e.g., Albrecht et al., 2016). The 200 ms pre-outcome interval was used for baseline correction. During artifact rejection, segments were discarded according to the following criteria: amplitudes exceeding ±100 µV, voltage shifts of 200 µV within 200 ms, voltage steps of 50 µV between adjacent data points, or abnormally low activity (i.e., less than 0.5 µV within a 100 ms window). On average, applying these criteria led to the exclusion of 1.80 % ($SD = 3.92$) of segments for active learning, and 2.20 % ($SD = 3.82$) of segments for observational learning data (but note that active learning data from 1 SAD

patient and observational learning data from 1 SAD and 1 OCD patient were excluded entirely due to excessive noise resulting in >25% discarded segments). The remaining artifact-free segments were exported for further data processing in MATLAB (version R2020a; The MathWorks Inc., Natick, Massachusetts, USA).

ERP component scoring procedure

Outcome processing was assessed via FRN/RewP and feedback-P3, measured in a fronto-central (Fz, FCz, FC1, FC2) and a centro-parietal cluster (Cz, CP1, CP2, Pz) electrode cluster, respectively. To account for latency differences, ERP components were scored separately for active and observational learning, following the procedure described in Vahedi et al. (2025):

For each electrode cluster, we calculated a composite waveform as the unweighted mean of the grand average (GA) waveforms for win and loss, pooled across electrodes within its respective cluster, i.e.,

$$COMP = \frac{pooled\ GA_{win} + pooled\ GA_{loss}}{2}$$

Next, each ERP component's (peak) latency was identified within each composite waveform, using a priori search windows based on current literature. The latency for FRN/RewP quantification was based on the local minimum within the time window 200–350 ms after feedback presentation (Faßbender et al., 2023), whereas the latency for P3 quantification was based on the local maximum within the 250-500 ms post-feedback interval (Polich, 2007). Finally, each ERP component was scored at the single-trial level, separately for each electrode within its respective cluster, by calculating the mean amplitude in a ±30 ms window centered around the (peak) latency identified in the composite waveform. The resulting time windows used to extract the FRN/RewP and P3 from each participant are provided in Table 2.

[insert Table 2 here]

Statistical Analyses

Data were analyzed at the single-trial level using (generalized) linear mixed-effects models ([G]LMMs) in R (version 4.1.0; R Core Team, 2021) via the *lme4* package (Bates et al., 2015). Contrast weights for all categorical fixed effect predictors were set using deviation coding (e.g., -0.5, 0.5). To test for OCD-specific effects, diagnostic group (OCD, HC, SAD) was specified as a three-level categorical factor, with OCD set as the reference level. Accordingly, all group-related main and interaction effects were estimated as separate planned contrasts with respect to OCD (i.e., OCD vs. HC, and OCD vs. SAD; see Vahedi et al., 2025).

For all models, we aimed to implement the maximum feasible random-effects structure, by including all by-participant random slopes and intercepts as well as their correlation, as supported by the data (see Barr et al., 2013). For ERP analyses, we additionally incorporated a random intercept by electrode. We performed automated model selection via the *buildmer* package (Voeten, 2020), in which the inclusion of random-effects terms was evaluated using stepwise likelihood-ratio tests (LRTs). Model parameters were optimized using the *bobyqa* algorithm with a maximum of 1e6 function evaluations. For LMMs, *p*-values were computed using Satterthwaite's approximation for degrees of freedom as implemented in the *lmerTest* package (Kuznetsova et al., 2017). For GLMMs, *p*-values were derived from Wald *z*-tests. For all analyses, the threshold for statistical significance was set to $p < .05$. Significant interaction effects were resolved using the *emmeans* package (Lenth, 2022), with Holm-adjusted *p*-values (Holm, 1979) used to correct for multiple comparisons where appropriate. A detailed overview of the results, including model formulae, is provided in the Supplement. Data were cleaned from invalid trials prior to model fitting (excluded trials: behavioral 3.11%, EEG data: 6.00%).

Task performance

To examine the presence of motivational biases in decision-making, we ran a GLMM on trial-level binary choice accuracy data (incorrect/correct) using a binomial logit-link function. Fixed effect predictors included the between-subject factor group (*OCD [=reference], HC, SAD*) as well as the within-subject factors agency (*active [=reference], observational*), required response (*go [=reference], nogo*), and cue valence (*win [=reference], avoid-losing*). With these predictors, the presence of motivational biases would be indexed by a significant required response × cue valence interaction effect.

EEG

Outcome processing was analyzed by running two complementary LMMs for the dependent variables FRN/RewP and P3 amplitude, respectively. As stated above, and in accordance with Albrecht et al. (2016), EEG analyses were restricted to trials with win and loss outcomes only, thus excluding draw trials. For both LMMs, fixed effect predictors included the categorical between-subject predictor group (*OCD [=reference], HC, SAD*) as well as the within-subject predictors agency (*active [=reference], observational*), response type (*go [=reference], nogo*), and outcome valence (*win [=reference], loss*). Notably, diverging from the behavioral analysis, *response type* codes the actual rather than required response that was committed/observed on a given trial. Moreover, to control for unspecific temporal effects in outcome processing, the continuous predictors *block* and (within-block) *trial number* (both centered before inclusion) were added as continuous covariates of no interest. To prevent overfitting, those predictors were included as fixed main effects only, i.e., not in interaction with other predictors. Using these predictors, action-biased outcome processing was expected to manifest in a response type × outcome valence interaction effect.

To ensure a sufficient number of trials for the assessment of the FRN/RewP, we verified that at least 10 trials were included for each combination of predictors (see Bellebaum & Daum, 2008; Ichikawa et al., 2010). The same criterion was applied to the P3. If for a given predictor combination, this criterion was violated, we excluded the data only for this specific predictor combination. By applying these criteria, further 3.09 % of trials had to be excluded.

Results

[insert Figure 2 here]

Task performance

Descriptive task performance data are visualized in Figure 2a. A detailed overview of inferential statistics is provided in Table S3 in the Supplement. GLMM results revealed significant main effects of cue valence (win>avoid-losing), b = -0.28 (SE = 0.09), z = -2.97, p = .003, required response (go>nogo), b = -1.05 (SE = 0.15), z = -7.21, p < .001, and agency (active>observational), b = -0.37 (SE = 0.11), z = -3.30, p = .001. Across the whole sample, our results replicated the presence of motivational biases as revealed by a significant cue valence × required response interaction, b = 2.42 (SE = 0.30), z = 8.16, p < .001, with overall better performance in GW relative to GAL, b = -1.49 (SE = 0.18), z = -8.40, p_{adj} < .001, and NGAL relative to NGW, b = 0.93 (SE = 0.13), z = 5.34, p_{adj} < .001. Moreover, the significant agency × cue valence × required response interaction indicated that motivational biases were attenuated following observational compared to active learning, b = -1.42 (SE = 0.48), z = -2.98, p = .003 (also see the Supplement for an independent analysis confirming motivational biases in observational learning). Closer examination of this effect revealed that this attenuation was confined to go learning, driven by a selective decrease in GW performance following observational compared to active learning, b = -1.10 (SE = 0.26), z = -4.15, p_{adj} < .001 (see

Figure 2b). Importantly, there were no significant effects involving the predictor group (*p*s ≥ .062).

EEG

Feedback-locked GA ERP waveforms are shown in Figure 3 (see also Figures S1 and S2 in the Supplement for topographical maps). A detailed overview of inferential statistics for all LMM analyses is provided in Tables S4-S5 in the Supplement.

[insert Figure 3 here]

FRN/RewP

FRN/RewP results replicated well-established main effects of outcome valence, b = -0.72 (SE = 0.31), t(73.25) = -2.36, p = .021, and agency, b = -2.89 (SE = 0.46), t(70.87) = -6.30, p < .001, with overall more positive amplitudes for win compared to loss and for active compared to observational learning.

Group differences between OCD patients and HCs emerged, as the respective group × agency interaction contrast was significant, b = -2.77 (SE = 1.12), t(70.81) = -2.47, p = .016. While for HCs, the FRN/RewP was generally more positive for self- compared to other-related outcomes, b = 3.95 (SE = 0.76), t(67.73) = 5.22, p_{adj} < .001, no such self-other distinction in the FRN/RewP was found for OCD patients (p_{adj} = .158). Aiming to further explore whether this effect was driven by alterations in active and/or observational learning, we additionally probed simple effects of group. While for active learning the FRN/RewP did not distinguish between groups (p_{adj} = .909), for observational learning the FRN/RewP was marginally more positive in OCD patients relative to HCs, though Holm-correction prevented this difference from reaching statistical significance (p_{adj} = .063). Additionally, the group × agency interaction contrast was significant for the OCD versus SAD comparison, b = -2.37 (SE = 1.15), t(72.27) = -2.06, p

= .043. Probing this effect revealed that SAD patients, like HCs, showed a more positive FRN/RewP for self- compared to other-related outcomes, b = 3.55 (SE = 0.80), t(70.95) = 4.44, $p_{adj} < .001$, though simple effects of group did not yield significant differences for neither active (p_{adj} = .497) nor observational learning (p_{adj} = .430). Taken together, these results suggest disrupted self-other distinction in the FRN/RewP in OCD patients compared to both HCs and SAD patients (see Figure 4a).

Finally, group differences between OCD and SAD were additionally reflected in the significant group × response type interaction contrast, b = -1.17 (SE = 0.56), t(63.82) = -2.10, p = .040. While simple effects of neither group nor response type were significant ($p_{adj} \geq .172$), descriptive data suggest that this interaction was driven by a reversal of response type coding with (descriptively) more negative FRN/RewP amplitudes for nogo versus go in OCD, and for go versus nogo in SAD patients.

[insert Figure 4 here]

P3

Crucially, P3 results revealed no significant effects involving the predictor group (ps ≥ .062). Instead, there were significant main effects of outcome valence, b = 1.12 (SE = 0.37), t(64.07) = 3.03, p = .004, and agency, b = -6.49 (SE = 0.80), t(69.10) = -8.08, $p < .001$, with more positive amplitudes for loss compared to win, and for active compared to observational learning. Moreover, the agency × outcome valence interaction was significant, b = -1.43 (SE = 0.69), t(61.71) = -2.06, p = .044, with significant outcome valence coding only for active, b = 1.83 (SE = 0.61), t(63.39) = 2.98, p_{adj} = .008, but not for observational learning (p_{adj} = .277; see Figure 4b). Beyond that, there was a significant response type × outcome valence interaction effect, b = -1.11 (SE = 0.55), t(56.14) = -2.02, p = .048, with the effect of outcome valence being

significant only for feedback following go, $b = 1.68$ ($SE = 0.40$), $t(72.33) = 4.17$, $p_{adj} < .001$, but not nogo ($p_{adj} = .280$; see Figure 4c). Further exploring simple effects of response type did not reveal significant differences for win ($p_{adj} = .267$) or loss ($p_{adj} = .364$). Analyzing the P3 in a fronto-central electrode cluster (i.e., P3a; Polich, 2007; Ullsperger, Fischer, et al., 2014) reproduced these results (see Table S6 of the Supplement).

Discussion

The present study examined to what extent motivational biases are altered in OCD patients, whether alterations depend on agency, and whether they are reflected in outcome processing as assessed with EEG. While motivational biases were generally attenuated for observational relative to active learning, we did not find these biases altered in OCD. Still, we found some differences in outcome processing, with OCD patients showing altered self-other distinction in the FRN/RewP. These findings offer novel insights into motivational decision-making and outcome processing in OCD, with their implications discussed in detail below.

Motivational biases may be unaltered in OCD

Overall, behavioral results replicated well-established motivational biases in decision-making, with better task performance in GW and NGAL compared to GAL and NGW (e.g., Ereira et al., 2021; Guitart-Masip, Economides, et al., 2014; Guitart-Masip et al., 2012; Vahedi et al., 2024). Moreover, motivational biases were generally attenuated for observational compared to active learning (see below for a discussion on that). Contrary to our hypotheses, however, the results did not provide evidence for altered motivational biases in OCD patients compared to HCs (and SAD patients). This finding is somewhat surprising, given the suggested role of the striatum and the PFC in driving and regulating motivational biases (Cavanagh et al., 2013; Guitart-Masip, Duzel, et al., 2014), and given fronto-striatal dysfunction in OCD (e.g., Pauls et

al., 2014). Despite this apparent discrepancy, the present finding aligns with recent work indicating that motivational biases may be unaltered in OCD (Marzuki et al., 2024; Scholz et al., 2026).

It is currently debated whether motivational biases constitute a Pavlovian response bias, an instrumental learning bias, or an interaction of both (de Boer et al., 2019; Guitart-Masip et al., 2012; Swart et al., 2017). Notably, whereas OCD has been linked to impaired instrumental learning (e.g., Gillan et al., 2011; Vahedi et al., 2025), Pavlovian learning appears largely intact (Myles et al., 2025). Given that we did not find altered motivational biases in OCD, this may be due to motivational biases primarily relying on, or being maintained by, the intact Pavlovian system. Alternatively, the strength of motivational biases is thought to decrease as controllability increases (Csifcsák et al., 2020; Dorfman & Gershman, 2019; Raab et al., 2024; but see Sedlinská et al., 2023). Alterations in agency, such as heightened control beliefs commonly observed in OCD (Reuven-Magril et al., 2008; Salkovskis et al., 2000), may thus have counteracted and therefore normalized otherwise enhanced motivational biases. Note, however, that we did not collect ratings of perceived controllability, which could have supported this argument; therefore, this interpretation must be regarded as speculative.

Altered self-other monitoring during outcome processing in OCD?

Although we did not find group differences in motivational biases, ERP results revealed OCD-related differences in early stages of outcome processing as reflected in the FRN/RewP. Contrary to our hypotheses but consistent with the behavioral null findings, these effects did not involve alterations in action-biased outcome processing. Instead, whereas the FRN/RewP distinguished consistently between self- and other-related outcomes in HCs, such differentiation was not found in OCD patients. While agency modulations have been typically discussed in

relation to outcome valence coding, the FRN/RewP is typically more positive for self-compared to other-related outcomes, even independently of outcome valence (Bellebaum et al., 2010; Itagaki & Katayama, 2008; Leng & Zhou, 2010). Accordingly, disrupted differentiation between self- and other-related outcomes in OCD may indicate altered self-other distinction in outcome processing.

Attempts to clarify whether this effect was driven by alterations in active and/or observational learning hinted at processing differences in observational learning, though this effect did not survive Holm-correction and only reached trend-level significance. Yet, altered observational learning appears plausible given that OCD has been frequently linked to an aberrant sense of agency (Borrelli et al., 2024; Gentsch et al., 2012; Grossmann et al., 2025; Szalai, 2019), including inflated responsibility beliefs, an illusory sense of control (Reuven-Magril et al., 2008; Salkovskis et al., 2000), and heightened affective responses when observing others (Jansen et al., 2020). Accordingly, it could be speculated that OCD patients remained similarly engaged even when outcomes were not self-evaluative but reflected events outside their control. However, from a theoretical perspective, the finding that the FRN/RewP in OCD patients lacked differentiation between self- and other-related outcomes could also reflect reduced self-monitoring, i.e., differences in active learning. Although this interpretation would align with previous evidence of reduced connectivity within the self-subsystem of the default mode network (Beucke et al., 2014; also see Fornaro & Vallesi, 2024), OCD has been more consistently associated with increased self-monitoring (cf. Norman et al., 2019). Again, whether the effect of disrupted differentiation between self- and other-related outcomes reflects alterations of active and/or observational learning mechanisms remains speculative, though alterations in observational learning appear most plausible.

In any case, this finding contrasts with previous evidence from our group using the same sample, which showed enhanced outcome valence coding in the FRN/RewP in OCD in active but not observational learning (Vahedi et al., 2025). By contrast, OCD-related differences found here did not depend on outcome valence. Although against our hypotheses, this finding is not too surprising, given the inconsistency of FRN/RewP findings in the literature, providing evidence for attenuated, enhanced, and unaltered outcome processing in OCD (see e.g., Endrass et al., 2013; Luo et al., 2020; Nieuwenhuis et al., 2005). Critically, it must be noted that this is the first study to investigate outcome processing in OCD using the orthogonalized go/nogo task. This paradigm differs substantially from paradigms used in previous studies in that it requires both active (*go*) and passive (*nogo*) responding and win and loss outcomes are provided in distinct win and avoid-losing contexts. Along these lines, the large variability of previous results on outcome processing in OCD may suggest high context dependence. Still, although OCD patients showed valence-independent alterations in outcome processing in this study, i.e., altered self–other monitoring, these differences did not translate into behavior.

Contrary to the FRN/RewP, we did not find OCD-related alterations in later outcome processing reflected in the P3. This may have to do with their differential functional roles in learning. While the P3 may be more involved in updating and implementing behavioral adaptation (Ullsperger, 2024), the FRN/RewP appears to reflect a more basal reinforcement learning signal, independent of action implementation (Cavanagh & Holroyd, 2026). Consistent with this idea, Albrecht et al. (2016) demonstrated that attenuated motivational biases in schizophrenic patients were accompanied by altered outcome processing in the P3. Crucially, in our study, behavioral data did not provide evidence for altered motivational biases in OCD which may therefore explain why there were no group effects for the P3.

Comparisons with SAD patients

To determine which findings may be uniquely related to OCD, we compared OCD patients with SAD patients. We did not find differences in motivational biases between OCD and SAD. This result is unsurprising given the considerable phenotypic overlap between OCD and SAD (Carpita et al., 2020), as well as partially shared neural mechanisms (Endrass et al., 2014; Weidt et al., 2016; also see Goodwin, 2015). Accordingly, although prior work has shown that motivational biases can be altered in certain mental disorders (e.g., Albrecht et al., 2016; Ousdal et al., 2018), our data suggest neither OCD nor SAD may be affected (but see Peterburs et al., 2022 for divergent results from a non-clinical SAD sample).

Still, differences between OCD and SAD emerged at the neural level during outcome processing. Most interestingly, whereas self-other distinction in the FRN/RewP was found to be disrupted in OCD patients, it was intact in SAD (but see the Supplement). Moreover, we found subtle differences in response type coding in the FRN/RewP. However, supplementary dimensional analyses did not provide clear evidence for such OCD-related effects. Accordingly, while OCD may be related to altered processing of self- versus other-related outcomes, which may be different to phenotypically similar but nosologically distinct disorders such as SAD, these processing differences may still (at least partly) involve transdiagnostic, disorder-general mechanisms.

General effects on motivational biases and outcome processing across the whole sample

While only expected in OCD patients, motivational biases were attenuated in observational compared to active learning across the whole sample, diverging from findings by Peterburs et al. (2021). This attenuation may point to differential neural mechanisms, with observational relative to active learning relying less strongly on the striatum (Bellebaum et al.,

2012; Kobza et al., 2012). Given the striatum's role in motivational biases (e.g., de Boer et al., 2019; Perosa et al., 2020; Richter et al., 2021; Richter et al., 2014), reduced striatal engagement during observational learning may have contributed to weaker bias expression. Notably, attenuated motivational biases for observational learning were driven by diminished GW performance in the present study. This generally aligns with the assumed functional architecture of the striatum (Collins & Frank, 2014) and recent evidence for biased instrumental learning (Swart et al., 2017), suggesting that when participants do not perform actions themselves, the typical learning advantage for rewarded action may not arise (or arise less strongly; but see results from choice-based repetition behavior in the Supplement providing only limited support for biased instrumental learning). Still, albeit attenuated, motivational biases persisted in observational learning (see Supplement), suggesting that apart from differential mechanisms in active and observational learning underlying bias attenuation, there may also be common mechanisms.

Regarding the neural mechanisms, ERP evidence revealed action-biased outcome processing only in the P3 but not the FRN/RewP. This contradicts previous reports of enhanced FRN/RewP outcome valence coding for action versus inaction (Bikute et al., 2022; Di Bernardi Luft et al., 2024; Yeung et al., 2005). However, note that these studies did not employ classical learning tasks, as participants were instructed to act or to withhold action. By contrast, the P3 showed outcome valence coding for action but not inaction. Importantly, however, direct comparisons of action versus inaction within win (and loss) proved to be non-significant, thereby contrasting with Schevernels et al. (2016). Thus, while supporting action-biased outcome processing, the lack of significant action-inaction differences suggests that this finding is more likely to reflect a *general* action bias, rather than biased instrumental learning with facilitated

learning from rewarded action and impaired learning from punished inaction (Swart et al., 2017). Accordingly, intact outcome valence coding for action but not inaction may support effective value updating and learning, ultimately aligning with our behavioral results showing better performance for go compared to nogo conditions. Alternatively, this finding could also reflect a frequency effect, as action was overall more frequent than inaction, possibly further mediated by learning. In any case, action-biased outcome processing in the P3 did not depend on agency, hence possibly constituting one common mechanism involved in active and observational learning that may underly motivational biases.

Limitations and future directions

Several limitations must be acknowledged. First, pharmacological treatment has been shown to modulate motivational biases (Guitart-Masip, Economides, et al., 2014; Scholz et al., 2022; Swart et al., 2017), which may have masked relevant effects, e.g., DA drug treatment was shown to remediate RPE processing in OCD patients (Murray et al., 2019). In addition, most patients presented with at least one comorbid mental disorder. This critically limits interpreting group effects as disorder-specific (even when including a clinical control group), as they may also reflect transdiagnostic and disorder-general mechanisms. Since the present sample only contained very few unmedicated and/or comorbidity-free patients, we were unfortunately unable to conduct subgroup analyses. Moreover, a limitation of the orthogonalized go/nogo task when assessing response type effects on outcome processing is that it leads to unequal and/or limited numbers of available trials per condition, hence it is advisable to aim to increase the number of available trials in future studies. Another limitation is that studying observational learning, with both (reinforced) learning and (non-reinforced) test blocks, complicated the application of computational modelling that could have provided additional insight into the mechanisms

underlying motivational biases. Furthermore, observational learning was based on virtual observation. Although Peterburs et al. (2021) showed similar effects for virtual and in-person observational learning in a healthy sample, clinical research may benefit from more ecologically valid environments, e.g., social observation and/or interaction. Last, OCD specificity was only assessed relative to SAD. Future studies should extend these comparisons to other anxiety disorders, such as generalized anxiety (Xiao et al., 2011) disorder or specific phobia (Lehnen & Pietrowsky, 2015), or even adopt a fully dimensional approach (see Morris & Cuthbert, 2012). Despite these limitations, we believe our findings are relevant in that they highlight possible alterations in self- versus other monitoring in OCD, thereby opening new perspectives toward characterizing the pathophysiology of OCD, e.g., within a second-person neuroscience framework (Schilbach, 2016; Schilbach et al., 2013).

Conclusion

In conclusion, the present study showed that although motivational biases were attenuated in observational relative to active learning across the whole sample, these biases were not altered in OCD. However, OCD patients did exhibit distinct neural patterns in outcome processing, with disrupted self-other distinction in the FRN/RewP. Similar results were found when comparing OCD patients to a clinical control group of SAD patients, suggesting altered self-other distinction in outcome processing as a particular characteristic of OCD. Accordingly, whereas motivational influences on learning and decision-making may not differ in OCD, our findings suggest altered sensitivity to self- versus other-related information during outcome processing. Future research, especially in the domain of observational learning (or social interaction), is warranted to gain additional insights into such “social” alterations in the pathophysiology of OCD.

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1064 **Table 1**

Sample characteristics after exclusions ($N = 81$).

	HC ($n = 28$)	OCD ($n = 26$)	SAD ($n = 27$)
Demographics			
age (in years)	33.18 (12.24)	32.96 (10.58)	31.37 (11.66)
sex (*n* female:male)	16:12	16:10	21:6
handedness (*n* right:left:ambidextrous)	24:3:1	23:2:1	25:1:0[a]
Psychometric features			
verbal IQ[b]	110.54 (14.64)	116.08 (11.84)	113.37 (17.73)
comorbidities (*n* with:without a history of comorbid disorders)[c]	–	19:7	19:8
medication status (*n* medicated:unmedicated)[d]	–	17:9	13:14
BDI-II	2.93 (4.47)	17.08 (9.72)	17.11 (10.63)
OCI-R	7.57 (6.48)	28.35 (14.40)	12.59 (9.84)
OBQ-D	3.14 (0.89)	4.48 (1.13)	4.09 (1.16)
Y-BOCS	–	20.12 (7.30)	–
LSAS	–	–	83.96 (22.18)

Note: Data are presented as means with standard deviations (*SD*) in parentheses, except for sex, handedness, comorbidities, and medication status, which are reported as counts. Abbreviations: HC = healthy controls; OCD = obsessive-compulsive disorder; SAD = social anxiety disorder; BDI-II = Beck Depression Inventory-II; OCI-R = Obsessive-Compulsive Inventory-Revised; OBQ-D = Obsessive-Beliefs Questionnaire; Y-BOCS = Yale-Brown Obsessive-Compulsive Scale; LSAS = Liebowitz Social Anxiety Scale.

[a] missing data on handedness for one patient in the SAD group

[b] verbal IQ was estimated using the Mehrfachwahl-Wortschatz-Test B (MWT-B)

[c] detailed overview about the history of comorbid disorders can be obtained from Table S1 in the Supplement

[d] detailed overview about current use of psychotropic medication can be obtained from Table S2 in the Supplement.

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Table 2

Scoring procedure.

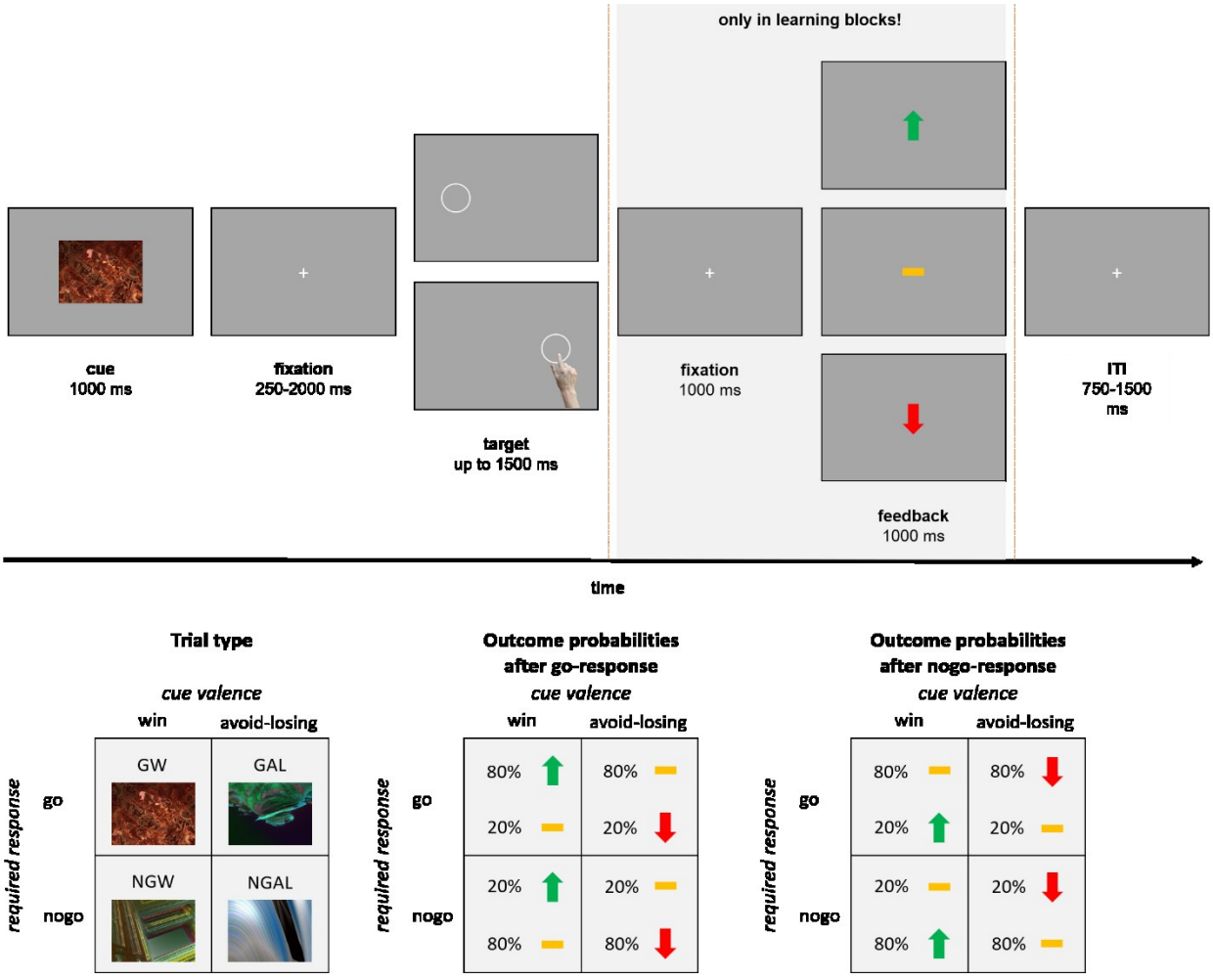
ERP component	Cluster	Search Window	Extraction Time Window
FRN/RewP	fronto-central (Fz, FC1, FC2, FCz)	200-350 ms[a]	active: 222-282 ms observational: 237-297 ms
P3	centro-parietal (Cz, CP1, CP2, Pz)	250-500 ms[b]	active: 345-405 ms observational: 357-417 ms

Note: Abbreviations: ERP = event-related potential, FRN/RewP = feedback-related negativity/reward positivity.

[a] FRN search window was based on Faßbender et al. (2023)

[b] P3 search window was based on Polich (2007)

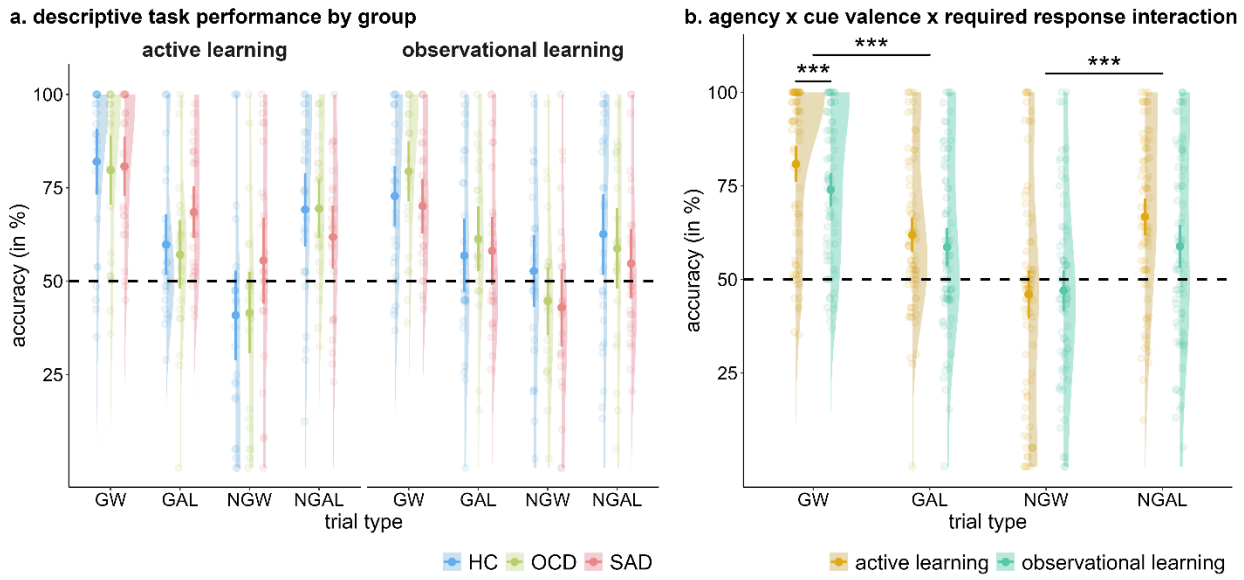
Figure 1



Note. Schematic illustration of the sequence and timing of stimulus presentation of a single trial for each cue condition. Test trials ended after the target detection task, thus no feedback was provided. Conversely, during learning, feedback was provided as one of two possible outcomes. For win cues, the favorable outcome was a gain of ten points, indicated by an upward pointing green arrow, while the unfavorable outcome was to neither gain nor lose points, indicated by a yellow horizontal bar. For avoid-losing cues, the favorable outcome was to avoid point loss, indicated by a yellow horizontal bar, whereas the unfavorable outcome was a loss of ten points. Abstract fractal images (Mathôt et al., 2015; obtained from

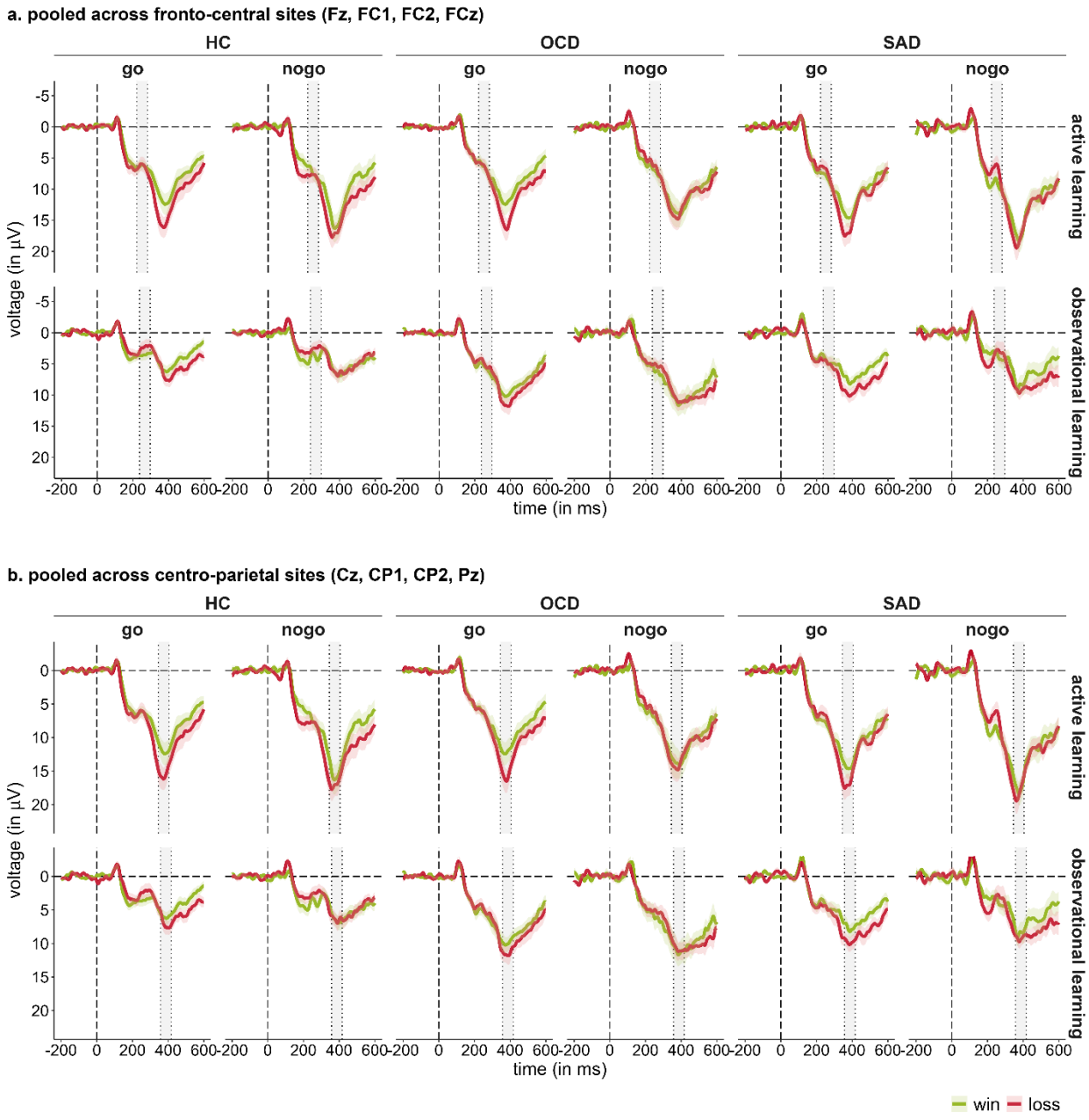
https://github.com/smathot/materials_for_P0010.5) were used as cues and randomly assigned to the four learning conditions at the beginning of each test session.

Figure 2



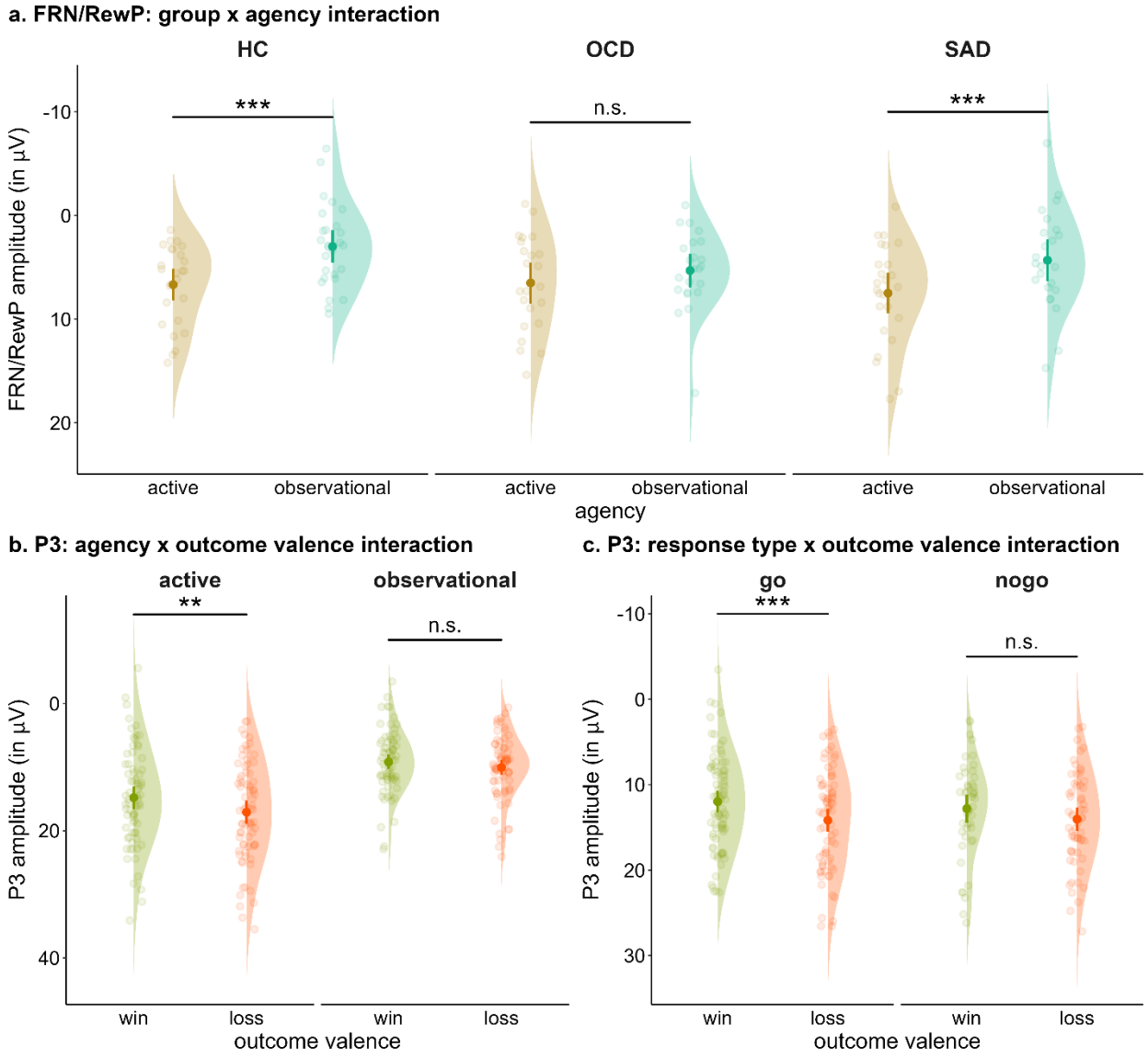
Note: Choice accuracy in test trials. **a.** provides descriptive task performance data, separately by diagnostic group and task variant. **b.** shows the descriptive result pattern underlying the significant agency × cue valence × required response interaction effect with asterisks indicating significant differences yielded from simple-effects analyses. The dashed horizontal line indicates chance-level performance (=50%). Data represent group-level means with error bars indicating 95% confidence intervals. Transparent dots represent subject-level means. Abbreviations: GW = go to win; GAL = go to avoid-losing; NGW = nogo to win; NGAL = nogo to avoid-losing; HC = healthy controls; OCD = obsessive-compulsive disorder; SAD = social anxiety disorder. n.s. not significant, *$p < .05$, **$p < .01$, ***$p < .001$

Figure 3



Note: Feedback-locked grand average ERP waveforms. Data are visualized as mean ± standard error. Gray-shaded regions indicate the extraction time windows used to score the feedback-related negativity/reward positivity (FRN/RewP) across fronto-central sites (**a.**), and the P3, across centro-parietal sites (**b.**). Abbreviations: ERP=event-related potential.

Figure 4



Note: Descriptive result patterns underlying ERP analyses. **a.** represents descriptive patterns underlying the FRN/RewP results. **b.-c.** represent descriptive patterns underlying the P3 results. Data represent group-level means with error bars indicating 95% confidence intervals. Transparent dots represent subject-level means. Asterisks indicate significant differences yielded from simple-effects analyses. Abbreviations: HC = healthy controls; OCD = obsessive-

compulsive disorder; SAD = social anxiety disorder.

n.s. not significant, *$p < .05$, **$p < .01$, ***$p < .001$

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Declaration of Generative AI and AI-assisted technologies in the writing process

AI-assisted writing tools were occasionally used during internal revision of the original draft to proof the document for language errors and improve readability. AI-generated rewording was carefully reviewed and adopted only if it contributed significantly to a better understanding of the content. The authors take the full responsibility for the content of this work.

Ethics declaration

Ethical approval

All procedures performed in this study were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent

Informed consent was obtained from all individual participants included in the present study.

Conflict of interest

Authors J.V., A.B., I.C., L.S., B.C-S., C.B., R.P., and J.P. declare that they have no conflicts of interest.

Data availability

Data and code to reproduce all analyses in this manuscript as well as the Supplement can be found on the Open Science Framework (https://osf.io/dg7ka/overview?view_only=587d8ddb4c74404c97b0556222019d8d).