The (In)Stability of Social Preferences: Neuroendocrine Mechanisms and Methodological Perspectives

Inaugural Dissertation

zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen-Fakultät
der Heinrich-Heine-Universität Düsseldorf

vorgelegt von

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Essen, Oktober 2025

The (In)Stability of Social Preferences

aus dem Institut für Experimentelle Psychologie
der Heinrich-Heine-Universität Düsseldorf

Gedruckt mit der Genehmigung der
Mathematisch-Naturwissenschaftlichen Fakultät der
Heinrich-Heine-Universität Düsseldorf

Berichterstatter:

1. Prof. Dr. Tobias Kalenscher

2. Prof. Dr. Gerhard Jocham

Tage der mündlichen Prüfung: 03.03.2026

Cover Art

This cover art illustrates how the two main neuromodulators of the acute stress response, cortisol and noradrenaline, shape social behavior in distinct ways. Although they do not directly counteract each other, they seem to drive behavior in different directions depending on the social and situational context: cortisol tends to promote affiliation, while noradrenaline tends to promote separation. In stressful situations, these seemingly opposing influences may complement each other, enabling both the pursuit of protection through affiliation and the readiness to confront or withdraw from potential threats. The tug-of-war depicted here symbolizes this dynamic interplay. The rationale to this analogy is explored in the following manuscript.

Danksagung

Dankbarkeit ist wohl das Wort, das am besten beschreibt, was ich empfinde, wenn ich auf meine Promotionszeit zurückblicke. Dankbarkeit für die vielen bereichernden Erfahrungen, die ich machen durfte und Dankbarkeit für die Menschen, die meinen Weg begleitet und ausgemacht haben, die mich angefeuert und mit mir mit gefiebert haben.

Zunächst möchte ich Tobi, Felix und Paul danken, die mich immer wieder ermutigt haben, über mich hinauszuwachsen und mich neuen Herausforderungen zu stellen. Danke für die wertvollen Ratschläge, die Unterstützung und stets konstruktives Feedback. Auch allen anderen ComPsy Kolleg*innen möchte ich für ihr Feedback und den Austausch danken. A special thanks goes out to Irina and Douman for countless inspiring discussions about life, science, feminism and politics. The time we spent working together is something I will always treasure.

Das Beste, was passieren konnte, ist dass ich diesen Weg gemeinsam mit José gestartet habe. Ohne dich hätte die Promotion nur halb so viel Spaß gemacht. Ich bin Dir so dankbar für jeden Moment, in dem Du hinter mir standest, mir Mut zugesprochen, Feedback und Deine Perspektive gegeben hast. Ich bin dankbar für jeden Wortwitz und jedes Lied, dass wir geteilt haben. Und ich bin dankbar für Dein Remake von Alpha und lache gerade wieder, während ich es mir durchlese.

Ohne die vielen Studierenden, die mit viel Herzblut meine Projekte unterstützt haben, wären diese gar nicht möglich gewesen. Ganz besonders danken möchte ich Damon, Karina und Julian für die unglaublich großartige Zeit, die wir zusammengearbeitet haben, für Eure wertvollen intellektuellen Beiträge und dafür, dass ich Euch auf Eurem Weg ein Stück begleiten durfte. Es war mir eine Ehre, Eure Abschlussarbeiten zu betreuen und ich bin gespannt, wo Eure Wege hinführen.

Zum Schluss möchte ich den Menschen danken, die meine Art zu denken, zu hinterfragen und meinen Blick auf das Leben geprägt haben, meine Familie und Freund*innen, insbesondere meine Mama, mein Papa, meine Bonusmama und meine Schwestern, Kira und Bele. Ihr wart schon immer meine größten Cheerleader, habt stets ein offenes Ohr und eine Umarmung parat und ich weiß, ihr seid immer an meiner Seite. Mein größter Dank gilt Torben. Danke für jeden Kaffee und jeden Frühstückskuchen, den Du mir gemacht hast, jede Runde, die Du mit dem Hund gegangen bist, aber vor allem danke für Deine Geduld, Deine emotionale Unterstützung und Deine unendliche Ruhe und Zuversicht, dass alles gut wird, mit der Du jeden Selbstzweifel ausgehebelt hast. Danke!

Zusammenfassung

Sozialverhalten ist nicht konstant, sondern hoch flexibel und entsteht aus dem Zusammenspiel neurobiologischer Mechanismen und sozial-emotionaler Rahmenbedingungen. Ein zentraler Einflussfaktor ist Stress. Die Beeinflussung des Sozialverhaltens durch Stress zeigt, dass soziale Präferenzen weniger stabil sind, als ökonomische Modelle voraussetzen und stellt damit die Grundannahme der Entscheidungskonsistenz infrage. Die Studien dieser Dissertation untersuchten, wie Stress-Neuromodulatoren Sozialverhalten und Entscheidungskonsistenz beeinflussen, wie neurobiologische Grundlagen flexibles Sozialverhalten ermöglichen und wie methodische Einschränkungen unsere Schlussfolgerungen begrenzen. In zwei psychopharmakologischen Studien haben wir gezeigt, dass die zentralen Stress-Neuromodulatoren, Cortisol und Noradrenalin, das Sozialverhalten kontextabhängig beeinflussen. Unter wahrnehmbarer Bedrohung förderte Cortisol kooperatives Verhalten gegenüber der eigenen Gruppe und Noradrenalin Feindseligkeit gegenüber anderen Gruppen. In neutraleren Situationen blieben Sozialverhalten und Entscheidungskonsistenz hingegen unverändert. Die Ergebnisse verdeutlichen, dass Stress keine einheitlichen Wirkungen entfaltet, sondern Verhalten, abhängig vom Verhältnis von Cortisol und Noradrenalin, den situativen Anforderungen sowie den jeweiligen sozialen Beziehungen, in Richtung Kooperation oder Konflikt verschieben kann. Um die neurobiologischen Grundlagen prosozialen Verhaltens weiter zu ergründen, untersuchten wir in einer weiteren Studie Personen mit selektiven Läsionen der basolateralen Amygdala (BLA). Die Ergebnisse zeigten, dass die BLA eine zentrale Rolle bei der flexiblen Anpassung prosozialen Verhaltens an sozial-emotionale Distanz spielt. Das legt spekulativ nahe, dass die BLA auch an den beobachteten Stresseffekten beteiligt sein könnte. Schließlich nahmen wir eine methodische Perspektive ein und zeigten, dass gängige Maße der Entscheidungskonsistenz nur unzureichende Reliabilität aufweisen. Das stellt frühere Schlussfolgerungen in Frage und verdeutlicht, wie sehr belastbare Ergebnisse von methodischen Entscheidungen abhängen. In einer Zeit zunehmender globaler Gewalt ist es entscheidend, die neurobiologischen Grundlagen zu verstehen, die Sozialverhalten in Richtung Kooperation oder Konflikt lenken, und dabei ist methodische Strenge für aussagekräftige Erkenntnisse unverzichtbar.

Keywords: Stress, Cortisol, Noradrenalin, Rationalität, soziale Präferenzen, Intergruppenkonflikt, Amygdala

Abstract

Social behavior is not stable, but highly flexible and arises from interactions between neurobiological mechanisms and social-emotional context. Stress is one of the crucial drivers. The effect of stress on social behavior suggests that social preferences are less stable than economic models assume, thereby challenging the fundamental assumption of choice consistency. The studies in this dissertation examined how stress neuromodulators influence social behavior and choice consistency, how neural substrates enable flexible social behavior, and how methodological limitations constrain our inferences. Across two psychopharmacological studies, we showed that the main stress neuromodulators, cortisol and noradrenaline, influence social behavior in a context-dependent manner. Under salient threat, cortisol promoted cooperative behavior toward one's own group, and noradrenaline promoted hostility toward other groups. In contrast, in more neutral settings, social behavior and choice consistency remained unchanged. These results illustrate that stress does not exert uniform effects on social behavior but may tip the scale toward either cooperation or conflict depending on the balance between cortisol and noradrenaline, the situational demands, and the social relationships involved. To further explore the neural basis of prosocial behavior, in a further study we examined individuals with selective lesions of the basolateral amygdala (BLA). The results demonstrated that the BLA plays a central role in flexibly adapting prosocial behavior to social-emotional distance. This speculatively suggests a possible role for the BLA in the observed stress effects. Finally, we took a methodological perspective and showed that common measures of choice consistency lack reliability. This calls into question prior conclusions and underscores how much robust results depend on methodological decisions. In a time of increasing global violence, it is crucial to understand the neurobiological underpinnings that drive social behavior toward cooperation or conflict, and methodological rigor is indispensable for meaningful insights.

Keywords: stress, cortisol, noradrenaline, rationality, social preferences, intergroup conflict, amygdala

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General Introduction

"In some sense, the current state of research on prosocial behavior resembles a field of wild flowers: On the one hand, it carries a beautiful diversity in form and expression. On the other hand, the field is disordered, wild, and untamed." (Pfattheicher et al., 2022, p. 124)

The Puzzle of Social Behavior

Humans are deeply social beings. They are driven by a fundamental need for connection (Baumeister & Leary, 1995) that is closely tied to physical and mental health (Cacioppo & Cacioppo, 2014; Cohen, 2004; Fratiglioni et al., 2004; Holt-Lunstad et al., 2010). Across cultures this social orientation manifests in remarkable, though culturally variable, levels of *prosocial behavior* (Henrich et al., 2005) that benefits both individuals and societies (Box 1). At the individual level, prosocial behavior is linked to well-being and happiness and can even buffer the effects of stress (Dunn et al., 2008; Hui et al., 2020; Park et al., 2017; Raposa et al., 2016). At the societal level, it supports economic success, strengthens social cohesion, and underpins collective efforts to shared challenges, such as climate change (Fehr & Fischbacher, 2003; Gross & De Dreu, 2019; Hauser et al., 2014; Knack & Keefer, 1997; Kosse & Tincani, 2020).

Yet, this propensity for connection coexists with an equally striking propensity for division. On a global scale, violent conflicts between groups and nations have reached historic highs (Raleigh & Katayoun, 2023; United Nations, 2020, 2023b), and polarization within societies is deepening, often fueled by moralization of opposing groups (Finkel et al., 2020; United Nations, 2023a). Thus, just as humans are willing to *cooperate* (Box 1), they are also willing to inflict profound harm on one another.

The coexistence of such opposing tendencies reflects a common tension in human sociality: people sometimes cooperate, even at personal costs, and at other times turn to conflict and harm. A range of theories have been proposed to explain the drivers of social behavior, pointing, e.g., to individual-level motivations such as the rewards of helping (Andreoni, 1990) or expectations of reciprocity (Falk & Fischbacher, 2006), as well as to group-level dynamics like social identity (Tajfel & Turner, 1986) and competition over resources (Sherif, 1966). This illustrates the complexity of human social behavior, which arises from the interaction of social-contextual factors and underlying neurobiological mechanisms. Understanding this interplay is essential for explaining not only the origins of prosocial behavior but also the shifts toward competition and conflict.

Social Decision-Making and Social Preferences

Social behavior involves making decisions that affect not only the decision-maker but also other people, such as whether to help a co-worker on their project or to continue one's own work. These decisions strongly depend on who the other person is. In fact, prosocial behavior decreases with greater social-emotional distance to the recipient, a phenomenon known as *social discounting* (Jones & Rachlin, 2006). Similar patterns also emerge in group contexts, where individuals differentially favor members of their own group (*in-group*; Box 1) over members of other groups (*out-groups*; Box 1). Such intergroup-biased behaviors are encompassed in the phenomenon of *parochial altruism* (Box 1; Choi & Bowles, 2007). This can take the form of *parochial cooperation* (Box 1), where individuals cooperate more with their in-group than with out-groups (Balliet et al., 2014; De Dreu et al., 2020), or *parochial competition* (Box 1), where such cooperation is combined with hostility toward out-groups (De Dreu et al., 2020). Typically, parochial cooperation exceeds parochial competition (Böhm et al., 2020).

Beyond such forms of social categorization, a range of contextual and individual factors also shape these decisions. In both interindividual and intergroup settings, the contextual framing has been shown to affect behavioral outcomes. For example, individuals are more generous toward others when a choice is framed as taking money away from others rather than as sharing money with them (Sellitto et al., 2021). Similarly, framing intergroup tasks in terms of collective outcomes rather than individual payoffs promotes competitive tendencies toward out-groups (Weisel & Zultan, 2021), suggesting that individual and group decision-making may involve at least partly different processes. Hostile behavior toward out-groups is also more likely under conditions of resource uncertainty or inequality, or when the out-group is perceived as threatening (Böhm et al., 2016; De Dreu et al., 2022; Halevy et al., 2010). Finally, individual characteristics such as age, also play a role, with older individuals tending to behave more prosocially than younger ones (Engel, 2011; Lockwood et al., 2021).

Together, this suggests that individuals systematically weigh their own and others' costs and benefits when making social decisions. These trade-offs are encapsulated in what is known as *social preferences* (Box 1), i.e., latent constructs that describe what people value in choices affecting other individuals and groups (Fehr & Charness, 2025). Social preferences underlie both prosocial and competitive behaviors, and like all preferences, they are not directly observable, which means they cannot be measured directly. Instead, they are typically inferred from systematic patterns of observable choice behavior.

Economic Games as Measures of Social Decision-Making

To study social decision-making and preferences, researchers commonly rely on experimental economic games. In these games, participants receive a monetary endowment (i.e., a budget) and make (repeated or one-shot) choices on how to allocate this money among different options. These tasks provide direct measures of behavioral outcomes but additionally their structure often allows to infer underlying social preferences from different allocation patterns.

The most basic game paradigm is the *dictator game* (Box 1), in which the participant decides how much of their endowment to share with another person, who is either designated, such as a friend or stranger, or an anonymous person. Sharing is typically interpreted as driven by altruistic motives (Engel, 2011).

In group contexts, a classic paradigm is the *Intergroup Prisoner's Dilemma – Maximizing Difference paradigm* (IPD-MD; Box 1; Halevy et al., 2008), which elicits behavior toward in-group and out-group members. Participants in this game are assigned to an in-group (typically three members) and play against an opposing out-group of equal size. They then decide how to allocate their endowment across three options. Contributions to the "keep pool" are retained by the participant, which suggests a focus on individual payoff and can be interpreted as selfish free-riding (i.e., profiting from others' cooperative contributions). Contributions to the "within-group pool" are multiplied by a factor (e.g., 1.5) and then distributed among all in-group members, reflecting cooperation that benefits the group but potentially comes at a personal cost if the others free-ride. Thus, within-group pool contributions are interpreted as parochial cooperation (De Dreu et al., 2020). Contributions to the "between-group pool" generate the same in-group profit as within-group pool contributions, but at the same time they incur equal costs for each out-group member, such that the same amount credited to in-group members is deducted from out-group members. Such contributions reflect a similar cooperative motive toward the in-group, but show an additional focus on harming the out-group, and are hence interpreted as parochial competition (De Dreu et al., 2020).

The Generalized Axiom of Revealed Preference

The process of deriving (social) preferences from observed behavior relies on the assumption that choice patterns are consistent and reflect stable underlying preferences. Revealed Preference Theory (Afriat, 1967; Houthakker, 1950; Samuelson, 1938) provides a

non-parametric framework to assess this assumption, with the *Generalized Axiom of Revealed Preference* (GARP; Box 1; Afriat, 1967; Houthakker, 1950) as its central criterion. The basic idea is that if an option A is chosen over another option B when both are affordable, then A is revealed preferred to B, i.e., it is at least as good or better than B. If A is chosen despite being more expensive than B, this implies a strict revealed preference for A. GARP requires that such revealed preferences are internally consistent: if a chain of choices implies that A is revealed preferred to B, then B should never be strictly revealed preferred, i.e. it should never be chosen over A unless A has become too expensive and is no longer affordable. Otherwise, the choices would be inconsistent and violate GARP.

Notably, if a set of choices satisfies GARP, then it is possible to construct a preference representation from this choice set that rationalizes the observed behavior (Afriat, 1967). In this sense, GARP provides a benchmark condition for treating choices as the expression of coherent preferences. Applied to social decision-making, GARP allows us to ask whether behaviors such as generosity shown in a dictator game can be represented as consistent social preferences, such as preferences for altruism or reciprocity (Andreoni & Miller, 2002; Falk & Fischbacher, 2006). This rests on the assumption that preferences remain stable at least across the observation period, given that everything else remains equal.

In sum, social decision-making refers to the observable behaviors through which individuals navigate social interactions, while social preference models aim to capture the motivational processes that underlie these behaviors. Modeling social preferences is useful not only for interpreting behavioral regularities, but also for predicting future choices and linking individual motives to larger political and societal outcomes such as voting, policy attitudes, polarization, and collective action (Fehr & Charness, 2025; Fisman et al., 2017; Kerschbamer & Müller, 2020; Müller & Renes, 2021). In this sense, decision-making and preferences represent complementary levels of abstraction in the study of social behavior and cognition. Their expression, however, is contingent on contextual, individual, and biological factors, with the *social brain* (Box 1) providing a key substrate for how social motives are implemented.

Box 1. Definitions

Altruism: Refers to behavior that benefits others while incurring a cost to oneself (Pfattheicher et al., 2022).

Cooperation: Refers to behaviors that contribute to a collective good, often at some immediate personal cost. While withholding contributions (free-riding) can yield higher individual payoffs, widespread cooperation maximizes collective outcomes and can ultimately benefit all group members (Rand & Nowak, 2013; Van Dijk & De Dreu, 2021).

Dictator Game: An economic decision-making game designed to measure prosocial behavior (specifically altruism). Participants receive a monetary endowment and are asked how much of it they would like to share with another person (either anonymous or designated). The other person has no say in the matter (Engel, 2011).

Fight-or-Flight: A biobehavioral response to acute stress characterized by either confronting a threat (fight) or escaping from it (flight), originally associated with activation of the sympathetic adrenal medullary system (Cannon, 1932).

Generalized Axiom of Revealed Preference (GARP): An economic choice consistency criterion and a hallmark of economic rationality. If a set of choices satisfies GARP, then it is possible to construct a preference representation from this choice set that rationalizes the observed behavior (Afriat, 1967; Houthakker, 1950; Samuelson, 1938).

In-Group vs. Out-Group: The in-group is the group to which a person belongs or feels they belong, while the out-group refers to all groups to which a person does not belong or with which they do not identify (Böhm et al., 2020).

Intergroup Conflict: A conflict of interests, values, or beliefs between individuals belonging to opposing groups (Böhm et al., 2020; Halevy & Landry, 2024). Various theories attempt to explain its origins, emphasizing, for example, the role of social identity (Tajfel & Turner, 1986), competition over resources (Sherif, 1966), or evolutionary pressures (Choi & Bowles, 2007). However, no single theory accounts for the phenomenon exhaustively (see Böhm et al., 2020 for a review).

Intergroup Prisoner's Dilemma – Maximizing Difference Paradigm (IPD-MD): An economic decision-making game designed to measure behaviors toward in-groups and out-groups in an intergroup conflict setting. Participants are assigned to an in-group and play against an opposing out-group of equal size. They receive a monetary endowment and are asked to distribute this across different options: keeping it, contributing to a collective in-group benefit, or contributing to an in-group benefit that simultaneously imposes costs on the out-group. This structure allows to measure both cooperation toward the in-group and hostility toward the out-group (Halevy et al., 2008).

Parochial Altruism: Originally defined as prosocial behavior toward the in-group combined with harmful behavior toward the out-group (Choi & Bowles, 2007), it is now used more broadly as an umbrella term for intergroup-biased behaviors (Cacault et al., 2015).

Parochial Cooperation: Refers to cooperation with members of the in-group but not the out-group (De Dreu et al., 2020).

Parochial Competition: Refers to cooperation with members of the in-group combined with hostility toward out-group members (De Dreu et al., 2020).

Prosocial Behavior: An umbrella term describing all behaviors that benefit others.

Social Brain: A set of neural networks that support social cognition and behavior (Schilbach & Redcay, 2025), currently thought to include the social perception network, the mentalizing network, the empathy network, and the mirror network (Kennedy & Adolphs, 2012).

Social Discounting: The tendency for generosity to decline as the social-emotional distance to the recipient increases (Jones & Rachlin, 2006).

Social Preferences: Social preferences refer to the values and trade-offs individuals consider when making decisions that affect both themselves and others (Fehr & Charness, 2025). They are not observable, which means they cannot be measured directly. Instead, they are typically inferred from observable choice behavior using mathematical models.

Stress: Acute stress is often defined in terms of physiological reactions triggered by an actual or perceived disruption of internal stability, or homeostasis (Cannon, 1932; Selye, 1950). This view emphasizes stress as a biological response aimed at restoring balance. It has been refined by the concepts of allostasis, referring to adaptive changes in physiological states in response to stress that may help buffer future challenges, and allostatic load, which refers to the long-term costs of repeated or chronic stress system activation (McEwen, 1998; McEwen & Akil, 2020). However, viewing stress as a purely physiological process has also been criticized for neglecting its cognitive dimension (Koolhaas et al., 2011). From this alternative perspective, stress is described as the perception of uncontrollability or unpredictability, accompanied by characteristic physiological responses.

Tend-and-Befriend: A biobehavioral response pattern to stress characterized by affiliative behaviors toward others to form protective alliances, was originally proposed to be driven by the attachment-caregiving system (Taylor et al., 2000).

The Social Brain

The concept of a *social brain* (Box 1) refers to how social cognition and behavior are represented in the brain (Kennedy & Adolphs, 2012; Schilbach & Redcay, 2025). Early formulations discussed specific regions, such as the amygdala, orbitofrontal cortex (OFC), and the temporal cortex as subserving social information processing (Brothers, 2002). With the rise of functional magnetic resonance imaging (fMRI), this set of regions was expanded to also include e.g., the insula, temporoparietal junction (TPJ), or dorsomedial prefrontal cortex (dmPFC; Kennedy & Adolphs, 2012; Stanley & Adolphs, 2013). Importantly, none of these regions alone can represent social functions. Contemporary neuroscience has therefore moved toward a network perspective, emphasizing that social cognition and behavior emerge from the coordinated activity of multiple regions (Kennedy & Adolphs, 2012; Stanley & Adolphs, 2013). For example, the mentalizing network, including, e.g., the TPJ, supports cognitive aspects of empathy and perspective taking (Stanley & Adolphs, 2013; Tusche & Bas, 2021), and the social perception network, which involves the amygdala, is thought to support the detection of socially salient cues (Stanley & Adolphs, 2013). Yet, the idea of a distinct social brain remains controversial; whether these networks are truly specific to social cognition and behavior or whether they reflect general mechanisms that are applied in social contexts remains an open question (Lockwood et al., 2020; Stanley & Adolphs, 2013). One suggestion is that specificity may exist at different levels of explanation, for example, different rules may be

engaged in social settings, or the same rules are implemented in different neural networks (Lockwood et al., 2020).

Prosocial behavior and cooperation are aspects of social behavior that have consistently been linked to valuation, executive control, mentalizing and empathy networks (Tusche & Bas, 2021). For example, the vmPFC, a typical valuation area, has been identified as one critical area underlying prosocial motivation (Lockwood et al., 2024; Strombach et al., 2015). Cooperation further recruits mentalizing regions such as the TPJ, which supports other-regarding preferences as well as prefrontal control regions such as the dorsolateral prefrontal cortex (dlPFC) thought to support overcoming selfish impulses (Sanfey et al., 2003; Strang & Park, 2016; Strombach et al., 2015). By contrast, non-cooperation and responses to unfairness are more closely associated with the insula (Sanfey et al., 2003; Strang & Park, 2016). At the level of larger-scale social interaction, such as between groups of individuals, regions like the amygdala or OFC contribute to social categorization processes, including in-group versus out-group distinctions (Cikara & Van Bavel, 2014; Van Bavel et al., 2008). Thus, prosocial behavior emerges from the interaction of circuits and networks supporting valuation, executive control, and social cognition, rather than from any single region in isolation. Please note, however, that this overview is not a comprehensive review of the extensive literature on the neural bases of (pro)social behavior and cognition (see Kennedy & Adolphs, 2012; Sandhu et al., 2025; Stanley & Adolphs, 2013; Strang & Park, 2016; Tusche & Bas, 2021 for more comprehensive reviews).

Among the regions implicated in social behavior and cognition, the amygdala is particularly fascinating. Although it is often treated as a unitary structure, it is in fact a cluster of nuclei with partly distinct functions (Sah et al., 2003). This cluster is now thought to support social cognition primarily by directing attention to emotionally and socially relevant stimuli. In both animal and human studies, “the amygdala” has been implicated in processes such as social categorization, other-regarding preferences, and attentional focus during affective touch (Cikara & Van Bavel, 2014; Gothard & Fuglevand, 2022; Rhoads et al., 2023; Van Bavel et al., 2008). The precise roles of the different subnuclei in these processes remain less well understood. The basolateral amygdala (BLA), for example, has frequently been linked to social decision-making: it seems to modulate social preferences (Chang et al., 2015; Dal Monte et al., 2020) and to support learning about whom to trust (Rosenberger et al., 2019; Sladky et al., 2021). Such findings suggest that the BLA plays a critical role in enabling prosocial behavior. Paradoxically, however, selective BLA lesions do not necessarily disrupt prosocial behavior and may, in fact, even lead to unusually generous choices (Van Honk et al., 2013). In addition,

the BLA also contributes to non-social functions, including flexible representation of current incentive structures and taking action in response to threats (Hinz et al., 2025; Terburg et al., 2018). Thus, the amygdala, particularly the BLA, appears to play a central yet complex role in social cognition that requires further elucidation.

Biobehavioral Patterns of Stress Reactivity

Social behavior as well as the functions of the social brain cannot be understood independently of the environments in which they operate. Social interactions often occur in contexts of acute *stress* (Box 1), where physiological as well as psychological stress responses may influence whether individuals respond competitively or cooperatively.

Traditionally, social behavior under acute stress has been explained through the lens of the *fight-or-flight* (Box 1) response. This response pattern was first described by Walter Cannon as a reflex-like, adaptive reaction of the organism to acute or perceived threats (Cannon, 1914, 1932; Cannon & De La Paz, 1911). Inspired by his observations that intense emotions, such as fear or anger, triggered adrenal gland activity and adrenaline release (Cannon & De La Paz, 1911), Cannon proposed that emotional arousal activates the *sympathetic adrenal medullary* (SAM) system, preparing the body for immediate action: either to confront the threat (*fight*) or to escape from it (*flight*; Cannon, 1914, 1932). The involved bodily changes, such as increased heart rate, blood pressure, and energy availability, are all organized to support the physical effort necessary for fight or flight, creating an integrated mind-body defense system (Cannon, 1914, 1932).

This model has since been used to explain antagonistic behavioral tendencies following acute stress, including heightened aggression and selfishness (e.g., Steinbeis et al., 2015). However, not all social stress responses are characterized by confrontation or avoidance. In fact, acute stress may also involve affiliative or prosocial behavior (e.g., Margittai et al., 2015; Stahlecker & Häusser, 2025), a response pattern that was first described in the *tend-and-befriend* theory (Box 1; Taylor et al., 2000).

The theory was introduced by Taylor et al. (2000) as a biobehavioral alternative to fight-or-flight and underscores the protective role of social relationships in regulating stress and supporting survival. It posits that under evolutionary pressures, especially in the context of caregiving, humans and other animals have developed alternative strategies to fighting or fleeing. Specifically, *tending* involves behaviors that protect and soothe offspring or close others, while *befriending* refers to forming and maintaining social alliances for mutual

protection and support (Taylor, 2006; Taylor et al., 2000). It highlights the central role of social relationships and prosocial behavior in behavioral stress responses.

Neurobiologically, tend-and-befriend responses are thought to be facilitated by the attachment-caregiving system, with oxytocin and opioids playing a central role (Taylor, 2006, 2012; Taylor et al., 2000). These pathways were proposed as analogous to the SAM system in fight-or-flight (Taylor, 2006, 2012; Taylor et al., 2000). Originally, the response pattern was argued to be female-specific, in part due to estrogen's oxytocin-enhancing effects (Taylor et al., 2000). However, later research challenged the idea that tend-and-befriend is exclusive to women (Geary & Flinn, 2002; Taylor, 2012). Studies have since shown that men also exhibit affiliative and prosocial responses to stress, such as increased generosity (e.g., Von Dawans et al., 2012). Thus, although the expression of prosocial tendencies following acute stress may vary to some degree by gender, the tendency to seek social affiliation under stress is a broadly human one.

Evidence on the effects of acute stress on social behavior is highly mixed. Much of the literature has been guided by the assumption that tend-and-befriend, and fight-or-flight tendencies are mutually exclusive. Within this framework, findings of increased prosociality after stress, especially toward socially close individuals, are typically interpreted as support for tend-and-befriend (Margittai et al., 2015; Tomova et al., 2017; Von Dawans et al., 2012, 2019). In contrast, findings of reduced prosociality are often taken as evidence for fight-or-flight (FeldmanHall et al., 2015; Steinbeis et al., 2015; Vinkers et al., 2013). Yet other studies report no robust changes at all (Passarelli & Buchanan, 2020; Potts et al., 2019; Veszteg et al., 2021). A recent meta-analysis reflects this heterogeneity, concluding that the impact of acute stress on social behavior is complex and remains difficult to characterize (Nitschke et al., 2022).

Given this heterogeneity, it is now widely acknowledged that acute stress effects on social behavior are more complex than dichotomies between tend-and-befriend and fight-or-flight would suggest (Faber & Häusser, 2022; Von Dawans et al., 2021). Current accounts, instead, propose that acute stress interacts with the demands of the social situation and individual characteristics, enabling an adaptive response that may take either affiliative or antagonistic forms (Faber & Häusser, 2022). A similar approach argues that tend-and-befriend and fight-or-flight are not fundamentally opposed, but rather represent complementary components of the acute stress response, each supported by partly distinct physiological systems (Margittai et al., 2018; Schweda et al., 2019).

Physiological Pathways of Stress Reactivity

Acute stress often refers to the physiological response to an actual or anticipated disruption of homeostasis – an equilibrium or steady state of physiological processes (Cannon, 1932; Chrousos, 2009; but see Box 1). This disruption may be caused by a variety of internal or external stimuli, so-called stressors, triggering a nuanced and complex cascade of physiological, neuroendocrine and behavioral adaptations that serve to restore the homeostatic state (Chrousos, 2009; De Kloet et al., 2005). The two central systems orchestrating this adaptation process are the SAM system and the *hypothalamic-pituitary-adrenal* (HPA) axis.

The SAM system is the fast-acting branch of the stress response. Upon stressor detection, the locus coeruleus increases noradrenaline release and a cascade of neuroendocrine responses is initiated via the sympathetic nervous system (Hermans et al., 2011, 2014; Ulrich-Lai & Herman, 2009). Sympathetic neurons in the spinal cord project through pre- and paravertebral ganglia to the adrenal medulla, which releases adrenaline and stimulates further noradrenaline release (Hermans et al., 2014; Ulrich-Lai & Herman, 2009). This response unfolds within seconds to minutes and leads to an increase in heart rate, blood pressure, and energy availability as well as increased arousal and vigilance, while non-essential vegetative functions such as digestion or reproduction are down-regulated (Chrousos & Gold, 1992; Joëls & Baram, 2009; Ulrich-Lai & Herman, 2009). The response of the SAM system is typically transient and abates by the time the stressor is resolved (Joëls & Baram, 2009).

In contrast, the HPA axis governs a slower, longer-lasting component of the stress response. Activation begins in the paraventricular nucleus of the hypothalamus, which releases corticotropin releasing hormone (CRH) and arginine vasopressin (AVP; Hermans et al., 2014; Ulrich-Lai & Herman, 2009). These hormones trigger the release of adrenocorticotropic hormone (ACTH) from the pituitary which then stimulates the adrenal cortex to release glucocorticoid hormones, i.e. cortisol (Ulrich-Lai & Herman, 2009). This affects immune responses and glucose metabolism, further amplifying energy mobilization and availability, and thus complementing and potentiating the SAM system reaction (Chrousos & Gold, 1992; Habib et al., 2001; Ulrich-Lai & Herman, 2009).

The HPA axis can conceptually be divided into early non-genomic and delayed genomic cortisol responses (De Kloet et al., 2005; Groeneweg et al., 2011; Hermans et al., 2014). Early effects occur within minutes even though it takes up to 30 minutes for cortisol to reach peak levels (De Kloet et al., 2005; Groeneweg et al., 2011). Genomic effects take much longer to develop and by then glucocorticoid levels typically have returned to baseline (De

Kloet et al., 2005; Groeneweg et al., 2011). These effects involve changes to gene transcription and are thought to be involved in terminating the stress response and promoting stress recovery (De Kloet et al., 2005; Hermans et al., 2011, 2014; Joëls & Baram, 2009). Importantly, the HPA axis is self-regulatory: cortisol levels exert negative feedback on the hypothalamus and pituitary, thereby dampening further CRH and ACTH release. This mechanism protects against excessive or prolonged glucocorticoid exposure, which can impair immune function, reproduction, and cognitive processes (Habib et al., 2001; Hermans et al., 2011).

While the SAM system is largely catecholamine-driven and the HPA axis glucocorticoid-driven, the stress response is more complex overall and involves interactions with additional neuromodulators, such as dopamine and serotonin (Joëls & Baram, 2009) as well as oxytocin (Groeneweg et al., 2011). Additionally, the two stress systems interact closely with each other (Chrousos & Gold, 1992). Glucocorticoids can potentiate catecholamine signaling and some cortisol effects are dependent on adrenergic activity (Groeneweg et al., 2011; Hermans et al., 2011). Thus, the acute stress response involves an intricate and flexible response across immediate and delayed timescales, with noradrenaline mostly driving immediate responses and cortisol being involved in both immediate and delayed responses.

Cortisol and Noradrenaline in Social Behavior

These temporal and functional dynamics of the stress systems have been argued to extend beyond physiology to social behavior. Specifically, cortisol has been proposed to facilitate tend-and-befriend responses, and noradrenaline has been associated more closely with fight-or-flight (Margittai et al., 2018; Schweda et al., 2019). Empirical support for this distinction is still limited. Nevertheless, cortisol has relatively consistently been linked to more affiliative and prosocial behaviors (Berger et al., 2016; Duque et al., 2022; Margittai et al., 2018; but see Strojny et al., 2024). For example, Margittai et al. (2018) demonstrated via pharmacological manipulation of cortisol and noradrenaline that participants in a social discounting task were more willing to share with socially close others under the isolated influence of cortisol, but this effect did not occur when both cortisol and noradrenaline were engaged. They interpreted their findings as indicating that cortisol supports tend-and-befriend tendencies and considered the fact that noradrenaline attenuated this effect as support for noradrenaline promoting fight-or-flight tendencies. Importantly, direct evidence linking noradrenaline to more antagonistic, or even aggressive tendencies is sparse (Haden & Scarpa, 2007; Nelson & Trainor, 2007; Takagishi et al., 2009). One reason is that many studies on the effects of stress on social behavior have focused exclusively on cortisol (e.g., Strojny et al.,

2024). Another reason is that experimental tasks often do not allow for explicitly harmful behavior, or conflate harmful behavior with helpful behavior, making it difficult to identify fight-or-flight-like responses. An exception is a study by Schweda et al. (2019), using the IPD-MD paradigm. They found no overall effect of stress on social behavior. However, they observed tentative evidence that cortisol was associated with prosociality (when controlling for testosterone), while increased heart rate, reflecting sympathetic activation, was related to more harmful tendencies. Together, these findings provide preliminary support for the idea that cortisol and noradrenaline promote distinct social behavioral tendencies, but conclusive evidence is still lacking.

Cortisol and Noradrenaline in the Brain

Importantly, cortisol and noradrenaline likely affect cognition and behavior through their effects on large-scale brain networks (Hermans et al., 2014). Stress modulates activity in areas of the default mode network, the salience network, and the executive control network, which subserve diverse cognitive functions and correspond to some regions of the social brain (Hermans et al., 2014; Van Oort et al., 2017). For example, the default network overlaps with mentalizing areas and has been implicated e.g., in emotion regulation (Stanley & Adolphs, 2013; Van Oort et al., 2017). The amygdala, a core region of the social perception network (Kennedy & Adolphs, 2012), is also involved in the salience network, which supports attentional focus and vigilance (Hermans et al., 2014; Kennedy & Adolphs, 2012). Lastly, the executive control network is associated with planning and goal-directed behavior and includes regions like the dlPFC (Hermans, 2014), which has been implicated in cooperative behavior (Hermans et al., 2014; Strang & Park, 2016).

During early stress responses, noradrenaline upregulates the salience network while both noradrenaline and potentially cortisol downregulate executive control, whereas in the aftermath of stress, this pattern is instead reversed (Arnsten, 2009; Hermans et al., 2011, 2014). This reflects a temporary shift of metabolic resources toward vigilance and away from goal-directed control during acute stress, which reverses during stress recovery (Hermans et al., 2014). In sum, acute stress seems to alter activity in brain networks that overlap with regions implicated in social cognition and behavior, which suggests a neural mechanism through which stress may modulate social behavior.

Experimental Induction of Stress

In controlled laboratory experiments, stress is typically induced using different stress paradigms. The gold standard is the Trier Social Stress Test (TSST; Kirschbaum et al., 1993), which involves socio-evaluative aspects and is considered a psychosocial stressor. Here, stress is induced by having participants prepare and then perform a mock job interview in front of a jury panel and have them do mental arithmetic tasks. The TSST has been shown to reliably activate physiological stress responses alongside subjective feelings of stress and anxiety (Kirschbaum et al., 1993). The TSST is considered a relatively natural stressor, but it does not allow for causal conclusions on the effects of stress neuromodulators. Hence, another approach is to simulate the physiological stress response using pharmacological agents. This involves administering drugs that enhance or suppress cortisol and noradrenaline release (Von Dawans et al., 2021). Hydrocortisone, for example, is a synthetic form of cortisol and induces glucocorticoid activity, while yohimbine is an alpha-2 adrenergic receptor antagonist that promotes the release of noradrenaline. Importantly, while pharmacological approaches allow for causal inferences, they are unable to replicate the full complexity of naturally occurring stress (see "*Limitations and Future Directions"*).

Research Questions

A great deal has already been learned about social behavior and its neural basis. Above all, it is evident that social behavior is complex and multifaceted, shaped by various internal and external factors, such as stress. This complexity is mirrored in the heterogeneity of research findings, and many questions remain about the neural underpinnings of social behavior, and the specific role stress plays in this context.

This dissertation seeks to contribute to resolving some of the seemingly contradictory findings. The aim is to advance our understanding of how stress neuromodulators and neural substrates shape social preferences and behavior. Additionally, a core assumption in models of social preferences is GARP-based choice consistency, which rests on the idea that preferences are stable. Stress effects on social behavior, however, challenge the notion that preferences remain stable despite dynamic changes in neuromodulator activity. Thus, taking a more methodological perspective, a second aim of this dissertation is to examine the robustness of choice consistency across such conditions, and whether it can be reliably measured to support psychologically meaningful conclusions about (social) decision-making.

In study 1, we examined the role of cortisol and noradrenaline in generosity toward socially close and distant others, as well as in prosocial choice consistency. Using a psychopharmacological approach with hydrocortisone and yohimbine, we repeatedly measured generosity in an adapted dictator game that enabled GARP-based analyses of choice consistency across fluctuating neuromodulator levels. Previous work has shown that within specific phases of the stress response, such as the early or late stage, the assumption of choice consistency holds (Cettolin et al., 2020; Nitsch et al., 2021). Here, we tested whether dynamic changes in neuromodulator activity reduce the consistency of prosocial choices. For this, we calculated consistency across all decisions made throughout the experiment, aggregating across pre- and post-administration timepoints.

In study 2, the focus was then broadened to consider the psychometric properties of these GARP-based consistency measures. Although they are often treated as indicators of decision-making quality (e.g., Choi et al., 2014; Drichoutis & Nayga, 2020), their theoretical grounding in psychology is limited. We therefore investigated more systematically whether they are reliable across different task paradigms and over time, to test whether they can support robust conclusions and carry psychological meaning beyond their meaning in economic theory.

Next, in study 3, we examined the interaction between stress neuromodulators, social context, and situational demands using an intergroup conflict paradigm, where participants faced potential out-group threat. Creating such a threatening context likely increases the salience of competitive behavior (Halevy et al., 2010). However, research directly testing stress effects in intergroup contexts is scarce, with only one prior study addressing this question (Schweda et al., 2019). Building on this gap, we employed the same psychopharmacological approach as in study 1 to test how cortisol and noradrenaline influence behavior in the IPD-MD. Specifically, we hypothesized that cortisol would promote cooperative behavior consistent with tend-and-befriend, whereas noradrenaline would promote antagonistic, competitive behavior in line with fight-or-flight.

Finally, beyond neuroendocrine mechanisms, it is equally important to understand the neural substrates of social preferences to obtain a more comprehensive picture of social behavior and potential stress effects. The amygdala and the BLA, are particularly interesting in this context, since they are known to be modulated by acute stress (Hermans et al., 2014). However, the role of the BLA in social behavior is complicated. Evidence suggests that impaired BLA function is associated with both reduced and increased prosocial tendencies. In study 4, we therefore investigated the role of the BLA in social decision-making, using a sample of participants with highly selective BLA lesions.

Beyond their theoretical importance, these questions also carry societal relevance. In an age marked by increasing intergroup tension and political polarization (Raleigh & Katayoun, 2023; United Nations, 2020, 2023a, 2023b), understanding how decisions that affect others are shaped by neurobiological mechanisms and external factors such as stress may offer critical insights into the dynamics of social cohesion and conflict.

Summary of Research Projects

Study 1 – Stress Neuromodulators and Social Choice Consistency

Lüpken, L.M.*, Schnitzler, A., Kalenscher, T., currently in revision at Hormones & Behavior. No Effect of Glucocorticoid and Noradrenergic Activity on Consistency in Prosocial Choice.
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Please note that this section summarizes my own research, which is why some parts of the text closely mirror the original publication. The summary also includes some of the original figures for illustration. The original article is available in the appendix.

Introduction

Stress effects on social behavior are often contradictory, which may reflect distinct effects of stress neuromodulators. Cortisol has been linked to prosocial behavior (Duque et al., 2022; Margittai et al., 2018; Schweda et al., 2019), and noradrenaline to more antagonistic tendencies (Haden & Scarpa, 2007; Nelson & Trainor, 2007; Schweda et al., 2019). Pharmacological studies show that cortisol can increase generosity, but this effect is offset by noradrenaline (Dashti et al., 2025; Margittai et al., 2018). Thus, stress may bias social preferences toward prosocial or antagonistic tendencies depending on the prevailing neuromodulatory profile.

Social preferences, like all preferences, cannot be observed directly but must be inferred from choice behavior. This inference critically depends on stable preferences and internal choice consistency, formalized by the GARP (Afriat, 1967; Houthakker, 1950; Samuelson, 1938). Meaningful estimation of (social) preferences is possible only if choices adhere to GARP.

Previous research shows that choices often remain consistent even under challenging conditions such as sleep deprivation, alcohol consumption, or acute stress (Burghart et al., 2013; Castillo et al., 2017; Cettolin et al., 2020; Nitsch et al., 2021). However, these studies examined behavior *within* a specific internal state (e.g., a specific time window of the stress response; Nitsch et al., 2021). It remains unclear whether choice consistency also holds *across* dynamically shifting internal states, such as the time-dependent cortisol and noradrenaline responses to acute stress (Hermans et al., 2014; Joëls & Baram, 2009). This is a crucial gap: if preferences systematically change with neurohormonal states – as previous research suggests (Dashti et al., 2025; Margittai et al., 2018) – choices may be consistent within each state but inconsistent when aggregated, e.g., if someone acts selfishly at baseline but generously at cortisol peak. Such state-dependent changes would mislead economic preference modeling and undermine the core assumption of choice consistency in economic theories of (social) decision-making.

To address this, we pharmacologically manipulated cortisol and noradrenaline action in a placebo-controlled double-blind psychopharmacological study. This design allowed us to test whether choice consistency is preserved across dynamically fluctuating neurohormonal states, or whether systematic changes in preferences reduce overall consistency. We hypothesized that cortisol would increase generosity, whereas noradrenaline would counteract this effect, thereby reducing choice consistency when choices are aggregated across time.

In sum, we contribute to economic theory by testing the robustness of the choice consistency assumption under dynamic internal states and extend the literature on how stress neuromodulators shape social preferences and behavior.

Methods

We conducted a double-blind, placebo-controlled psychopharmacological study with a final sample of 119 mixed-gender healthy participants to examine the differential effects of cortisol and noradrenaline on generosity and GARP-based choice consistency. Participants were pseudo-randomly assigned to one of four drug conditions: hydrocortisone (H; n = 30), yohimbine (Y; n = 29), hydrocortisone + yohimbine (H+Y; n = 31), or placebo (P; n = 29). Salivary cortisol levels and salivary alpha-amylase activity (as a proxy for noradrenergic activity; sAA; Nater & Rohleder, 2009) as well as heart rate and subjective stress and mood ratings were assessed repeatedly throughout the experiment.

To assess changes in generosity and test whether choice consistency is maintained across changing neurohormonal states, participants completed an incentivized modified dictator game adapted from Andreoni & Miller (2002) at four time points relative to drug intake: -20 mins (block 0 / baseline), + 25 mins (block 1), + 60 mins (block 2), + 190 mins (block 3). In each trial, participants allocated a monetary budget between themselves and either a best friend or a stranger (20 unique trials per measurement and recipient type). We varied budget constraints (5 – 20 EUR) and prices of giving or keeping money (1 – 3 EUR) across trials to allow for GARP-based analyses. Prices were like an exchange rate: for example, at a price of 1 EUR for keeping and 3 EUR for giving money, participants received the full amount they allocated to themselves, but the recipient received only one-third of the amount allocated to them. The order of trials was pseudorandomized across the session.

Prosocial decision-making was quantified as the average proportion of the budget participants shared with the other person ("*share score*"), calculated separately for each recipient type (friend vs. stranger) in each measurement block. Choice consistency was assessed using the CCEI (Afriat, 1972, 1973), calculated across all choice made in the experiment, i.e., across all blocks. The CCEI measures how closely choices align with GARP: it identifies the most severe GARP violation and determines the minimum budget reduction required to eliminate all violations. Scores range from 0 to 1, with higher values indicating greater consistency.

We used a mixed-factorial Bayesian analysis of variance (ANOVA) to test for drug and social distance effects on share scores across blocks and on CCEI scores, using uninformative

default priors (Rouder et al., 2012). Full methodological and analytical details are reported in the original paper in the appendix.

Results

Cortisol levels increased over time in the hydrocortisone and hydrocortisone + yohimbine groups but remained stable in the yohimbine and placebo groups. For sAA, we found no evidence of a drug x block interaction (Figure 1). Instead, sAA was elevated in blocks 1 and 3 across all participants. Exploratory analyses of area under the curve with respect to increase (AUC_I; Pruessner et al., 2003) indicated clear increases in sAA activity in the yohimbine and hydrocortisone + yohimbine groups ($AUC_I > 0$), but not in the hydrocortisone or placebo groups ($AUC_I \not> 0$). This suggests stronger sAA responses in participants who received yohimbine relative to a generally elevated response across all participants. The absence of a clear interaction effect is not surprising, as sAA is an indirect and noisy marker of central noradrenergic activity, correlating only weakly with serum noradrenaline (Nater et al., 2006; Rohleder & Nater, 2009). General autonomic activity, such as arousal during drug intake, may also have masked drug-specific effects on sAA activity.

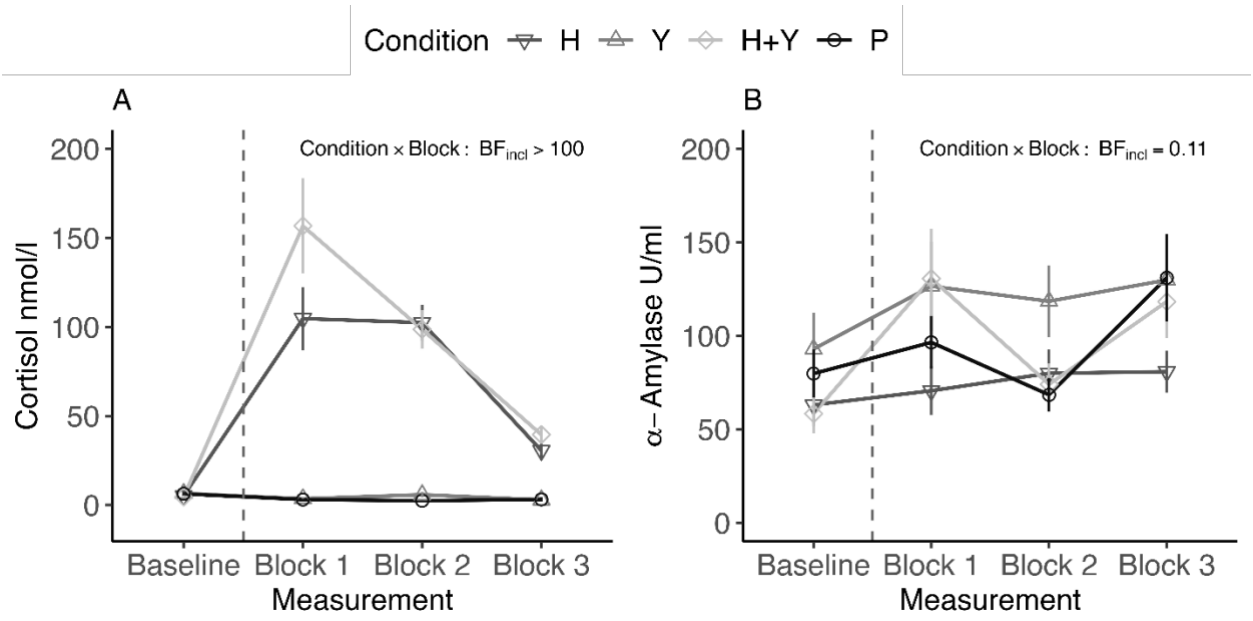

Figure 1. Manipulation check. (A) Mean salivary cortisol levels (± standard error of the mean, SEM), and (B) mean sAA activity (± SEM) across measurement blocks by drug condition. The vertical dashed line indicates drug administration (after baseline and before block 1). Blocks correspond to approximate minutes post-intake: Baseline ~ +24 min, Block 2 ~ +59 min, Block 3 ~ +180 min. Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone + yohimbine, P = placebo, nmol/L = nanomoles per liter, U/ml = units per milliliter.

We found evidence against effects of drug condition and its interactions with block, social distance, or both, as well as against a block × social distance interaction on share scores.

Instead, there was evidence for main effects of social distance and block: participants shared more with best friends than with strangers and sharing declined over time (Figure 2). For choice consistency, we found evidence against main effects of drug or social distance, and against a drug x social distance interaction on CCEI scores (Figure 2), indicating they were unaffected by the pharmacological manipulation. Full results are reported in the original paper in the appendix.

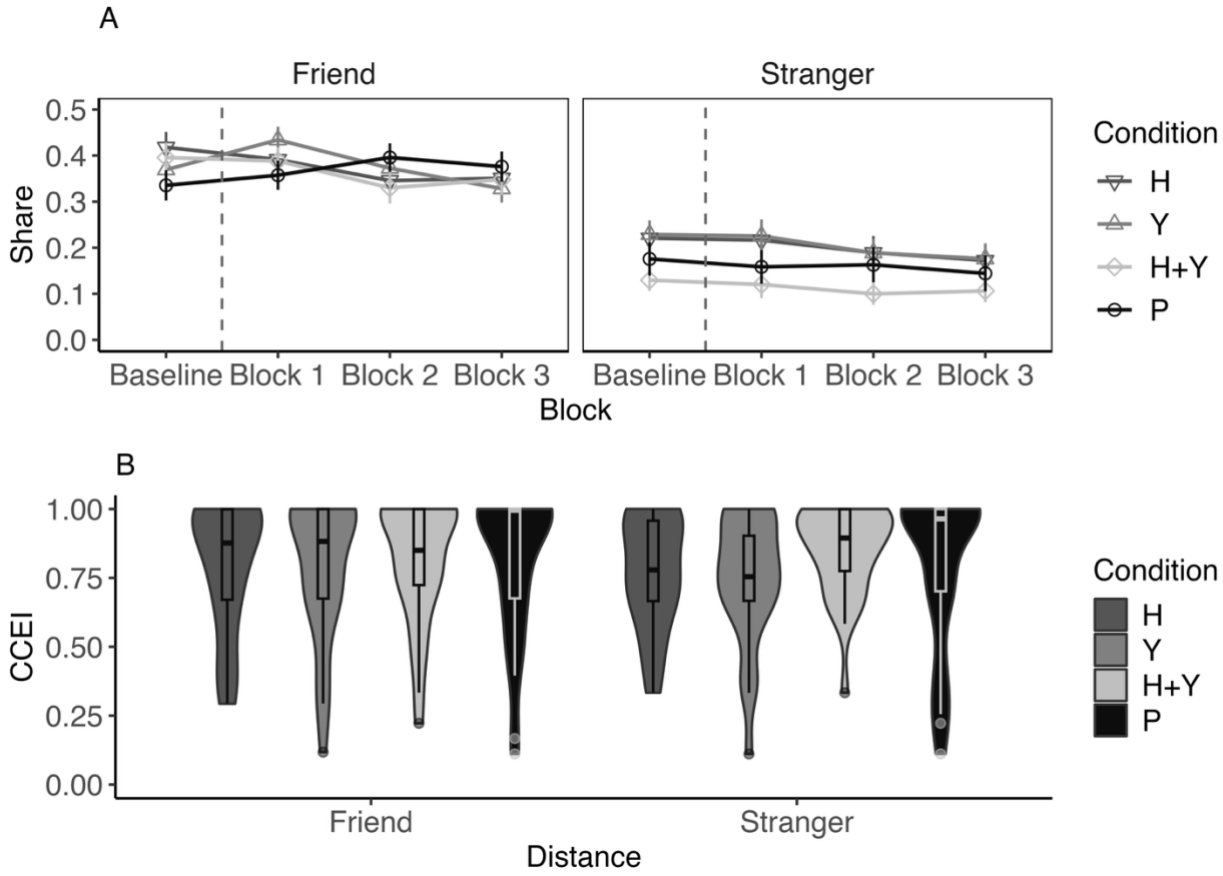

Figure 2. Prosocial decision-making and choice consistency. (A) Mean share score (± SEM) across measurement blocks by drug condition, separately for recipient type (friend or stranger). The vertical dashed line indicates drug administration (after baseline and before block 1). Blocks correspond to approximate minutes post-intake: Block 1 ~ +25 min, Block 2 ~ +60 min, Block 3 ~ +190 min. (B) Mean CCEI score (± SEM) by drug condition, separately for recipient type (friend or stranger). Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone and yohimbine combined, P = placebo.

Discussion

Contrary to our hypotheses, neither sharing behavior nor choice consistency were affected by hydrocortisone, yohimbine, or their combination. Across all drug conditions, participants shared more with friends than strangers, replicating the social discounting phenomenon (Jones & Rachlin, 2006), but they shared less over time.

These results extend prior work on the robustness of choice consistency during altered cognitive or neurohormonal states (Burghart et al., 2013; Castillo et al., 2017; Cettolin et al., 2020; Nitsch et al., 2021). Importantly, whereas these studies examined within-state consistency, we show that consistency is also preserved across transitions in neurohormonal states. This suggests that even across dynamic internal states, social preferences remain sufficiently stable to satisfy the core assumption of preference-based choice models, implying that it is not necessary to account for transient but unobservable stress states in economic analyses of choices and preferences.

We did not, however, replicate earlier findings that hydrocortisone increases generosity toward close others and yohimbine offsets this effect (Margittai et al., 2018). Differences in task design may explain this discrepancy: our paradigm introduced transaction costs (prices of giving or keeping money), repeated within-subject measurements, and budget lines as response scales. These features may have increased cognitive demands or masked subtle motivational shifts observed in simpler tasks, in line with Nitschke et al. (2022).

Recent findings suggest that stress does not uniformly increase or decrease prosocial behavior; instead, its effects depend on the specific needs triggered and the contextual stimuli present (Dashti et al., 2025; Faber & Häusser, 2022). Thus, while stress neuromodulators can shape social behavior in some contexts, their effects are not universal and may be absent in others, depending on the structure of the choice environment and social setting.

Overall, we show that standard economic modelling and preference analyses are robust to dynamically changing neurohormonal states, and that behavioral effects of stress neuromodulators are more context-dependent than previously assumed.

In the next study, we aimed to more broadly evaluate the psychometric properties of choice consistency measures, given their limited theoretical grounding in psychology, a point made particularly relevant by the null effects observed here.

Study 2 – Reliability of Choice Consistency

Nitsch, F.J.*, Lüpken, L.M., Lüschow, N., Kalenscher, T., 2022. On the reliability of individual economic rationality measurements. Proc. Natl. Acad. Sci. 119, e2202070119. https://doi.org/10.1073/pnas.2202070119

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Please note that this section summarizes my own research, which is why some parts of the text closely mirror the original publication. The summary also includes some of the original figures for illustration. The original article is available in the appendix.

Introduction

Economic rationality is commonly defined as consistent choice behavior that aligns with a decision maker's preferences and budget. Any such set of choices can be reconciled with a structure of wants, cost efficiency, and transitivity (Afriat, 1973). Formally, GARP requires that if someone incurs costs to choose one option over another, they should never choose the latter when both are equally affordable (Houthakker, 1950; Samuelson, 1938; Varian, 1982). While rational choice theory is theoretically elegant and widely applied, it has long faced descriptive, predictive, and normative criticism (Harless & Camerer, 1994; Rieskamp et al., 2006; Tversky, 1975). Nevertheless, psychology, behavioral economics, and neuroeconomics try to identify (neuro)psychological correlates of economic rationality, often interpreting it as a psychological trait (Nitsch & Kalenscher, 2020, 2021), an extension beyond the original economic framework (Varian, 2006). Yet, the validity of such measures has rarely been scrutinized, perhaps due to the strong economic-theoretical foundation. Thus, here, we rigorously test the reliability of these GARP-based rationality measures across multiple datasets and study contexts.

Methods

Across three studies (studies 2a, 2b, and 2c) as well as analyses of published datasets, we assessed the reliability of contemporary measures of economic rationality, i.e. choice consistency, based on the GARP (Afriat, 1967; Houthakker, 1950). We focused on the two most prominent indices: the CCEI (Afriat, 1972) and the HMI (Heufer & Hjertstrand, 2015; Houtman & Maks, 1985). The HMI, like the CCEI measures how closely choices align with GARP and reflects the largest subset of choices that satisfies GARP.

Study 2a included 53 participants from the control group of a larger experiment. Participants completed three different versions of a modified dictator game (diagram, bundles, and slider task; Andreoni & Miller, 2002; Choi et al., 2014; Harbaugh et al., 2001). Each task was administered twice within the same session, separated by a filler task. In each task and measurement, participants made 20 hypothetical decisions, allocating a budget between themselves and their best friend. Both the budget (2 – 10 EUR) and the prices of keeping and giving money (1 – 3 EUR; akin to exchange rates) varied across decisions, to allow for GARP-based analyses. We included attention check trials for each task and measurement and excluded data from a measurement if the check was failed. The task versions varied in complexity and

visual presentation (see below and Figure 3), allowing us to assess reliability both within (test-retest reliability) and across formats (inter-method reliability).

In the diagram task (Choi et al., 2014), participants made their choice using a cartesian coordinate display that depicted both the budget and the prices (represented by the steepness of the budget line). This interface allowed for a continuous allocation of the budget: participants chose a point on the diagonal budget line, reflecting an allocation of money between themselves and their best friend, with the corresponding payouts displayed in an info box. In the bundles task (Harbaugh et al., 2001), the budget line was divided into discrete points, presented as five discrete choice options (bundles), from which participants chose the one they liked best. In the slider task (Garagnani, 2020), participants chose a point on a horizontal slider, again reflecting an allocation of money between them and their best friend. Like the diagram task, this format allowed for a continuous allocation of the budget but concealed the prices. The effective payouts were again shown in an info box (Figure 3).

Study 2b was preregistered (https://osf.io/wfd4z/) and aimed to replicate and extend study 2a in a larger sample (N = 148) with double the number of trials (40 instead of 20 per task). The filler task was removed. Participants again completed all three tasks (diagram, bundles, and slider task) twice, in randomized order within each measurement. Fatigue levels were monitored once after each measurement to ensure tolerability of the longer format.

Study 2c followed up with a subset of study 2b participants (~5 months later, N = 97) to replicate findings in participants already familiar with the tasks. We aimed to examine longer-term test–retest reliability, and to test whether low reliability was driven by mistake choices. Compared with study 2b, only the diagram task was administered (2 × 40 trials). In addition, after completing the task twice, participants were also given the opportunity to revise a random subset of 10 prior decisions (following Breig & Feldman, 2021, Figure 3). For each potential revision, the original choice was first displayed as a reminder, after which participants could redo their choice. To assess long-term reliability, we collapsed the 2 x 40 trials of studies 2b and 2c each.

To test for the reliability of both the CCEI and the HMI, we calculated intraclass correlation coefficients (ICC) of type consistency to assess both inter-method (across task versions) and test-retest reliability (within task versions, across measurements). Following established guidelines, we interpreted ICCs < 0.50 as poor, 0.50–0.75 as moderate, 0.75–0.90 as good, and > 0.90 as excellent (Koo & Li, 2016). Additionally, to assess the reliability of contemporary rationality measurements more generally, we reanalyzed five published datasets, applying either test–retest or split-half reliability depending on whether the original dataset

included multiple or single measurements: Choi et al. (2007; C07), Choi et al. (2014; C14), Kurtz-David et al. (2019; K19), Nitsch et al., (2021; N21), and Ahn et al. (2014; A14).

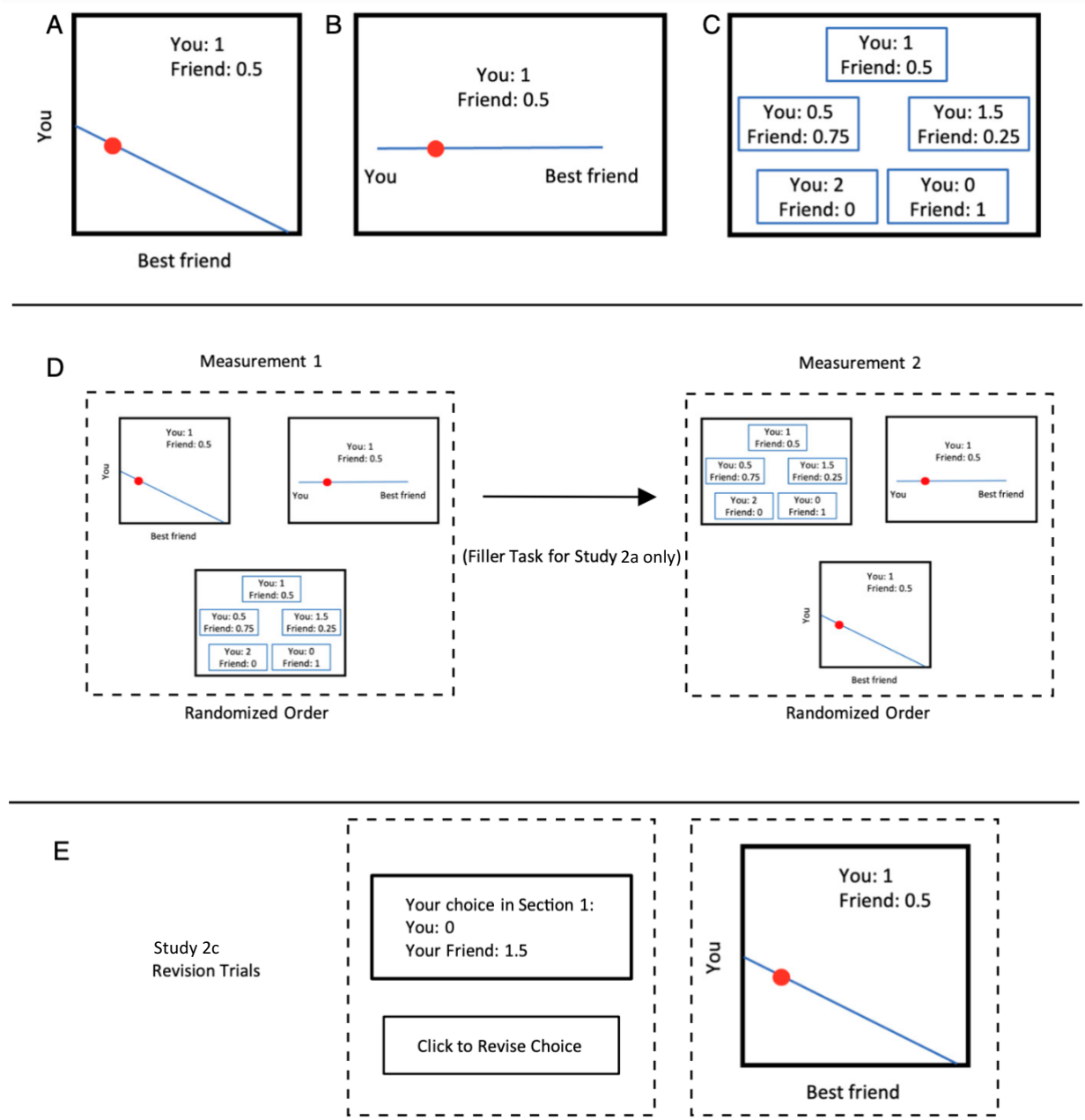

Figure 3. Task versions used to measure rationality. We manipulated the way the decision problem was presented in three task versions: (A) diagram, (B) slider, and (C) bundles. (D) Experimental structure of studies 2a and 2b. All task version blocks were presented in randomized order for two measurements each. (E) Example trial of the choice revisions in study 2c. Participants first saw their prior choice and then had the opportunity to either remake or revise that decision.

Finally, in an exploratory analysis, we tested whether low reliability of the CCEI and HMI was driven by measurement error or by small true differences between individuals. To estimate measurement error, we calculated within-subject coefficients of variation (WSCV)

from repeated measures for each task; lower WSCV values indicate lower measurement error (Quan & Shih, 1996). Full methodological and analytical details are reported in the original paper in the appendix.

Results

Overall, across the three studies and the published datasets, neither the CCEI nor the HMI exhibited good or excellent reliability (see Figure 4). Notably, in all three studies the number and configuration of trials were sufficient: participants displayed significantly higher rationality than random choosers (Bronars, 1987).

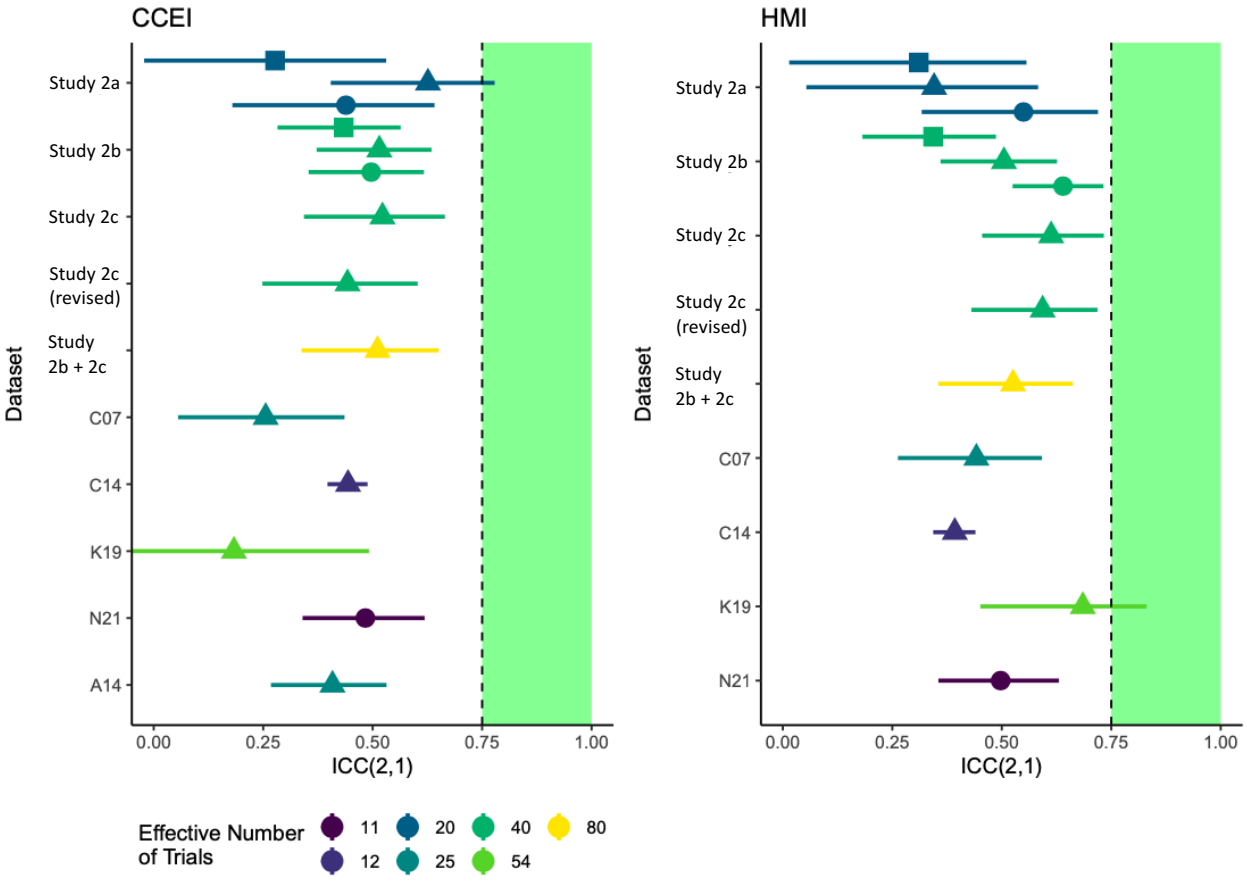

Figure 4. Test-retest and split-half reliability of CCEI and HMI. Depicted are the ICC estimates and 95% confidence intervals of the test-retest/split-half reliability of CCEI (Left) and HMI (Right) across all eight datasets. Symbols indicate which task version was used: triangles indicate the diagram task, circles indicate the bundles task, and rectangles indicate the slider task. The dashed vertical line and subsequent green area indicate the range of good reliability according to common standards. The effective number of trials is the number of trials per measurement (test-retest reliability) or split (split-half reliability).

In studies 2a and 2b, inter-method reliability across task versions was poor for both CCEI and HMI at both measurements. Test-retest reliability varied: the CCEI in the diagram task (studies 2a and 2b) and the HMI in the diagram task (study 2b) and bundles task (studies

2a and 2b) reached moderate levels, whereas reliability was poor in all other cases. Thus, neither CCEI nor HMI reached good (i.e., sufficient) reliability.

In study 2c, we again found only moderate, and thus insufficient, reliability for both indices in the diagram task (the only task version included in this study). Long-term reliability was comparable to short-term reliability, with both indices reaching only moderate levels. Interestingly, allowing participants to revise a subset of prior choices did not improve either rationality or test–retest reliability.

Analyses of published datasets showed a similar pattern. For the CCEI, split-half or test–retest reliability was poor in four of five datasets and moderate in one; for the HMI, it was poor in three of four datasets and moderate in one. Thus, low reliability is not unique to our study designs but appears to be a broader issue in the field.

Finally, our exploratory analysis of WSCV indicated that when measurements included at least 20 trials, WSCV values were relatively small, suggesting low measurement error.

Discussion

We showed that the psychometric reliability of widely used behavioral measures of choice consistency, specifically the CCEI and HMI, is generally moderate to poor across choice domains, task structures, study contexts, populations, sample sizes, and measurement designs. These findings, replicated across three original studies and five published datasets, suggest that current revealed preference-based methods are limited in distinguishing between individuals, in line with recent work (Enkavi et al., 2019; Pedroni et al., 2017; Rakow et al., 2020).

Importantly, our analyses indicate that this limitation is not primarily due to high measurement error: response revision did not improve reliability, and WSCV was sufficiently low with at least 20 trials. Instead, the data suggest a lack of true individual differences. Most participants behaved highly consistent, and individual scores predicted future behavior less well than the population mean.

This has direct implications for research attempting to link choice consistency scores to psychological or sociodemographic variables. We caution against interpreting revealed preference consistency as a stable individual trait without stronger evidence of reliability and validity (Flake & Fried, 2020). More broadly, these results raise doubts about the validity of economic choice consistency as a psychological construct, which lacks a clear theoretical grounding in psychology, despite its use as a proxy for decision quality and cognitive function (Burghart et al., 2013; Choi et al., 2014; Chung et al., 2017; Nitsch et al., 2021).

Practical limitations, such as the number of trials, may constrain reliability improvements. While longer tasks may reduce measurement error, they risk participant fatigue and potential biases in decision strategy. Moreover, our inability to replicate improved choice consistency through choice revision (Breig & Feldman, 2021) suggests that such interventions may depend strongly on task design. A different design may, thus, have the potential to improve choice consistency and reliability.

Overall, the reliability of individual-level choice consistency measurements based on revealed preferences should not be assumed. Even under optimized conditions, reliability remains modest, raising concerns about their suitability for individual differences research.

The low reliability of choice consistency measures cautions against overinterpreting the null effect on social preference stability in study 1 (Hedge et al., 2018; Karvelis & Diaconescu, 2025). More broadly, the results so far suggest that stress neuromodulators may not exert uniform effects on social behavior but instead act in ways that depend on the specific social context and situational demands (Faber & Häusser, 2022; Nitschke et al., 2022). Intergroup conflict and competition may represent such a context: when individuals are confronted with potential out-group threat, decisions about cooperation and hostility become particularly salient (Halevy et al., 2010). In the next study, we therefore examined how cortisol and noradrenaline influence behavior in intergroup conflict settings.

Study 3 – Stress Neuromodulators and Intergroup Conflict

Dashti, D.[1], Lüpken, L.M.[*1], Seidisarouei, M., Forbes, P.A., Schnitzler, A., Kalenscher, T., 2025. Dissociable Glucocorticoid and Noradrenergic Effects on Parochial Cooperation and Competition in Intergroup Conflict. Proc. Natl. Acad. Sci. 122(29), e2502257122. https://doi.org/10.1073/pnas.2502257122

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Please note that this section summarizes my own research, which is why some parts of the text closely mirror the original publication. The summary also includes some of the original figures for illustration. The original article is available in the appendix.

Introduction

Stress changes social behavior, yet its effects remain contradictory. Classic accounts emphasized antagonistic "*fight-or-flight*" responses (Cannon, 1932), supported by evidence of stress-induced violence, selfishness, reduced trust, and competitiveness (e.g., Bendahan et al., 2017; Klaw et al., 2016; Potts et al., 2019; Vinkers et al., 2013; Zhang et al., 2021). In contrast, more recent research provides evidence for a "*tend-and-befriend*" response (Taylor et al., 2000), characterized by increased generosity and prosociality (e.g., Margittai et al., 2015, 2018; Singer et al., 2017; Von Dawans et al., 2012; Zhen et al., 2021). Thus, while stress clearly affects social behavior, it remains unclear whether it promotes antagonistic or affiliative responses (Nitschke et al., 2022).

These divergent effects may reflect dissociable stress pathways: the SAM system, driven by noradrenaline, has been linked to more aggressive and competitive responses (Haden & Scarpa, 2007; Margittai et al., 2018; Miczek & Fish, 2005; Nelson & Trainor, 2007), while the HPA axis, via cortisol, has been implicated in prosocial and affiliative behavior (Berger et al., 2016; Duque et al., 2022; Margittai et al., 2018; Schweda et al., 2019), particularly toward socially close others (Margittai et al., 2015, 2018). Whether an individual prioritizes cooperation or adopts more competitive strategies also depends on group membership (De Dreu et al., 2020). For example, studies on combatants show extremely stressful experiences may heighten both in-group bonding and aggression against out-groups (Whitehouse et al., 2014), a phenomenon termed "*parochial competition*" (Bernhard et al., 2006; De Dreu et al., 2020).

Based on this, we hypothesized that cortisol promotes parochial cooperation (cooperation toward the in-group), whereas noradrenaline fosters parochial competition (in-group support coupled with hostility toward out-groups).

Methods

We conducted a double-blind, placebo-controlled psychopharmacological study to examine the differential effects of cortisol and noradrenaline on parochial cooperation and competition. Ninety mixed-gender participants were pseudo randomly assigned to one of four drug conditions: hydrocortisone (n = 24), yohimbine (n = 22), hydrocortisone + yohimbine (n = 20), or placebo (n = 24). Stress neuromodulator activity was assessed repeatedly via salivary cortisol levels and sAA activity (as a proxy for noradrenergic activity; Nater & Rohleder,

2009), and heart rate and subjective stress ratings were recorded repeatedly throughout the experiment.

Following drug administration and a 60-min break, participants completed an adapted version of the IPD-MD (Halevy et al., 2008), which measures both cooperative behavior toward the in-group (parochial cooperation) and hostile behavior toward the out-group (parochial competition; De Dreu et al., 2020). Participants were assigned to a three-member group (in-group) and played against three opposing out-groups. In each round, they decided how to allocate a monetary endowment (10 EUR, or less; see below) across three pools: [1] the "*keep pool*", where allocations were retained by the participant; [2] the "*within-group pool*", where each in-group member, including the participant, received half of the allocation (parochial cooperation); and [3] the "*between-group pool*", which produced the same in-group benefit, but additionally, deducted half of the allocation from each out-group member's payoff (parochial competition; Figure 5).

Importantly, we manipulated initial aggression by the out-group across the three rounds (none, moderate, or strong aggression). Before making their decision, participants were shown how much money the out-group had deducted from them and their in-group members (0, 2, or 5 EUR), which reduced their endowment accordingly (10, 8, or 5 EUR). The order of rounds was pseudorandomized, and participants were informed that one round would be randomly selected at the end, with its outcome added to their final payoff.

Behavioral data were analyzed using two linear mixed-effects models on the percentage of budget allocated to the within-group pool and the between-group pool. Allocations to the keep pool were excluded from analysis to ensure that the remaining dependent variables were independent of each other. The models included "*drug condition*" and "*aggression by the out-group*" as predictors. Control analyses and robustness checks confirmed that results were not driven by demographic, hormonal, or affective confounds. Additionally, when considering "*gender*" as an additional predictor, we found no main or interaction effects on any of the outcome variables. Changes in biomarkers (cortisol, and sAA) were assessed in separate ANOVAs on the AUC_I (Pruessner et al., 2003), with the factors "yohimbine" (yes vs. no) and "hydrocortisone" (yes vs. no). Full methodological and analytical details are reported in the original paper in the appendix.

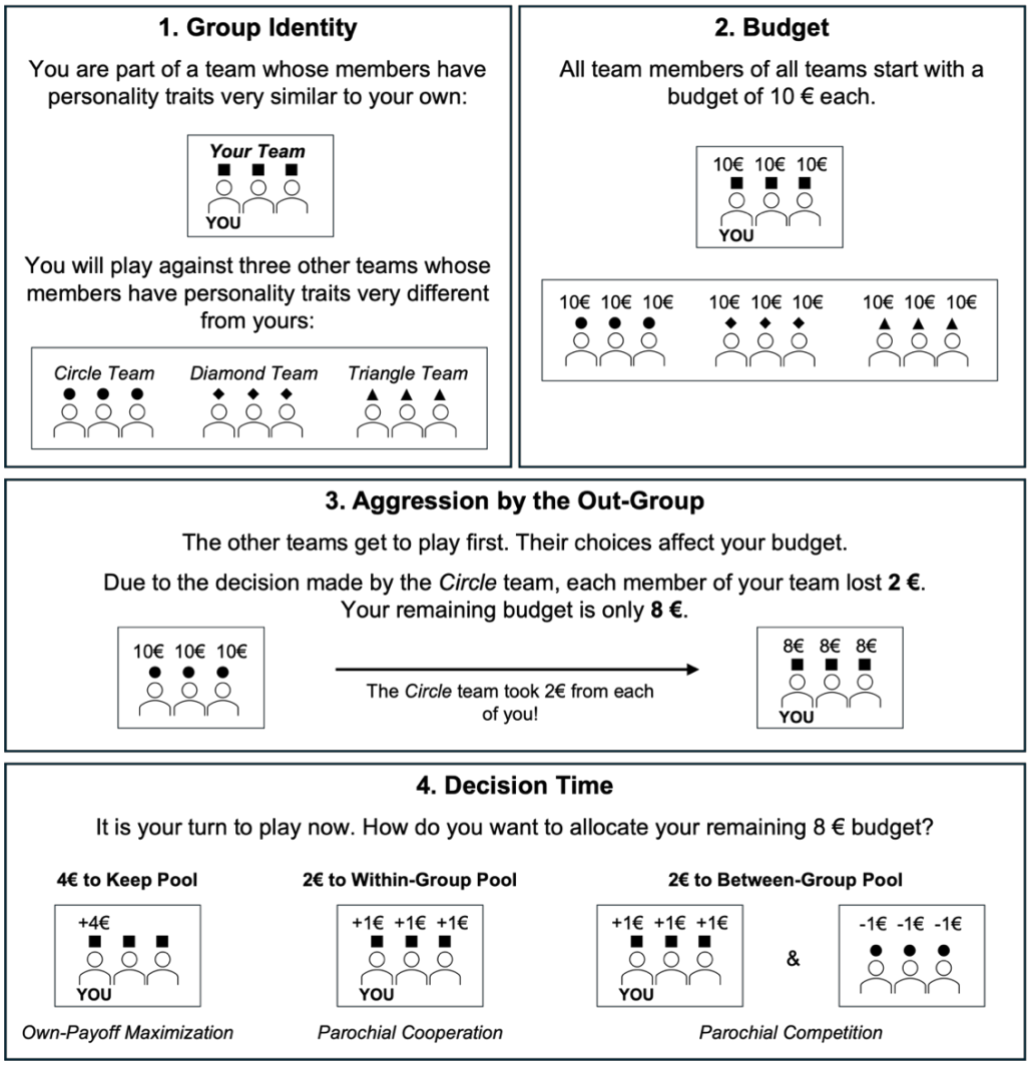

Figure 5. Logic and example trial of the IPD-MD. Each participant was first assigned to a team (panel 1) and told that they would have a budget of 10€ (panel 2). Next, each participant learned whether, and how much money, the out-group (here: the circle team) had deducted from them and the other in-group members (panel 3). They then allocated their remaining budget across the three options (panel 4).

Results

Yohimbine and hydrocortisone effectively manipulated noradrenergic and glucocorticoid activity: yohimbine significantly increased the AUC_I of sAA, and hydrocortisone significantly increased the AUC_I of cortisol. No interaction between yohimbine and hydrocortisone was observed for either measure. These results confirm successful manipulation of activity of the two neurobiological stress systems.

Participants who received hydrocortisone allocated significantly more money to the within-group pool compared to those in the placebo group, indicating that cortisol enhanced parochial cooperation. This effect was not observed when hydrocortisone was combined with

yohimbine, nor with yohimbine alone. Additionally, higher levels of out-group aggression reduced within-group pool allocations (Figure 6).

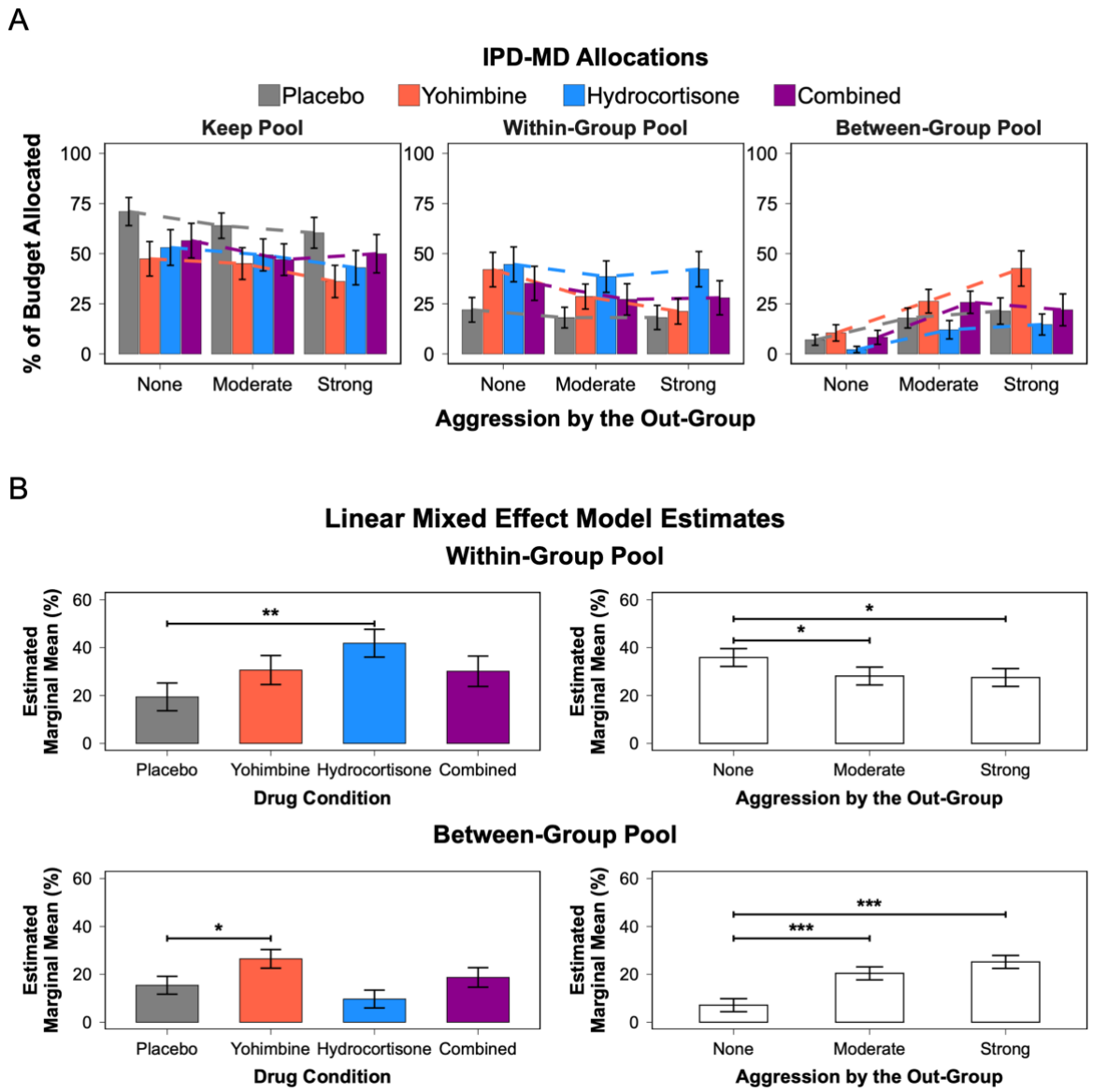

Figure 6. Hydrocortisone and yohimbine differentially affect parochial cooperation and competition. (A) Mean percentage (± SEM) of budget allocated to keep-, within-group and between-group pools in the IPD-MD at different levels of aggression by the out-group, shown separately for the four drug conditions. (B) Estimated marginal means (± SEM) of allocations to the within-group and between-group pool shown separately for the four drug conditions and levels of aggression by the out-group.
* $p < .05$, ** $p < .01$ and *** $p < .001$.

Participants who received yohimbine allocated significantly more to the between-group pool compared to those in the placebo group, suggesting that increased noradrenergic activity enhanced parochial competition, i.e., cooperating with the in-group while harming the out-group. This effect was not observed when yohimbine was combined with hydrocortisone, nor with hydrocortisone alone. Additionally, participants responded to increasing levels of out-

group aggression with higher between-group allocations, consistent with a retaliatory behavioral pattern (Figure 6). Full results are reported in the original paper in the appendix.

Discussion

Here, we showed that, consistent with our hypotheses, the stress neuromodulators cortisol and noradrenaline affect intergroup social behavior in distinct ways: cortisol promotes parochial cooperation, i.e., generosity toward the in-group, while noradrenaline promotes parochial competition, i.e., favoring the in-group while harming the out-group. Notably, participants in the yohimbine group kept less money for themselves than those in the placebo group, suggesting their motivation was not purely self-serving but rather aimed at prioritizing in-group welfare while simultaneously directing resources against the out-group. Out-group behavior also played a role: independent of drug group, participants retaliated against out-group aggression by shifting from cooperation to competition, in line with previous research (Halevy et al., 2010).

These effects align with the respective roles of the HPA axis and the SAM system in the neurohormonal stress response (Hermans et al., 2014; Joëls & Baram, 2009), suggesting noradrenaline heightens group-based antagonism during early phases of acute stress, and cortisol facilitates in-group focused cooperation and conflict avoidance during post-stress vulnerability.

Our results help resolve the long-standing debate over whether stress primarily triggers fight-or-flight or tend-and-befriend responses (Cannon, 1932; Taylor et al., 2000). We show that these responses are not mutually exclusive but complementary, supporting flexible adaptation to social demands during and after stress. By experimentally dissociating neurohormonal systems, our study clarifies inconsistencies in prior work (Nitschke et al., 2022), which often overlooked the role of group membership, timing of stress phases, or the relative dominance of cortisol versus noradrenaline. This shifts the central question from whether stress makes people more or less prosocial to under what conditions, toward whom, and why (Faber & Häusser, 2022; Nitschke et al., 2022).

Finally, these results have broader societal implications. They resonate with a recent neurobiological model of war, which suggests neurobiological processes direct group behavior in war toward in-group protection and out-group harm (Bartal, 2024). Thus, the stress-boosted parochial competition, suggested here, is likely to maintain the self-perpetuating cycles of intergroup conflict.

Beyond neurohormonal mechanisms, it is equally important to understand the neural substrates of social preferences to obtain a more comprehensive picture of social behavior. The amygdala is particularly relevant in this context, as it is modulated by acute stress and stress neuromodulators (Hermans et al., 2014). In the next study, we therefore investigated the role of the BLA in social decision-making, using a sample of participants with highly selective BLA lesions. We focused on social discounting, which requires computing the value of rewards for oneself and for others as a function of social distance (Strombach et al., 2015).

Study 4 – The Basolateral Amygdala and Social Discounting

Kalenscher, T.*, Lüpken, L.M., Stoop, R., Terburg, D, van Honk, J., 2025. Steeper social discounting after human basolateral amygdala damage. Proc. Natl. Acad. Sci. 122, e2500692122. https://doi.org/10.1073/pnas.2500692122

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David Terburg: Resources, Writing - Review & Editing.

Jack van Honk: Investigation, Resources, Writing - Review & Editing.

Please note that this section summarizes my own research, which is why some parts of the text closely mirror the original publication. The summary also includes some of the original figures for illustration. The original article is available in the appendix.

Introduction

Animal and human studies have linked the amygdala, and particularly the BLA, to prosocial behavior, and lesions in these regions to more selfish or antisocial behavior (Anderson & Kiehl, 2012; Chang et al., 2015; Gangopadhyay et al., 2021; Haruno & Frith, 2010; Hernandez-Lallement et al., 2016; Rhoads et al., 2023; Scheggia et al., 2022). However, recent evidence from South-African participants with Urbach–Wiethe disease (UWD), which selectively affects the BLA (Rosenberger et al., 2019; Terburg et al., 2012; Van Honk et al., 2013, 2022), complicates this picture. UWD patients show hyper-altruistic and hyper-moral behavior (Hurlemann et al., 2010; Rosenberger et al., 2019; Scheele et al., 2012; Van Honk et al., 2013, 2022), suggesting that the BLA does not promote altruism or prosocial behavior per se. Instead, it may be critical for social-cognitive processes that weigh selfish against altruistic motives (Gangopadhyay et al., 2021; Rhoads et al., 2023). Thus, we hypothesized that human BLA lesions would alter social discounting, a phenomenon that explicitly requires balancing these motives (Strombach et al., 2015). Specifically, we predicted that the BLA fine-tunes prosociality as a function of the social-emotional distance between the participant and the recipient of help.

Methods

We examined social discounting behavior in five South African women with UWD and compared them to sixteen matched healthy female controls. UWD is a rare genetic condition causing highly selective, bilateral lesions to the BLA (Rosenberger et al., 2019; Terburg et al., 2012; Van Honk et al., 2013, 2022). Participants were matched on age, gender, income and socio-economic status, cultural-ethnic status, religion, and IQ (Terburg et al., 2012). All had basic education and were literate. Only women were included due to high substance abuse prevalence among men in the region. Participants with a history of secondary psychopathology, substance abuse or any acute or chronic disease other than UWD were excluded.

Social discounting was assessed using a modified, incentivized dictator game (as in, Archambault et al., 2020; Margittai et al., 2015, 2018; Schweda et al., 2020), where participants made real monetary decisions about how much of an endowment (200 South African Rand, approximately 11 US$) to share with others at varying levels of social-emotional distance. Participants were asked to assign real individuals to eight social distance levels. They provided names for social distance levels 1–3, 5, 10, and 20. Social distance 50 was defined as a person who the participants had seen several times, but did not know the name of, and social distance

100 was defined as a stranger on the street whom they did not know. Importantly, spouses and relatives were excluded to avoid household-sharing confounds.

The key outcome was the degree to which generosity declined with increasing social distance. We quantified this both in a model-free way, using the area under the curve (AUC; the normalized integral of the money shared with others; Jones & Rachlin, 2009), and in a model-based way, by fitting a hyperbolic discounting function to the amount of money shared across social distances (Jones & Rachlin, 2006). For each participant, we estimated two parameters: *V,* the intercept with the y-axis, which reflects generosity toward socially close others (Jones & Rachlin, 2006; Margittai et al., 2015), and *log(k)*, the discount rate, which captures the steepness of discounting with social distance.

We non-parametrically tested for group differences in AUC values and used bootstrapping to obtain 95% percentile-based confidence intervals for *log(k)* and *V* in the control group. We then examined whether the individual estimates from UWD participants fell within these intervals. To control for alternative explanations for behavioral differences (Beadle et al., 2022; Frühholz et al., 2017; Wu & Hong, 2022), participants also completed trait questionnaires on empathy (Leibetseder et al., 2007), personality (Rammstedt & John, 2007), and social network structure (Cohen et al., 1997). Full methodological details are provided in the original paper in the appendix.

Results

Across all participants, generosity decreased hyperbolically with social distance. However, while generosity toward close others (social distance 1) was comparable between UWD participants and controls, generosity in the UWD group declined more steeply with increasing social distance (see Figure 7).

The model-free analysis confirmed this pattern: UWD participants had significantly smaller AUC values than controls, indicating steeper social discounting. Additionally, the model-based analysis showed that all UWD participants had *log(k)*-parameters outside the control group's 95% confidence interval. Four UWD participants exhibited steeper discounting (higher *log(k)*) than controls, while maintaining generosity toward close others (*V* within 95% confidence interval of controls). In contrast, one UWD participant showed flatter discounting (lower *log(k)*) but also markedly reduced generosity overall, including toward her closest social tie (*V below* 95% confidence interval of controls). Importantly, no significant group differences were found in empathy, personality traits, or social network size. Full details on the results are provided in the original paper in the appendix.

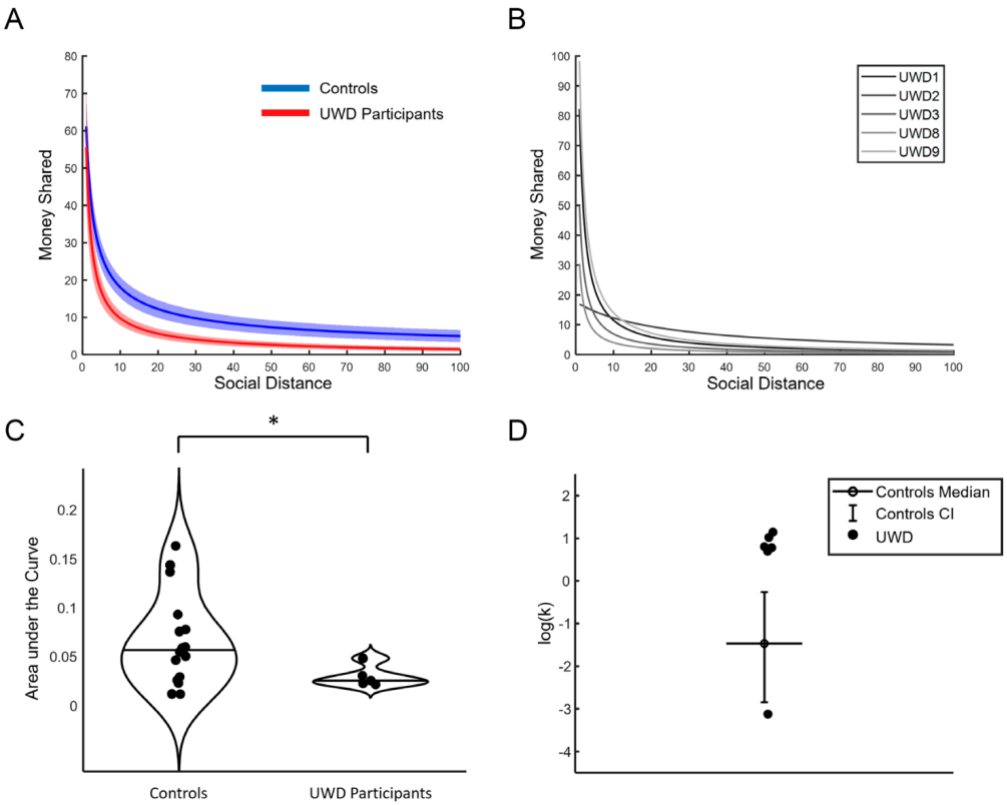

Figure 7. Social discounting in UWD participants. (A) Mean best-fitting hyperbolic social discount functions (solid lines; ±SEM; shaded areas) of control (blue) and UWD participants (red). (B) Best-fitting individual social discount functions of the five UWD participants. (C) Violin plots of the normalized AUC of the proportion of money shared across social distance. Horizontal lines: median AUCs; dots: data from individual participants. (D) log-transformed k-values [*log(k)*]. Controls' median of the bootstrap distribution (horizontal line) and 95% confidence interval (vertical line). The dots indicate the *log(k)*-values of the five UWD participants. *$p < 0.05$.

Discussion

We found that UWD participants with selective BLA lesions we less generous than controls, especially toward socially distant individuals. Four UWD participants showed a markedly steeper decline in generosity with increasing social distance, and one showed consistently low generosity. These differences were not explained by empathy, personality, or social network size. This pattern supports the view that the BLA does not simply promote altruism per se, but rather fine-tunes prosocial behavior based on social proximity.

Our results align with research showing that the BLA encodes the value of both own-rewards and rewards to others (Chang et al., 2015; Gangopadhyay et al., 2021). This suggests, BLA mediates the tradeoff between maximizing own-rewards and considering reward for others, particularly when social distance creates internal conflict (Strombach et al., 2015). BLA lesions compromise the computations underlying this tradeoff, resulting in a default strategy of maximizing self-interest, except toward very close others where helping may be the default.

Crucially, our results reconcile previous contradictory findings: BLA damage has been linked to increased generosity in some tasks (Rosenberger et al., 2019; Van Honk et al., 2013, 2022) but decreased generosity in others (Chang et al., 2015; Gangopadhyay et al., 2021; Hernandez-Lallement et al., 2016; Scheggia et al., 2022). We propose this reflects BLA's role in model-based social motivation, enabling flexible adjustments in generosity depending on context, such as down-regulating generosity in response to others' selfishness (Rosenberger et al., 2019), shifting between rule-based and utilitarian moral reasoning (Van Honk et al., 2022), or balancing self- and other-regarding motives in social discounting. Disruption of this model-based process can yield either more selfish or more prosocial behavior after BLA lesions, depending on the prevailing default response. Additionally, previous research rarely controlled for the social-emotional distance between participants and recipient, which may also contribute to inconsistencies in the literature.

Although our sample size was necessarily small due to the rarity of UWD, the focality and bilateral symmetry of lesions in this group (Terburg et al., 2012) are unprecedented in human lesion research. The exclusion of close relatives and household members from the social discounting task may have increased discounting rates in all participants, including controls. Nonetheless, our findings emphasize the BLA's critical role in calibrating prosocial behavior across social distances and offer a unifying explanation for prior mixed evidence on its role in prosocial behavior.

Unpublished Research Projects

Task Design Matters: The Role of Choice Format in Social Decision-Making

This project was conducted in collaboration with one of my master's students, Recep Dogan. I would like to explicitly acknowledge his contributions. While the initial idea for the project, as well as parts of the conceptualization and methodological design, originated with me, Recep played a significant role in further developing the conceptual framework and methodology. He also prepared the project's preregistration, developed the scoring approach that enabled us to compare prosocial behavior across conditions of varying number of choice options (see https://aspredicted.org/446z-v532.pdf), set up the online survey, and collected the data online. Here, I will only summarize the results that are most important to the broader conclusions of this dissertation.

Inspired by recent evidence that the number of available options (binary vs. open choice) moderates stress effects on social behavior (Nitschke et al., 2022), this project investigated how task design itself shapes conclusions about generosity in decision-making. Specifically, we explored whether varying the number of choice options in a dictator game (i.e., choice complexity) affects the amount of money participants are willing to share with an anonymous recipient. We also examined whether binary (discrete) and open-ended (continuous) choice formats yield comparable measures of generosity. Taking this methodological perspective, we aimed to address the comparability of findings across studies using different task implementations.

In this study, participants (N = 263) completed 15 trials of a dictator game in either a low (2 options) or high (4 options) choice complexity condition. In each trial, they received €60 and chose how much to share with another person. An open-choice format using a continuous slider (0–60€) was included as a final trial to assess whether allowing continuous as opposed to discrete choices would influence generosity.

The main finding was that the number of choice options had no significant effect on generosity (Figure 8). Participants shared similar proportions of money in the low and high complexity conditions, suggesting that varying the number of discrete options within a modest range (2 vs. 4) does not meaningfully influence generosity.

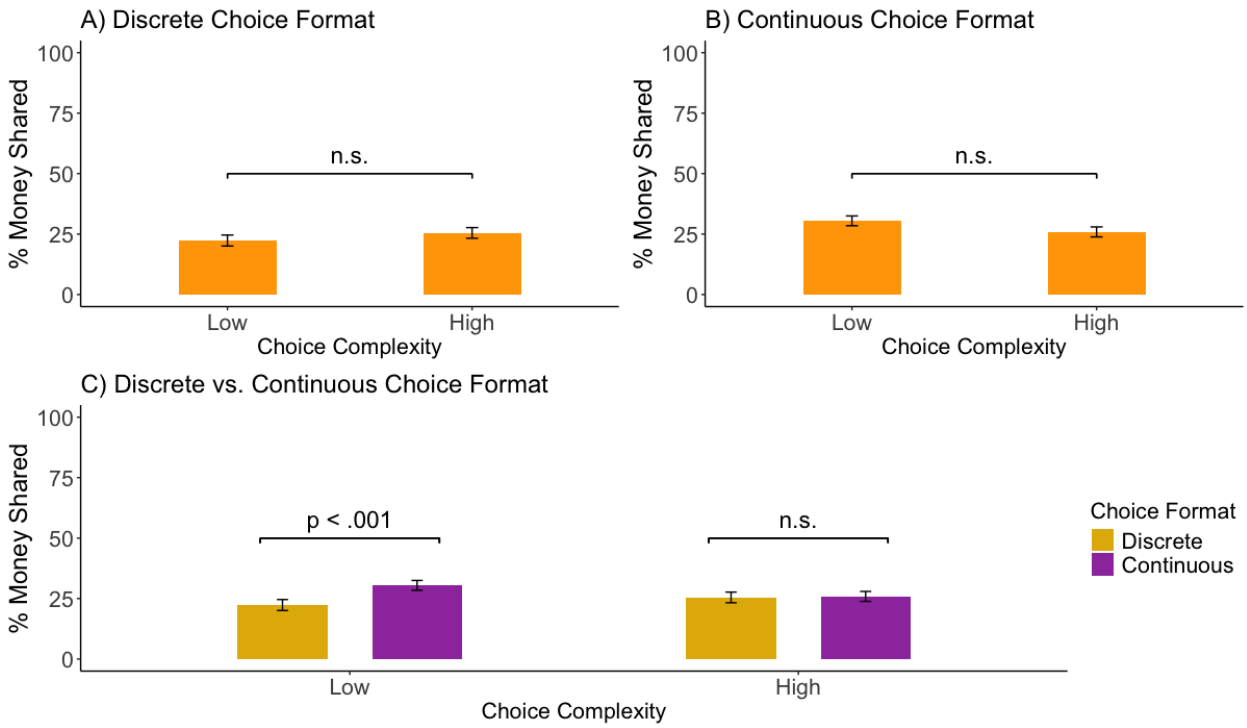

Figure 8. Generosity across choice formats and choice complexity. Mean (± SEM) percentage of money shared in the discrete (A) and continuous (B) choice formats for the low (2 options) vs. high (4 options) choice complexity conditions. (C) Mean (± SEM) percentage of money shared in the discrete vs. continuous choice formats, shown separately for low and high choice complexity.

However, a crucial exploratory result emerged when comparing the discrete binary choice format with the continuous open choice format: participants in the low-complexity condition shared significantly less in discrete choice trials than in the continuous open-choice trial (Figure 8). This difference was not observed in the high-complexity condition and could not be explained by a difference in generosity in the open-choice trial between the low- and high-complexity condition (Figure 8). These results suggest that generosity measured via binary choice formats is not directly comparable to that measured in open-choice formats.

This discrepancy raises important methodological concerns. Binary choice tasks, which are used in many experimental paradigms (e.g., Von Dawans et al., 2012, 2018, 2019), may artificially constrain behavior and under- or overestimate prosociality relative to more open choice formats. The choice architecture itself, particularly the flexibility of expressing nuanced generosity, appears to shape the observed behavior. Thus, our results caution against treating data from binary and open choice formats as interchangeable.

For the purposes of this dissertation, the key implication is that the choice format exerts an influence on measured prosociality. Therefore, when studying the effects of stress (neuromodulators) on social preferences, any comparison across studies must carefully account

for differences in choice format. This may potentially explain why choice complexity was found to moderate stress effects on social behavior (Nitschke et al., 2022).

Effort-Based Social Discounting: Beyond the Monetary Domain

The idea for this project was originally developed by Tobias Kalenscher. With helpful comments from David Terburg, we collaboratively developed the conceptual framework and methodological approach. Again, I would like to explicitly acknowledge the important contributions of two of my students, Karina Offermans and Julian Felix Grefer, without whom this project would not have been possible. They programmed the entire study in MATLAB – a programming language they learned specifically for this project – and conducted the data collection. Again, I will only summarize the results that are most important to the broader conclusions of this dissertation.

This project represents a first empirical step toward validating a novel measurement tool for assessing social discounting in the domain of physical effort. Because prosocial behavior often involves emotional or physical effort, recent research has begun to investigate prosocial effort directly (e.g., Lockwood et al., 2017). These studies have shown that people are less willing to choose an effortful option when it benefits others rather than themselves, and if they do, they tend to put in less effort (Lockwood et al., 2017, 2021, 2022). Stress may further reduce effort for others (Forbes et al., 2024). So far, it remains unclear whether the willingness to exert effort for others decreases systematically with increasing social distance, as is well established in the monetary domain (Jones & Rachlin, 2006; Margittai et al., 2015; Schweda et al., 2020; Strombach et al., 2015). To address this gap, we developed a novel effort-based social discounting task.

In this task, participants earned hypothetical monetary rewards for themselves and others by applying force to a hand dynamometer. Unlike previous paradigms (e.g., Lockwood et al., 2017), the magnitude of rewards for oneself or others was directly tied to the effort exerted, i.e., the more effort participants exerted, the higher the reward. Each trial required participants to exert effort to earn money either for themselves (social distance 0) or for another person at one of six increasing levels of social-emotional distance (1, 5, 10, 20, 50, 100; with 100 representing a total stranger). Each participant completed four measurement blocks, with short breaks (2 mins) in between.

Our key finding was that participants' willingness to exert effort declined systematically with increasing social distance, replicating the social discounting phenomenon in a new behavioral domain (Figure 9). This effect of social distance emerged both within

individual blocks and when averaging exerted effort across blocks. However, analyses also revealed a significant block x social distance interaction, indicating greater variability across blocks than in the aggregated data. Finally, there was no significant difference in exerted effort between social distances 50 and 100, either within blocks or in the aggregated data.

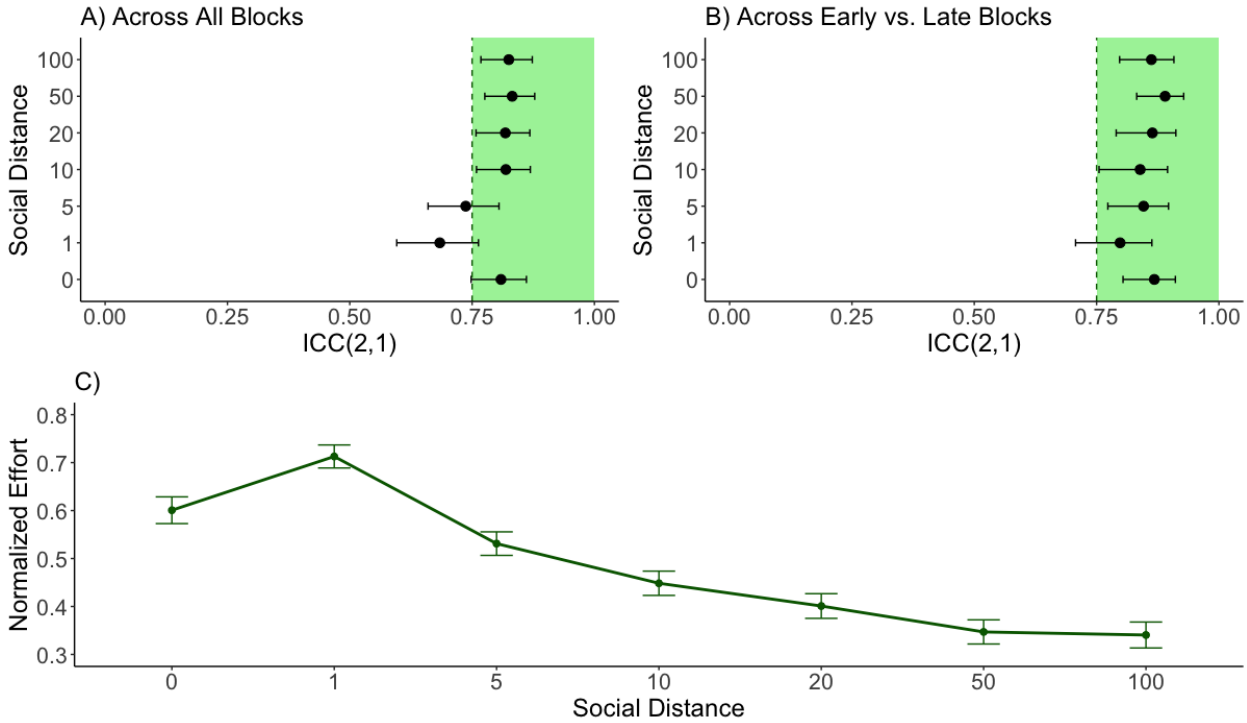

Figure 9. Test-Retest Reliability and Effort-Based Social Discounting. Intraclass correlation coefficients (ICCs) are shown for each social distance level (A) across the four repeated measurements and (B) across early (measurements 1+2 averaged) versus late (measurements 3+4 averaged) measurements. (C) Mean (± SEM) normalized exerted effort across social distance levels, averaged across all experimental measurements. Exerted effort was normalized to the maximum force participants could exert measured in three consecutive calibration trials in the beginning of the experiment.

We also assessed test-retest reliability of our measure, both across individual blocks and when averaging early (measurement 1+2) and late (measurement 3+4) blocks. Across blocks, ICCs generally indicated good reliability (ICCs > 0.75; Koo & Li, 2016), except at social distance 1 and 5. Reliability improved further when averaging across early and late blocks, reaching good levels across all social distances(Figure 9). This suggests that our effort-based social discounting task provides a reliable measure of social discounting in the effort domain, particularly when responses are aggregated across repeated measurements.

Surprisingly, participants exerted more effort for social distance 1 (a person very close to them) than for themselves. This is a reversal of the typical self-other gradient, in which people usually prioritize their own outcomes. One possible explanation is the lack of incentive compatibility in the task, which may have reduced strategic self-interest and revealed genuine

prosocial tendencies. This finding aligns with research indicating that individuals are sometimes more willing to work for others than for themselves when incentives are low (Imas, 2014) and may also reflect the "warm glow" associated with prosocial behavior (Andreoni, 1990). Together, these findings illustrate the value of effort-based paradigms in uncovering nuanced social preferences that may be obscured in purely monetary contexts.

The project contributes to the broader goal of developing more ecologically valid and domain-general measures of social preferences and behavior. It complements existing economic games by testing prosociality in the physical effort domain and lays the foundation for comparing effort-based and money-based social discounting in future studies. Going forward, we plan to (1) replicate this paradigm using incentive-compatible conditions and (2) include a traditional monetary dictator game social discounting task to systematically examine cross-domain validity.

General Discussion

Social behavior is neither constant nor easily captured. It arises from complex interactions between social-emotional context and neurobiological mechanisms and is further shaped by physiological and situational influences, such as stress. Across four studies, we demonstrate the nuanced effects of stress neuromodulators on social decision-making, the critical role of the BLA as a neural substrate in calibrating prosociality, and the challenges posed by limited reliability in behavioral measures.

Summary and Synthesis of Results

In study 1, we examined the effects of cortisol and noradrenaline on generosity and GARP-based social choice consistency in an interindividual choice setting using a psychopharmacological design with hydrocortisone and/or yohimbine. Neither choice consistency nor generosity were affected by stress neuromodulator activity, suggesting that the core assumption of economic preferences models – choice consistency – remains robust even across fluctuating neuromodulator activity.

Study 2 more broadly evaluated the psychometric properties of choice consistency by assessing the reliability of two of the most widely used indices of GARP-based choice consistency: the CCEI and the HMI. We found that both indices showed poor to moderate reliability, thus, falling short of common reliability standards (Koo & Li, 2016).

Next, in study 3, we were interested in how cortisol and noradrenaline shape behavior in an intergroup conflict setting. Using a psychopharmacological design similar to study 1, we investigated the effects of these neuromodulators on parochialism in the IPD-MD (Halevy et al., 2008). In contrast to study 1, we observed distinct effects: cortisol promoted parochial cooperation and noradrenaline promoted parochial competition. Additionally, the more aggressive the out-group was, the more participants shifted from pure in-group focused cooperation to parochial competition.

Finally, in study 4, we examined the neural substrates of social decision-making by investigating social discounting in a sample of participants with highly selective BLA lesions (Terburg et al., 2012). Compared to controls, lesion participants were as generous toward close social ties but substantially less generous toward distant others, suggesting a crucial role of the BLA in calibrating prosociality to social distance. This is in line with the idea that the amygdala contributes to social categorization processes (Cikara & Van Bavel, 2014; Van Bavel et al., 2008).

Together, these findings suggest that stress does not uniformly amplify or suppress prosocial or antagonistic tendencies. Rather, its behavioral consequences appear multifaceted and context-dependent, shaped by perceived social closeness, and the relative dominance of cortisol versus noradrenaline (study 3; see also Margittai et al., 2015, 2018). At the same time, the null effect in interindividual contexts (study 1), contrasted with distinct effects in intergroup conflict (study 3), implies that stress neuromodulator activity alone does not determine social behavior but instead may interact with contextual features, such as perceived threat or the complexity of the choice environment. Beyond this, evidence from participants with BLA lesions (study 4) illustrates a key neural substrate that underpins the flexible adaptation of prosocial behavior to social distance, emphasizing the importance of neurobiological mechanisms in adaptive social responding. This invites speculation that amygdala modulation during stress (Hermans et al., 2014) may be involved in sharpening or softening in-group–out-group boundaries. Finally, from a methodological perspective, the limited reliability of widely used GARP-based measures (study 2) raises concerns about the interpretability of previous research (including our own but see "*The Importance of Reliable Measures*"). Along with recent evidence on the low reliability of other behavioral measures (e.g., Enkavi et al., 2019), this underscores that advancing our understanding of (social) behavior requires more robust methodological tools.

Befriend "Us" But Fight "Them": A Biobehavioral Model of Social Stress Responses

The divergent findings between study 1 and study 3 point to a paradox: stress can leave social tendencies unchanged in some contexts yet profoundly shape them in others. This mirrors the broader heterogeneity in the literature (Nitschke et al., 2022; Von Dawans et al., 2021). Rather than interpreting these results as contradictory, they may be understood as different expressions of an adaptive stress response. Building on recent theoretical developments (Faber & Häusser, 2022; Nitschke et al., 2022; Von Dawans et al., 2021), I outline a biobehavioral model that integrates the fight-or-flight and tend-and-befriend perspectives. Specifically, the extent to which fight-or-flight and tend-and-befriend tendencies emerge and how they combine seems to be shaped by (1) the social context, (2) the situational demands, (3) the relative dominance of cortisol versus noradrenaline, and (4) their interactions with neural substrates. These processes are likely further modulated by individual-level characteristics, such as age or empathy (Azulay et al., 2022; Kamas & Preston, 2021; Lockwood et al., 2021), though these will not be discussed here in detail.

The Role of the Social Context

Human prosociality is not distributed equally. It typically declines with increasing social-emotional distance toward the recipient (Jones & Rachlin, 2006), and individuals tend to cooperate more with in-group than with out-group members, and under certain circumstances may even harm out-group members; especially so when it protects their in-group (Balliet et al., 2014; Böhm et al., 2016; Halevy et al., 2010; Weisel & Böhm, 2015).

Prior research suggests that social distance also moderates stress effects on social behavior (Huang et al., 2023; Nitschke et al., 2022). For example, stress (and especially cortisol) has been shown to amplify prosocial responses toward socially close, but not distant others (Margittai et al., 2015, 2018). In extreme contexts, such as violent conflict, stress may foster strong in-group bonding, while sustaining aggression toward outsiders (Whitehouse et al., 2014). Thus, social stress responses appear to be shaped by social categorization processes that can drive behavior toward cooperation or aggression, depending on the interaction partner.

This perspective aligns with our finding in study 3, where participants under the influence of stress neuromodulators cooperated more with their in-group but also competed stronger with the out-group, seemingly amplifying us versus them dynamics. However, it does not fully account for the null effect observed in study 1. Previous research suggests that interindividual and intergroup interactions differ systematically, for example in levels of cooperativeness (Böhm et al., 2020; Wildschut et al., 2003). Moreover, framing intergroup tasks around collective versus individual outcomes increases competitive tendencies, pointing to different underlying motivational strategies (Weisel & Zultan, 2021). Thus, one possible explanation is that the interindividual context in study 1 engaged different motivational processes than the group context of study 3.

The notion of group categorization as a driving force of behavior has, however, recently been criticized. Deschrijver and Ramsey (2025) argue that social categorization is grounded less in abstract group membership and more in perceived similarity or difference between individuals. From this perspective, in-group vs. out-group effects observed in laboratory tasks may partly reflect the artificial group boundaries imposed by the experimental design, whereas in reality such distinctions are more continuous than discrete. Thus, in real-world stress contexts, individuals may not rely solely on rigid group categories but instead differentiate between others based on perceived similarity or dissimilarity, guided by the most salient cues in the environment, that stress may amplify.

Additionally, the null effect in study 1 stands in contrast to prior findings in interindividual contexts (Margittai et al., 2015, 2018) and the findings of study 3 diverge to some extent from Schweda et al. (2019). While their data provided some indication that cortisol may foster cooperative tendencies and SAM-system activation more competitive ones (in line with study 3), they observed no overall effect of stress on intergroup conflict behavior in the IPD-MD. These comparisons suggest that although social context is an important moderator of stress effects on social behavior, it cannot by itself account for the divergent findings in the literature and in our own studies.

The Role of the Situational Demands

Stress has long been understood as an adaptive response to situation-specific demands (Cannon, 1932; Selye, 1950). In line with this, the literature seems to converge on the notion that the (social) situation is a decisive moderator of stress effects: stress does not arise in a vacuum but in the context of specific stressors that trigger certain needs (Faber & Häusser, 2022; Von Dawans et al., 2021). Specifically, Faber and Häusser (2022) recently argued that stress interacts with the situational demands and individual needs to produce adaptive behavior. For example, stress that elicits a need for social support may foster affiliative responses, whereas stress in the face of external threat may promote more defensive or aggressive behaviors. Accordingly, behavior under stress should not be expected to change in a straightforward way but to flexibly adapt to the respective situation.

This framework aligns well with our findings. Individuals are generally reluctant to harm others (e.g., Halevy et al., 2008) unless they feel threatened or placed in a defensive position (e.g., Böhm et al., 2016). Study 3 created such a context by having the out-group move first, placing participants in a defensive role. Under these conditions, we observed distinct but complementary effects: noradrenaline amplified competitive behavior, while cortisol amplified affiliative behavior. Stress neuromodulators thus biased responses toward strategies that were adaptive in the context, i.e., befriending the in-group for mutual protection and confronting the out-group to counter threat.

By contrast, when situational demands were more neutral, stress effects were less pronounced, as in Schweda et al. (2019). They also used the IPD-MD paradigm, but without creating salient threat, i.e., the out-group did not move first. They found only weak associations between stress physiology and parochial behavior and no overall stress effect. Similarly, in study 1, the complexity of the task and the salience of the transaction costs likely shifted attention toward efficiency rather than social affiliation, thereby potentially attenuating effects

of stress neuromodulators. This fits with evidence that subtle design features, such as the specific choice environment (e.g., number of choice options), or framing of the task, can systematically alter social decision-making (Bergh & Wichardt, 2022; Nitschke et al., 2022; Schweda et al., 2020; Sellitto et al., 2021; our own unpublished data, see "*Task Design Matters: The Role of Choice Format in Social Decision-Making*").

The Role of Cortisol and Noradrenaline

The human stress response is temporally dynamic: first, the rapid activation of the SAM system triggers noradrenaline release, followed by a slower but more sustained activation of the HPA axis, leading to cortisol secretion (Hermans et al., 2014; Joëls & Baram, 2009). This temporal distinction of early and late stress responses has inspired the idea that noradrenaline and cortisol may exert distinct but complementary effects on behavior, promoting the flexible adaptation to demanding situations (Margittai et al., 2018; Schweda et al., 2019).

Our results on noradrenaline (study 3) suggest its primary role lies in protective behaviors under threat, cooperating with the in-group while aggressing against out-groups. This interpretation is consistent with prior evidence linking noradrenaline to aggression and heightened vigilance and with the idea that noradrenaline may heighten threat sensitivity (Haden & Scarpa, 2007; Haller et al., 1997; Miczek & Fish, 2005; Nelson & Trainor, 2007). This could explain why noradrenaline showed no isolated effects in non-threatening contexts (as in study 1 and Margittai et al., 2018). In the absence of salient threat, its protective function is not engaged.

Crucially, participants under the influence of noradrenaline did not simply act more competitively; they also kept less for themselves, thereby investing more overall into the group interaction. In other words, they sacrificed more personal resources to both harm the out-group and benefit the in-group. This tentatively suggests that noradrenaline may not only sharpen competitive drives but also enhance the willingness to sacrifice for the in-group. Such a blend of affiliative and antagonistic tendencies contrasts with prior work (Margittai et al., 2018), where no prosocial effects of noradrenaline were observed, and may be driven by the heightened hostility of our intergroup conflict context. Whether noradrenaline is best understood as primarily driving competition or instead as fostering a blend of cooperation with in-groups and hostility toward out-groups should be further explored in future research.

While evidence is not fully consistent (see e.g., study 1), a range of studies points toward a prosocial role of cortisol (Berger et al., 2016; Duque et al., 2022; Margittai et al., 2018), in line with the increased parochial cooperation we observed in study 3. Recently

Strojny et al. (2024) reported reduced altruistic punishment after pharmacological manipulation of cortisol (see also Vinkers et al., 2013), which they interpreted as diminished prosocial behavior. We argue, however, that reduced punishment under cortisol influence may instead reflect a harm-avoidance function: as the modulator of post-stress coping, cortisol may promote behaviors that prevent conflict escalation. Notably, participants under cortisol influence in study 3 still responded to aggression by the out-group, increasing competitive contributions with increasing out-group aggression. This indicates that cortisol does not blunt defensive reactivity but biases responses toward in-group affiliation, conflict avoidance and harm prevention, in line with what we termed an "accept what you get and avoid conflict mentality" (Dashti et al., 2025, p. 4). This interpretation aligns with cortisol's role in downregulating initial stress responses and preventing them from overshooting (De Kloet et al., 2005; Hermans et al., 2011). What remains unresolved is whether cortisol's cooperative bias extends beyond the in-group, as study 3 did not allow for direct cooperation with out-group members. Evidence from Margittai et al. (2018), however, suggests that cortisol is primarily linked to benefits for socially close others.

Interestingly, when cortisol and noradrenaline act in concert, under combined administration of hydrocortisone and yohimbine, social behavior seems to remain unchanged (study 3 and Margittai et al., 2018), implying that their individual effects offset each other. This supports the idea that the two neuromodulators regulate different aspects of social responding. Noradrenaline appears to bias behavior toward parochial competition, where in-group cooperation and out-group hostility are expressed simultaneously, while cortisol seems to promote parochial cooperation without the antagonistic component. Thus, rather than exerting strictly opposing effects, the two neuromodulators may emphasize different directions within the spectrum of group-focused responses. Importantly, in natural stress responses, cortisol and noradrenaline are indeed co-released, but typically one system dominates at a given time point (Hermans et al., 2014). This cautions against overinterpreting the null effect of combined pharmacological administration, which may not mirror naturally occurring stress dynamics.

Notably, cortisol and noradrenaline do not operate in isolation. Rather, they interact with other neuromodulator systems, including oxytocin and vasopressin (Groeneweg et al., 2011; Heinrichs et al., 2003; Heinrichs & Domes, 2008), both of which are also implicated in social cognition and behavior (Meyer-Lindenberg et al., 2011). Oxytocin, in particular, has often been portrayed as a "prosocial hormone", yet its effects are not always affiliative. For example, oxytocin has been linked not only to cooperation but also to competitive reactions, depending on the social context (De Dreu et al., 2010, 2011; Zhang et al., 2019). Similar to

cortisol and noradrenaline, oxytocin is increasingly understood as supporting adaptive, context-sensitive responses rather than exerting a simple prosocial bias (Bartz et al., 2011; Marsh et al., 2021).

Interestingly, early oxytocin increases have been associated with stronger cortisol responses, whereas later oxytocin increases were linked to faster stress recovery (Engert et al., 2016). This suggests that oxytocin may initially amplify cortisol release, thereby supporting affiliative tendencies, that may help buffer stress (Raposa et al., 2016) and then facilitate downregulation of the stress response. Speculatively, cortisol and oxytocin may thus interact to promote prosocial responding under stress to support coping. Clarifying the dynamics of this interaction remains an open question for future research.

In sum, different neuromodulator constellations may promote distinct social behavioral outcomes: elevated cortisol may facilitate affiliative behavior and coping, potentially amplified by oxytocin or vasopressin; in contrast, heightened noradrenaline may bias behavior toward vigilance and competitive strategies that protect the in-group and fight the out-group. Yet, these effects are far from uniform. Given the adaptive nature of human social behavior, it is plausible that neuromodulators do not impose fixed behavioral patterns but instead enable flexible, context-sensitive responses through their dynamic interplay with each other, neural systems, and individual-level characteristics.

The Role of the Social Brain

Additionally, acute stress modulates activity across large-scale brain networks, particularly the salience network, the default mode network, and the executive control network (Arnsten, 2009; Hermans et al., 2014; Van Oort et al., 2017), which overlap with social brain regions, such as the amygdala or TPJ (Kennedy & Adolphs, 2012). These networks subserve different cognitive functions: the salience network focuses attention on relevant cues, such as threat; the default mode network is involved in self-referential thought and emotion regulation; and the executive control network supports higher-order cognition and goal-directed behavior (Hermans et al., 2014; Van Oort et al., 2017).

Noradrenaline has been implicated in upregulating salience network activity while downregulating the executive control network (Arnsten, 2009; Hermans et al., 2011, 2014). This fits well with the idea that noradrenaline heightens threat sensitivity, biasing the brain toward fast, protective reactions. By contrast, during the recovery phase of stress, when (genomic) cortisol is more influential, these effects appear reversed: activity in the salience network is dampened while activity in the executive control network increases (Hermans et al.,

2014). This shift may support more deliberative, reflective processes that favor harm avoidance and affiliation. Thus, the lens of stress-induced reallocation of neural resources provides a plausible mechanism by which cortisol and noradrenaline exert their influence on social behavior. Direct evidence for this mechanism in the social domain is limited but a few recent studies have begun to bridge this gap. Specifically, they have linked changes in social behavior under acute stress to activation changes in different brain regions, such as increased activity in salience-related regions like the TPJ (Chang et al., 2025; Wang et al., 2024) and decreased activity in executive control regions like the dmPFC (Kim et al., 2025). This lends tentative support to the idea that stress effects on social behavior are mediated by shifts in salience and executive control networks. However, the precise neural mechanisms and the specific role of cortisol and noradrenaline in this remain unresolved.

Within this framework, our findings on the BLA (study 4) add an important piece. The amygdala, as part of the salience network, has been implicated in social categorization processes (Cikara & Van Bavel, 2014; Van Bavel et al., 2008). Our results suggest that the BLA plays a crucial role in regulating social behavior across social distance, fine-tuning prosocial responses. Speculatively, this implies that BLA upregulation during acute stress, when noradrenaline dominates, sharpens social categorization into “us vs. them” or “friend vs. enemy”, thereby facilitating the parochial behaviors we observed in study 3. Conversely, amygdala downregulation in the aftermath of stress, when cortisol peaks, may reduce sharp self–other distinctions, enabling more inclusive or forgiving social responses that help prevent renewed conflict.

Putting the Pieces Together

No single influencing factor described in this chapter can account for all the diverging findings in the literature. Taken together, however, they can be integrated into a model of biobehavioral stress responses that provides a powerful framework for understanding these findings and a basis for future research (Faber & Häusser, 2022; Von Dawans et al., 2021). This model moves beyond the traditional dichotomy of fight-or-flight versus tend-and-befriend, illustrating that these response patterns are in fact complementary aspects of an overall adaptive repertoire. Which response emerges or whether both occur simultaneously, depends on the social context, the situational demands and the underlying neurobiology. Importantly, both models were originally based on the idea that stress responses serve as biobehavioral defense mechanisms (Cannon, 1932; Taylor et al., 2000). From this perspective,

it is plausible that social stress responses involve any behavior, be it cooperative or competitive, that best protects the individual from the adverse consequences of the stressful situation.

In early acute stress, when a threat is imminent, the most adaptive responses include not only fighting or fleeing to eliminate the threat but also supporting and protecting socially close others. Our results suggests that this is at least to some degree supported by noradrenaline. Interestingly, this is aligns with Cannon's (1932) original conceptualization of fight-or-flight as an immediate protective reaction, which he linked to activation of the SAM system. Once the immediate threat subsides, however, behavior that (re-)builds social connection may become more adaptive, which supports coping but potentially also helps expand the social network for mutual protection in the future. Our results suggest that this is likely modulated by cortisol, potentially in interaction with oxytocin, the neuromodulator central to the tend-and-befriend framework (Taylor et al., 2000). Finally, both noradrenaline and cortisol may shape neural substrates involved in these behaviors, providing a mechanistic basis for how temporal shifts in stress physiology recalibrate social decision-making.

Methodological Perspectives

The Importance of Reliable Measures

In study 2, we demonstrated that GARP-based choice consistency measures exhibit limited reliability. This raises questions about the interpretability of our findings from study 1. Although it has been argued that low reliability poses less of a problem for experimental manipulations and between-subjects designs (Hedge et al., 2018), recent work challenges this view. Karvelis and Diaconescu (2025) instead suggest that such designs may be equally vulnerable to low reliability leading to over- or underestimation of effects. In study 1, however, we generally observed no drug effects on social choice behavior, i.e., generosity remained unchanged. Thus, while low reliability may have attenuated differences in choice consistency between drug conditions, the overall null effect on social choice behavior makes such differences unlikely to have emerged in the first place.

More generally, though, this finding also casts doubt on other work using such measures. A major risk is treating unreliable measures as stable psychological traits and thus ascribing unwarranted psychological meaning to them. For example, GARP-based measures have often been equated with decision-making quality (e.g. Choi et al., 2014). Thus, findings of group differences in choice consistency have sometimes been interpreted as evidence that one group makes worse decisions than another, which risks being misused as justification for

existing disadvantages (e.g., poverty or gender inequality). Recently, high choice consistency observed in GPT outputs was even interpreted as evidence of good decision-making ability and used to argue for its suitability as a decision-making assistant (Chen et al., 2023). Yet, an alternative explanation, in line with our finding of low between-subject variability, is simply that choice consistency is a low threshold that is easy to pass, and most agents, human or artificial, appear highly consistent.

Contrary to previous claims (Madar et al., 2024), our results suggest that choice consistency is unlikely to reflect a stable psychological trait or cognitive ability. Instead, it appears to function more like a state, contingent on the specific choice environment. This does not render GARP-based measures meaningless, but it does caution against overinterpretation. Importantly, our analyses indicate that low reliability is largely driven by limited between-subject variability. This suggests a way forward: to render these measures meaningful proxies of decision-making quality, future work must find ways to amplify genuine individual differences and by this potentially increase reliability. For now, GARP-based choice consistency indices may be better understood as descriptive features of choice patterns, indicating whether choices can be understood as coming from a coherent preference ordering, rather than as direct indicators of underlying psychological constructs.

Importantly, the problem of low reliability is not unique to GARP but extends to commonly used behavioral and fMRI based tasks (Elliott et al., 2020; Enkavi et al., 2019; Hedge et al., 2018). This underscores a broader problem: reliability cannot be treated as a given but must be routinely established and reported. Without reliable measures, even robust-looking effects risk reflecting task noise rather than stable phenomena, limiting replicability and generalizability across studies. Meaningful conclusions and theoretical developments therefore depend on the systematic evaluation and refinement of tasks to ensure that the constructs they aim to capture are measured reliably.

Rethinking Gender Differences in (Social) Behavior

In the study of social behavior and cognition (but also behavior and cognition more generally), sex / gender[1] is probably the most frequently discussed moderator. The key argument for gender differences in the effects of stress on social behavior has been

[1] While sex commonly refers to biological attributes and gender to socially constructed identities that may extend beyond a binary framework (Heidari et al., 2016), the two have not been clearly separated in much of the prior literature. Accordingly, the methodological points raised here apply to both. In what follows, I will use the term gender for consistency.

evolutionary. The tend-and-befriend response was originally theorized to be female-specific, based on the assumption that rearing offspring made fight-or-flight a suboptimal strategy for women (Taylor et al., 2000). This perspective was criticized early on (Geary & Flinn, 2002) and the model was later extended to men as well (Taylor, 2012), as evidence accumulated for tend-and-befriend responses in male participants (Margittai et al., 2015, 2018; Singer et al., 2017; Tomova et al., 2017; Von Dawans et al., 2012; Zhen et al., 2021). More broadly, even the assumption of strict gender division in early hunter–gatherer societies has been called into question (Haas et al., 2020; Kuhn & Stiner, 2006) further weakening the evolutionary case for gendered stress responses. Thus, the theoretical basis for expecting robust gender differences in social stress reactions appears weak.

Across our studies, reviewers most frequently recommended examining gender as a potential moderator. This likely reflects both the legacy of the tend-and-befriend framework and the fact that some studies have reported gender as a moderator in stress effects on social behavior (e.g., Nickels et al., 2017). Yet, in neither of our mixed-gender samples (studies 1 and 3) did we find any evidence that gender moderated the (null) effects. In fact, we found no main effects of gender on social behavior in either study.[2] This aligns with a recent meta-analysis that likewise reported no systematic support for gender as a moderator of stress effects on social behavior (Nitschke et al., 2022). Together, this suggests some tension between the emphasis placed on gender as a moderator and the current evidence base.

A second line of reasoning for expectations of gender differences is that women and men differ in physiological stress reactivity (Kirschbaum et al., 1999). While this is of course relevant, it is important to note that differences in physiological cascades do not automatically imply differences in behavioral outcomes. It has, for instance, been suggested that oxytocin may underlie prosocial responses in women, whereas vasopressin could serve a similar function in men (Taylor, 2012). In other words, different physiological implementations can converge on similar behavior.

More generally, it has been shown that observed gender differences often reflect contextual variables rather than fixed traits (Kettlewell et al., 2023; Levy et al., 2025). Meta-analyses suggest that when gender differences in behavior exist, they tend to be small (Hyde, 2005; Zell et al., 2015), and many can be explained by socialization processes (Eagly & Wood,

[2] Note that we observed a main effect of gender on choice consistency in study 1 but not on social behavior. This effect is difficult to interpret given concerns about the reliability of the measure and the possibility that other factors, such as social norms, contributed to it (see "*Supplementary Materials"* of the original paper in the appendix for a detailed discussion).

1999; Endendijk et al., 2017; Spencer et al., 1999). The focus of gender further risks overshadowing other, and perhaps more meaningful, individual differences. For example, Kamas & Preston (2021) showed that gender differences in prosocial behavior were largely explained by empathy; when men and women were equally empathic, their behavior was comparable. Neuroscientific work has likewise cautioned against interpreting gender differences in ways that reinforce dichotomized notions of "male" and "female" brains (Joel & Fausto-Sterling, 2016).

My goal here is not to argue that gender should be disregarded in research, but rather to caution against treating it as an automatically meaningful explanatory factor. Without clear, theory-driven accounts of how and under what conditions gender differences should emerge – biologically, psychologically, or socially – the risk is that gender becomes an easy but misleading explanation, potentially even reinforcing discriminatory notions. What is needed going forward is a more balanced evidence base. To this day, the majority of research on stress and social behavior is still based primarily on male samples (e.g., Strojny et al., 2024; see Nitschke et al., 2022 for a discussion), often justified by sex differences in HPA axis reactivity (e.g., Forbes et al., 2024; Kim et al., 2025; Margittai et al., 2015, 2018; Speicher et al., 2023). This practice limits generalizability and makes it difficult to draw meaningful conclusions about gender in meta-analyses. Therefore, it should be standard practice to include mixed-gender samples and address variation directly. With our mixed-gender samples, we aimed to contribute to improving the generalizability and inclusivity of this literature.

Limitations and Future Directions

The danger of post-hoc theorizing in the face of diverging findings (as I have done here) is that it risks turning into a catch-all explanation, invoked to rationalize null or contradictory findings. Thus, while the flexible, adaptive model of social stress effects neatly accounts for the at times seemingly contradictory findings in the literature, it also carries the risk of lacking falsifiability, meaning that future contradictory results may be too easily accommodated within it. To address this, future research should rigorously test the model by considering the factors proposed. For example, threatening contexts that allow for protective behavior should produce distinct noradrenaline effects characterized by more antagonistic tendencies toward outsiders, and contexts that allow for affiliative responding should produce distinct cortisol effects characterized by prosocial tendencies toward socially close others. Thus, future studies should be conceptualized to provide opportunities for both fight-or-flight and tend-and-befriend tendencies simultaneously.

Beyond this, research on social behavior and stress inevitably grapples with the complexity of social interactions, stress responses, and the methods used to study them. The studies presented here capture important aspects of these processes but necessarily simplify them. Accordingly, the following limitations should be understood as points that constrain the interpretation of the findings.

A central limitation to the generalizability of our findings from studies 1 and 3 is the way in which we manipulated the activity of stress neuromodulators. Although noradrenaline and cortisol are central aspects of the human stress response, they are released as end products of broader physiological cascades of the SAM system and the HPA axis, respectively. These cascades involve numerous additional mediators and interact with other neuromodulatory systems, meaning that in natural stress, cortisol and noradrenaline rarely act in isolation (Groeneweg et al., 2011; Joëls & Baram, 2009). Psychopharmacological manipulations, however, lack this complexity and can therefore only approximate natural stress (Sarmiento et al., 2024). Additionally, natural stress is accompanied by subjective feelings of stress (Koolhaas et al., 2011), whereas pharmacological manipulations typically do not elicit such experiences. In fact, participants are often unaware of any drug effects. Our (null) findings may, thus, reflect neuromodulator-specific processes, and clarifying their role in the overall complexity of natural stress remains an important task for future research.

Nonetheless, pharmacological manipulations offer unique advantages over psychosocial stress paradigms, such as the TSST (Kirschbaum et al., 1993). They avoid social evaluative confounds that can independently influence behavior and, crucially, allow for causal inferences about the roles of cortisol and noradrenaline. A promising direction for future research may be to combine both approaches to capture the advantages of each. For example, administering hydrocortisone and/or yohimbine alongside a psychosocial stressor, such as the TSST, could potentially better approximate natural stress while still isolating the causal role of specific neuromodulators.

Furthermore, stress in real life, especially in the context of threat, often arises from social encounters, so it seems reasonable that the source of stress might also play a role in behavior. Interestingly, stress reactivity itself does not seem to vary depending on whether the stressor comes from an in-group or an out-group (Halbeisen et al., 2023), but the behavioral consequences may still differ. To address this question, an approach could be to administer the TSST followed by an intergroup task such as the IPD-MD, varying whether the stress-inducing panel represents the out-group and whether this out-group behaves aggressively.

Overall, our findings and conclusions are based on controlled laboratory experiments, that can only approximate real social dynamics and thus arguably lack ecological validity. For example, social decision-making tasks constrain the forms of social behavior that can be expressed: dictator games typically make it impossible to express aggressive tendencies, which makes them unsuitable to study fight-or-flight tendencies, and it was recently argued that they also do not approximate tend-and-befriend behaviors well (Stahlecker & Häusser, 2025). The IPD-MD allows for expressing aggression, but only toward out-groups and only in ways that also benefit the in-group. Additionally, the IPD-MD does not allow for benefiting members of the out-group, making it impossible to draw conclusions about universal cooperation (Aaldering et al., 2018). Accordingly, any interpretation of social behavior must consider the affordances and constraints of the paradigms used.

Beyond this, stressful social interactions and intergroup conflicts often involve high stakes, strong emotions and are potentially enduring. Such features are difficult to reproduce in the lab and ethical concerns constrain what can be studied. For example, creating genuine interpersonal or intergroup conflict, let alone violent conflict, would be morally unacceptable. Laboratory paradigms therefore necessarily simplify these dynamics. Going forward, technological advances such as virtual reality may offer ways to better model the complexities of real-life social interactions while maintaining ethical safeguards. In addition, our project on effort-based social discounting offers another promising approach: effort-costs arguably simulate costs in social decision-making better than monetary costs (Lockwood et al., 2017); translating intergroup tasks into the domain of effort could therefore provide a way to more accurately represent intergroup behavior in the laboratory.

Finally, as is the case for most research on social behavior, our conclusions are constrained by the samples we used. Except for study 4, which used a South African sample, all other studies in this dissertation relied primarily on WEIRD (western, educated, industrialized, rich and democratic, Henrich et al., 2010) and PRIME (productive, researchable, independent, mobile, and educated; Lockwood & Van Den Bos, 2025) populations. In practice, this means that three of the four studies (and both unpublished projects) were conducted mainly with (German) university students. Although study 2 included a non-German online sample, it too was skewed toward highly educated individuals. These populations are far from representative of the global population, and prosociality varies substantially across cultures (Henrich, Ensminger, et al., 2010; Henrich et al., 2005; Henrich, Heine, et al., 2010). As with gender, what is needed is a more balanced evidence base. Replicating and extending findings

across multiple countries and cultural contexts will be crucial for testing the generalizability of stress effects on social behavior.

Another obvious next step for research on stress and social behavior concerns the underlying neural mechanisms. As discussed, the notion of stress-induced reallocation of neural resources provides a plausible framework for how cortisol and noradrenaline affect social behavior. Thus, replicating study 3 with the addition of neuroimaging could be an important step toward identifying the specific brain networks involved in these effects. However, this appears to be a difficult exercise: recent imaging studies investigating the effects of hydrocortisone and yohimbine on brain activity have, contrary to expectations, mainly produced null effects (Lipka et al., 2024; Metz et al., 2024; Rosada et al., 2024). These were interpreted, in part, considering the limitations of psychopharmacological manipulations. That is, it was suggested that the manipulation of cortisol and noradrenaline alone may not adequately reflect the complexity of stress and therefore may not produce the expected neural effects. Furthermore, it was discussed that the temporal effects of the drugs may not have been sufficiently accounted for, and thus effects may have offset each other (Lipka et al., 2024).

This suggests two challenges for future neuroimaging work. First, pharmacological approaches may be inherently restricted by the absence of the full cascade of physiological and psychological components of natural stress. Second, careful attention to timing will be critical to capture dynamic changes in neural activity. A further methodological challenge will be adapting the IPD-MD task for neuroimaging. While robust imaging analyses typically require large numbers of trials, simple repetition of trials in this task risks introducing confounds, such as increased selfishness in repeated games or learning and reciprocity (Böhm et al., 2020; Halevy et al., 2012; Van Dijk & De Dreu, 2021). Addressing these challenges will be crucial for advancing toward a mechanistic account of how stress neuromodulators shape social decision-making at the neural level.

Lastly, an exciting avenue for future research involves interbrain synchrony, i.e., the degree to which two or more individuals exhibit aligned neural activity during interaction (Schilbach & Redcay, 2025). Social interaction, by definition, involves more than one person, and it has been argued that this is reflected not only in behavior but also in coordinated brain activity across individuals (Hasson et al., 2012). Both animal and human studies have demonstrated that interbrain synchrony relates to key aspects of social dynamics, including the strength of interactions, the emergence of hierarchy, cooperation and competition, and performance in teams (e.g., Hu et al., 2017; Jiang et al., 2015; Kingsbury et al., 2019; Reinero et al., 2021; Yang et al., 2020; Zhang & Yartsev, 2019). Investigating how stress affects

interbrain dynamics could provide a powerful new lens for understanding how stress responses shape collective social behavior.

Conclusion

I opened this dissertation with a metaphor from Pfattheicher et al. (2022, p. 124) about prosociality research as a "field full of wild flowers.". Although this metaphor originally referred to definitional ambiguity, I believe it applies equally well to research on social behavior and its modulation by stress in general. The heterogeneity of approaches offers valuable perspectives that enrich our understanding yet also complicates synthesis.

The work presented here adds a few more "flowers" to this landscape. It shows the multifaceted nature of social behavior and its sensitivity to stress (neuromodulators) but also emphasizes that such effects are far from uniform. Which behavior emerges critically depends on the neuromodulator that dominates the stress response, whether the context is perceived as threatening, and the social relationship between interaction partners. The BLA emerges as a key neural substrate for flexibly expressing prosocial behavior toward close and distant others, and its modulation by cortisol and noradrenaline may provide a plausible mechanism by which stress accentuates us versus them tendencies. At the same time, limited reliability of current measures of choice consistency highlights the need for more robust tools.

Beyond the laboratory, these findings suggest that stress may tip the scale toward either cooperation or conflict in contexts of threat. As societies become increasingly polarized, it becomes crucial to identify the conditions under which stress amplifies or dampens group antagonism.

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Appendix

Eidesstattliche Erklärung

Ich, Luca Marie Lüpken, geb. 24.09.1996, versichere an Eides Statt, dass diese 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.

Essen, 01.10.2025

Luca Marie Lüpken

Study 1 – Original Paper

Lüpken, L.M.*, Schnitzler, A., Kalenscher, T., currently in revision at Hormones & Behavior. No Effect of Glucocorticoid and Noradrenergic Activity on Consistency in Prosocial Choice.
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Luca M. Lüpken: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Visualization, Supervision, Project Administration.

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No Effect of Glucocorticoid and Noradrenergic Activity on Consistency in Prosocial Choice

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Declarations of interest: The work was supported by a grant from the German Research Foundation (Deutsche Forschungsgemeinschaft, Bonn, Germany) to Tobias Kalenscher (grant-ID: DFG-KA 2675/7-1).

Abstract

Internal consistency in decision-making is a hallmark of economic rationality. It is a prerequisite to infer unobservable values and preferences from observed choices. This inference depends on the assumption that preferences remain stable, at least over short periods of time. However, growing evidence suggests that internal physiological states, such as short-term fluctuations in cortisol and noradrenaline after acute stress, can alter values and preferences. It is unclear whether this might lead to inconsistent choices across transitions in neurohormonal stress states. Here, we asked whether the stress neuromodulators cortisol and noradrenaline affect choice consistency in prosocial decision-making. We exogenously manipulated cortisol and/or noradrenaline action in a double-blind psychopharmacological study by administering hydrocortisone, yohimbine, both hydrocortisone and yohimbine, or placebo, to 129 participants. Prosocial decision-making was measured using a modified dictator game before and after drug administration, and choice consistency was quantified within the framework of the Generalized Axiom of Revealed Preferences (GARP). Our results indicate that neither cortisol nor noradrenergic activity affected choice consistency or prosocial decision-making, suggesting that social preferences remain stable despite changes in neurohormonal states. These findings underscore the robustness of choice consistency across changing neurohormonal states.

Keywords: choice consistency, rationality, social preferences, cortisol, noradrenaline, stress

1 Introduction

Stress changes how people make decisions. Stress effects on decision-making have been reported for a range of domains, including risk-taking, loss aversion, and social interaction (Margittai et al., 2018a, 2018b; Sarmiento et al., 2024; Starcke and Brand, 2012; Von Dawans et al., 2021). While the effects are often complex and somewhat unreliable (Forbes et al., 2024; Nitschke et al., 2022), some of these complexities may reflect distinct roles of the main stress neuromodulators cortisol and noradrenaline (Dashti et al., 2025; Margittai et al., 2018b; Schweda et al., 2019).

In the social domain, cortisol has been associated with affiliative and prosocial behavior (Berger et al., 2016; Dashti et al., 2025; Duque et al., 2022; Margittai et al., 2018b; Schweda et al., 2019), and noradrenergic activity has been linked to more antagonistic tendencies (Dashti et al., 2025; Haden and Scarpa, 2007; Nelson and Trainor, 2007; Schweda et al., 2019). For example, Margittai et al. (2018b) studied social discounting, that is, the decrease in financial generosity across social-emotional distance between participant and another person. They found that hydrocortisone administration (a synthetic form of cortisol) increased generosity toward socially close others, e.g., very good friends. This hydrocortisone-driven increase in generosity was mitigated by the additional administration of yohimbine (an alpha-2 adrenergic receptor antagonist that increases noradrenaline release). Similarly, Dashti et al. (2025) showed that cortisol promoted generosity toward in-group members, whereas noradrenaline promoted hostility toward out-groups. These findings suggest that stress-induced neuromodulatory changes bias social decision-making toward either prosocial or antagonistic tendencies, depending on the prevailing neuromodulatory profile, thus shifting the underlying social preferences.

Social preferences are latent constructs that capture how individuals value outcomes for themselves and others. They are central to models of collective behaviors and are assumed to underlie social decisions (Fisman et al., 2017; Kerschbamer and Müller, 2020). Because preferences are not directly observable, they must be inferred from choice patterns. For example, observing an individual's donation behavior toward a charity reveals something about their valuation of the charity's cause. A basic requirement for the inference of preferences from choices is internal consistency in choices – a hallmark

of economic rationality. The Generalized Axiom of Revealed Preference and related axioms (GARP; Houthakker, 1950; Samuelson, 1938) formalize this principle (not just in the social domain, but in general) by imposing logical constraints on observed choices. Put simply, if choice alternative A is chosen over alternative B, B cannot be preferred to A, since, otherwise, B would have been chosen. Additionally, if A is more expensive than B, yet it is still chosen, A must be strictly preferred to B. Violations of GARP indicate that choices cannot be rationalized by a stable preference function, undermining the ability to infer underlying preferences from choices (Afriat, 1967).

This is not merely a formal concern: economic models typically assume stable preferences, at least over short periods of time. However, if internal states, such as stress, alter social preferences, as prior studies suggest, this assumption may no longer hold, and preferences estimated in one internal state (e.g., at baseline) may not generalize to another (e.g., under stress).

Prior research has demonstrated that human choices often adhere to GARP under conditions of cognitive load or physiological strain, such as sleep deprivation, alcohol consumption, drug influence, acute stress, or menstrual cycle phases (Bedi and Burghart, 2018; Burghart et al., 2013; Castillo et al., 2017; Cettolin et al., 2020; Drichoutis and Nayga, 2020; Lazzaro et al., 2016; Nitsch et al., 2021). These findings have been interpreted as evidence that preference-based decision models are robust to such perturbations. However, these studies investigated choice consistency within a given internal state, e.g. within specific time windows of the stress response (Nitsch et al., 2021). They did not address whether choice consistency holds across dynamically shifting states, such as short-term changes in cortisol or noradrenaline in the neurohormonal stress response.

This is a crucial limitation. If preferences are stable within a state but shift between states, individuals may exhibit high block-wise consistency but violate GARP when choices are pooled. For example, someone may act selfishly at baseline and generously during cortisol peak; both patterns may be internally consistent within each neurohormonal state, but the combined choices across neurohormonal states would violate GARP. Such violations would reflect state-dependent shifts in preferences that go undetected unless these internal states are explicitly included in the model.

Thus, in sum, if preferences and choices systematically vary with neurohormonal states, as prior research suggests (Dashti et al., 2025; Margittai et al., 2018b), then behavior aggregated across states may no longer be rationalizable by a stable preference function, challenging a core assumption of economic modelling.

However, the question of whether choice consistency holds across dynamically shifting neurohormonal states has not yet been systematically investigated, even though neuromodulator levels such as cortisol and noradrenaline are known to fluctuate substantially over short time frames (Hermans et al., 2014; Joëls and Baram, 2009). Acute stress, for example, activates the sympathetic-adrenal-medullary (SAM) system and the hypothalamic-pituitary-adrenal (HPA) axis in a time-dependent manner, with noradrenaline peaking rapidly and cortisol rising more slowly but lasting longer.

We, therefore, set out to test whether choice consistency is preserved across neurohormonal stress states, or whether state-dependent shifts in preferences and choices reduce overall consistency. For this, we pharmacologically manipulated cortisol and noradrenaline action by administering the drugs hydrocortisone and / or yohimbine in a placebo-controlled double-blind psychopharmacological study. We hypothesized that, while the drug effects unfold over time, cortisol would increase generosity, whereas noradrenaline would counteract this effect (Dashti et al., 2025; Margittai et al., 2018b), thus reducing choice consistency. Crucially, we analyzed choice consistency by aggregating decisions across multiple time points within the same individuals across the entire experimental session, from baseline to post-drug administration. In sum, this allowed us to assess whether pharmacologically induced changes in neurohormonal states lead to systematic changes in preferences that manifest as reduced choice consistency when decisions are aggregated.

Hence, the contribution of our paper is twofold: first, we complement and extend the literature on the effects of stress on economic decision making by testing the robustness of choice consistency across different stress neuromodulator states. Second, we extend the literature on the effects of stress neuromodulators on social decision making.

2 Method

2.1 Participants

After excluding the data of one participant who reported concerns about the quality of their data, a total of 129 participants (male: n = 63, female: n = 64, non-binary: n = 2) aged between 18 and 35 years were included in the experiment. As described in Section 2.6, we took a Bayesian approach to our data analysis. Consequently, our sample size was determined using a pre-specified Bayesian stopping rule (Nitsch et al., 2021; Rouder, 2014; Schönbrodt et al., 2017): data collection continued until we achieved at least moderate evidence for or against our hypotheses, defined as a Bayes factor (BF) of $BF \geq 3$ in either direction (Jeffreys, 1939; Van Doorn et al., 2021). This threshold has been suggested as roughly analogous to a classical p-value of .05 (Jeffreys, 1961; Keysers et al., 2020).

Participants were included if they were healthy, did not smoke or drink alcohol excessively, did not take drugs and had a BMI between 19 and 26. Pregnant participants and psychology students from the second semester onwards were excluded from participation. Biologically female participants took a pregnancy test to ensure that they were not pregnant. Additionally, participants were instructed to abstain from exercise, sexual activity, alcohol consumption, and medication 24 hours before participation and to stop eating, smoking, and caffeine consumption two hours before participation.

Participants received a fixed compensation of €10 and could earn up to €90 additionally during the experiment. This additional compensation depended both on chance and on the choices participants made during the experiment.

The study was approved by the ethics committee of the University Hospital Düsseldorf and complied with the Declaration of Helsinki.

2.2 Pharmacological manipulation

Participants were pseudo-randomly assigned to one of four experimental groups: hydrocortisone (H; 20mg, Jenapharm, mibe GmbH; N = 31), yohimbine (Y; 20mg, Yocon-Glenwood, Cheplapharm Arzneimittel GmbH; N = 34), hydrocortisone and yohimbine (H+Y; N = 33), or placebo (P; N = 31). The

dosage corresponded to previous studies (Margittai et al., 2018b, 2018a). To ensure that participants could not infer which drug they had received, all groups received an identical number of pills.

2.3 Control measures

2.3.1 Physiological stress response

Cortisol and noradrenergic activation were measured using saliva samples (stress samples; Salivettes; Sarstedt AG & Co. KG, Nümbrecht, Germany) collected at four time points during the experiment (see Figure 1; note that we collected saliva probes at seven time points, but only analyzed four time points). After collection, the samples were frozen at -20°C until analysis by Dresden Lab Services GmbH. While cortisol was measured directly in saliva by immunoassay, salivary alpha-amylase, an indirect marker of noradrenergic activation (Nater and Rohleder, 2009), was determined by an enzyme kinetic method as described in Rohleder et al. (2006). Eight out of 516 total samples could not be analyzed due to insufficient saliva or contamination of the sample.

As an additional marker of sympathetic nervous system activation, heart rate (beats per minute, bpm) was measured at seven time points (Figure 1) throughout the experiment (using Polar A370 watches; Polar Electro Oy).

2.3.2 Subjective stress response

To assess subjective stress levels and mood, participants rated their perceived stress levels on a visual analog scale (VAS) ranging from 0 to 100 and completed the German version of the Positive and Negative Affect Schedule (PANAS, Watson et al., 1988) at four time points (Figure 1).

2.3.3 Sex hormone levels

Because HPA axis reactivity may be influenced by both menstrual cycle and hormonal contraceptives (Kirschbaum et al., 1999), we additionally assessed sex hormone levels (estradiol, progesterone and testosterone) using three saliva samples, collected in approximately 5-minute intervals (sex samples; SaliCaps; TECAN Trading AG) prior to drug intake. The samples were frozen at -20°C after collection and analyzed at Dresden Lab Service GmbH using LC-MS/MS procedure. The three samples were pooled for this analysis to obtain a more reliable result.

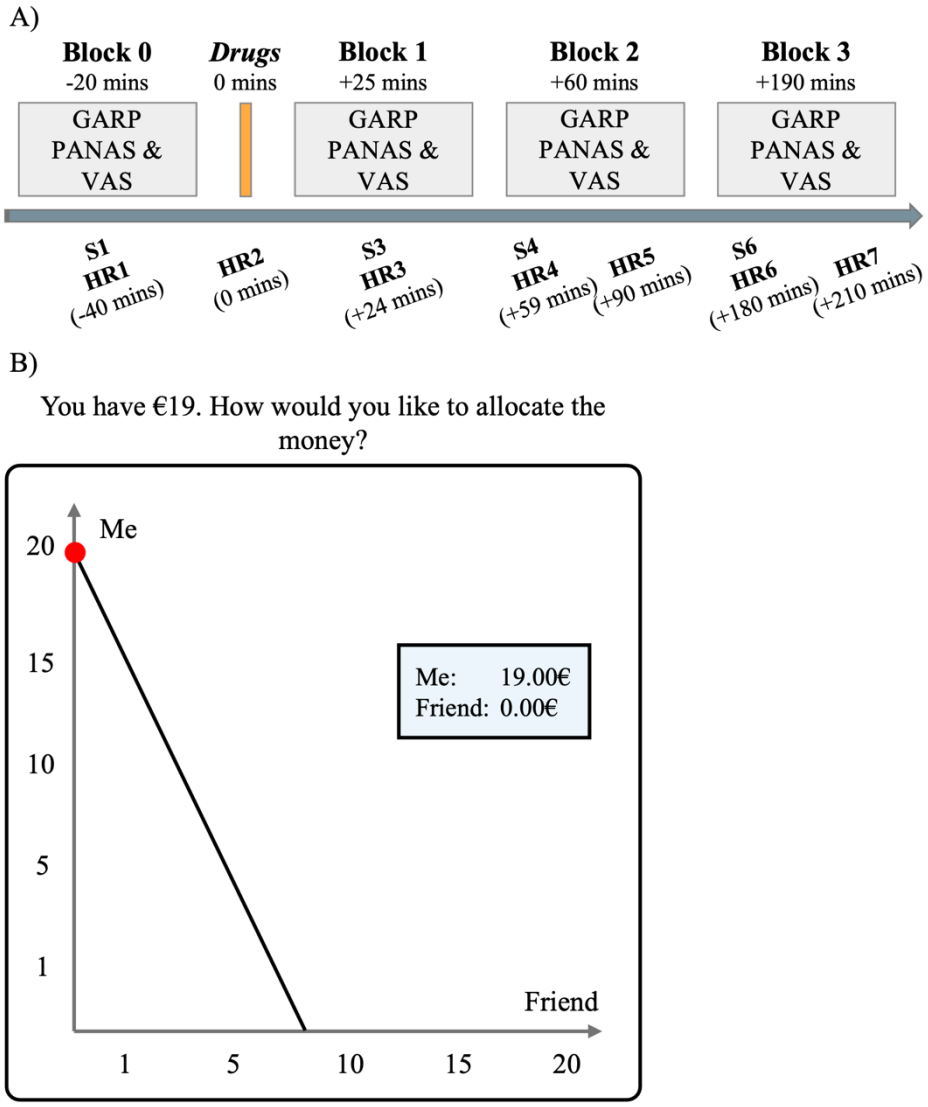

Figure 1. A) Experimental timeline. Trait measures were collected online before data collection in the lab. Saliva samples to analyze sex hormones were taken prior to block 0. Drug intake depended on the group allocation: Participants took either hydrocortisone, yohimbine, hydrocortisone and yohimbine combined, or placebo. Heart rate was measured continuously throughout the session, and values were extracted at the time points indicated in the figure. Abbreviations: S = stress saliva sample, HR = heart rate measurement, GARP = economic decision-making task (GARP task), PANAS = Positive and Negative Affect Schedule, VAS = Visual Analogue Scale for momentary stress. B) Illustration of an example trial of the GARP task. Here, participants had a budget of 19 EUR to allocate between themselves and their best friend by moving a red dot along a diagonal budget line, representing all possible allocation choices. The payouts for each person were displayed dynamically in the upper right corner as the dot was moved. In our task, sharing with others was costly, akin to transfer and transaction costs (see text for details): for example, in this trial, sharing with the best friend was more expensive than keeping money for oneself. Thus, here, if the entire budget of 19 EUR was shared with the best friend, they would receive only 9.50 EUR.

2.3.4 Trait measures

To verify successful group randomization and to control for potential confounding factors, we collected several trait measures via an online questionnaire prior to participation in the experiment. The online questionnaire took approximately 45 minutes to complete and included a list of the exclusion criteria as well as eleven questionnaires (see Supplementary Materials for a list).

2.4 Procedure

Prior to participating in the experiment, participants completed the online questionnaire, which included the trait measures and exclusion criteria. The experimental sessions always started at 2 pm to control for circadian variations in cortisol levels and lasted on average 4 hours and 15 minutes (SD = 0.18). Upon arrival at the lab, participants were given information about the experiment, gave informed consent, and filled in a screening questionnaire to check for exclusion criteria. Participants who met any of the exclusion criteria were excluded from participation. Subsequently, participants provided the three sex saliva samples as well as demographic information, including age, gender, education, and gross monthly income.

As mentioned, participants were pseudo-randomly assigned to one of the four pharmacological conditions (H, Y, H+Y and P; see above). All participants completed our experimental task (GARP task, see below) at four time points relative to drug intake: -20 minutes (block 0 / baseline), +25 minutes (block 1), +60 minutes (block 2), +190 minutes (block 3, see Figure 1). We opted for repeated measures of our GARP task to observe the evolution of choices and preferences as the drug effects unfolded. In addition to our experimental task, other tasks were completed at these time points (Moral Decision Task, EMCS, Singer et al., 2019; Affect Misattribution Task, AMT, Ling et al., 2023), the data of which will be reported elsewhere. After the last measurement block, the participants provided information about their beliefs about the effects of the drugs and guessed which drug they had received. Additionally, we emphasized the importance of data quality and acknowledged the potential challenges of maintaining attention during the lengthy experiment. Participants were then asked if they consented to the use of their data and were assured that there would be no repercussions for refusing.

During the shorter breaks immediately after drug intake and after block 1, participants were given simple 200-piece puzzles. During the longer break after block 2, participants watched emotionally neutral documentaries about nature and craftsmanship. Throughout the experiment, participants were asked not to use their phones or talk to each other.

2.5 GARP task

We employed a modified dictator game adapted from Andreoni and Miller (2002), in which participants allocate money between themselves and another person. In this game, we manipulated the social distance to the other person: participants decided on the allocation between either themselves and their best friend, or themselves and a stranger. To be able to quantify choice consistency within the GARP framework, we additionally manipulated the budget constraint as well as the prices of the money allocations to oneself and the other person, as explained in the following. In each trial, participants had varying amounts of money available to allocate between themselves and the other person, i.e., the budget constraint was variable. The prices for these allocations also varied from trial to trial, akin to transfer and transaction costs. This implies that participants or the other persons did not necessarily receive exactly what the participants allocated, but potentially less, depending on the transfer prices set for each trial. To illustrate, let's consider two scenarios with different price settings. If the price was set to 1/3, the participant kept precisely what they allocated to themselves, while the other person received only 1/3 of the participant's allocation to that person - equivalent to an exchange rate of 1/3. Conversely, if the price was 3, the participant kept only 1/3 of their allocation to themselves, while the other person received precisely what the participant allocated to that person. For further clarification, consider a trial with a budget of €20 and a price of 1/3. If the participant allocated, say, €5 to the other person and €15 to themselves, the participant would receive €15, while the other person would receive only €1.67, i.e., one third of the €5 allocated to the other person.

In contrast to Andreoni and Miller (2002), we used a graphical representation inspired by Choi et al. (2007) and analogous to the diagram task in Nitsch et al. (2022). In this representation, in each trial, participants saw a coordinate system in which the y-axis represented themselves, and the x-axis

represented the other person (best friend or stranger). Within this graphical space, participants chose by selecting a point along a diagonal line that represented all possible money allocation options based on the budget and price constraints of the trial. At the same time, they could check the current money allocation to themselves and to the other person (best friend or stranger) in a box in the upper right corner of the coordinate system (see Figure 1). The slope of the diagonal line reflected the price in each trial, i.e., a steeper line indicated a potentially higher maximum payout for the participant compared to the other person (best friend or stranger).

Participants made a total of 160 decisions throughout the experiment, with each decision involving either their best friend or a stranger as the recipient. Within each block, participants made 20 decisions with their best friend and 20 decisions with a stranger, for a total of 80 decisions per recipient type. The budget for each decision ranged from €5 to €20 in whole numbers, and the prices varied among 1/3, 1/2, 1, 2, or 3. This setup resulted in 15 budget levels and 5 price levels. All price x budget combinations were presented for both recipient types, resulting in 80 unique trials per recipient type. The order of the trials was pseudo-randomized across the experiment for each recipient type. We ensured that this task setup was sufficiently sensitive to detect GARP violations by running multiple simulations (see Supplementary Materials).

At the end of each measurement block, one decision made within that block was randomly selected, and the amount the participant allocated to themselves, and the other person (best friend or stranger) was added to the total payout. Thus, the money the participant allocated to themselves was paid out directly to the participant, while the money allocated to the other person was paid out to that person. The participant's best friend received their share by mail, while the stranger was a randomly selected individual encountered by the research team on campus. For example, if the randomly selected decision involved an allocation of €15 to the participant and €1.67 to a stranger, the participant would receive an additional €15 at the end of the study, while a random person on campus would receive €1.67.

On each trial, participants were given 20 seconds to make their allocation decision. The time limit was set to ensure that the time constraints of the experimental protocol could be met. Reaction time data

from a previous study indicated an average decision speed of 4 seconds. Thus, the 20-second time limit gave participants sufficient time to make their decision. In our experiment, participants took an average of 5.8 seconds to decide, confirming the adequacy of the time limit. On average, participants missed 2.89 (SD = 4.75) trials, indicating that while most decisions were made within the allotted time, there were occasional cases where the time limit was exceeded.

Prior to the baseline measurement, comprehension of the task and its payout structure was assessed using 5 comprehension questions. These questions addressed different aspects of the task, such as the possibility of earning additional money for oneself, understanding the allocation of money to friends and strangers, and understanding of the payout process. Participants could only proceed with the task if they answered correctly. If they answered incorrectly, the experimenter explained the task again to ensure correct understanding. In addition, participants were given 5 practice trials to familiarize themselves with the task and ensure that they understood how to interact with the task interface.

Each block included an attention check trial for decisions involving both the best friend and the stranger as the recipient, which occurred after half of the decisions within the block had been made for each recipient type. The intention behind these trials was to ensure participants' continued engagement and attention to the task instructions. Participants who failed all attention checks were excluded from the main analyses ($N = 10$), resulting in a final sample of 119 participants (H: N = 30, Y: N = 29, H+Y: N = 31, P: N = 29). Importantly, our results remained robust across a range of exclusion criteria based on attention checks. This included analyzing the full sample (i.e., including participants who failed all attention checks) as well as analyses applying increasingly stringent thresholds, such as excluding participants who failed at least one, two, or three checks (see Supplementary Materials).

2.5.1 Prosocial decision-making

To quantify prosocial decision-making, we calculated the proportion of the budget that participants shared with the other person for each trial. These proportions were then averaged per participant to obtain a mean "share" score for each recipient type within each measurement block.

2.5.2 Choice consistency

Several indices have been developed to quantify the extent to which participants make internally inconsistent choices in economic decision tasks, i.e., the extent to which they deviate from satisfying GARP. One of the most prominent of these indices is the Critical Cost Efficiency Index (CCEI; Afriat, 1973, 1972; Varian, 1993).

The CCEI measures how cost-efficient choices are: internally consistent choices are perfectly cost-efficient, while inconsistent choices are not. Cost-inefficiency means that an individual with inconsistent choices could have obtained alternative, but equally valued options for less money, thereby wasting some of their budget. For example, imagine someone's choice reveals that they value sharing 5 EUR with a friend at least as much as keeping 5 EUR to themselves. Later, they again choose to share 5 EUR with their friend, even though the price of sharing money has increased by 10% more than the price of keeping it. Knowing that keeping 5 EUR is at least as good as sharing 5 EUR, the decision-maker has overspent by at least 10%, making their choices 90% cost-efficient (example adapted from Nitsch et al., 2021, p. 105289).

The CCEI identifies the most severe violation of GARP and then determines the minimum amount by which the budget must be reduced to eliminate all GARP violations. It ranges from 0 (representing minimal choice consistency) to 1 (representing perfect choice consistency). Thus, the CCEI for the example above would be 0.9, reflecting a 90% cost-efficiency. For each participant, we calculated CCEI scores across all choices made in the experiment per recipient type following the methodology previously used by Nitsch et al. (2022).

2.6 Data analysis

We chose a mixed-factorial Bayesian analysis of variance (ANOVA) because it allows us to quantify evidence against effects (Van Den Bergh et al., 2020).

To test our hypotheses, we averaged across matched models to extract Bayes factors (BF) for each predictor (Van Den Bergh et al., 2020). Therefore, we used Bayes factors for inclusion ("BF_{incl}") to represent evidence in favor of a predictor and Bayes factors for exclusion ("BF_{excl}") to represent evidence

against a predictor. This approach efficiently handled the extensive model comparisons required for our hypotheses and maintains consistency.

We used uninformative default priors (Rouder et al., 2012) due to limited or inconclusive prior evidence on the effects of stress neuromodulators on choice consistency and prosocial decision-making. Bayes factors are interpreted as follows: inconclusive or weak evidence for $BF < 3$, moderate evidence for $3 \leq BF \leq 10$, and strong evidence for $BF > 10$ (Jeffreys, 1939; Van Doorn et al., 2021). Post-hoc tests with repeated analyses were corrected by fixing prior probabilities that the null hypothesis holds to 0.5 (JASP Team, 2024; Westfall et al., 1997).

To test our first hypothesis that cortisol would increase generosity, whereas noradrenaline would counteract this generosity-boosting effect of cortisol, social distance (friend, stranger) and block (baseline, block 1, block 2, block 3) were within-subject factors, and drug condition (H, Y, H+Y, P) was a between-subject factor. The dependent variable was the share score. To test the second hypothesis that the shift in prosocial choices over time would manifest as reduced choice consistency if all choices across the experiment were considered, we used a similar model but removed the within-subject factor block and instead used the CCEI as the dependent variable. To assess the effectiveness of the pharmacological manipulation, we used the respective subjective or physiological stress measure as the dependent variable, including only block as a within-subject factor and drug condition as a between-subject factor.

Additionally, we tested for group differences in each trait measure using Bayesian ANOVA for continuous measures and Bayesian contingency tables for categorical measures to rule out systematic group differences prior to our manipulation. We also evaluated the success of the double-blinding by using a Bayesian binomial test to determine whether subjects could correctly guess which substance they had received.

Preprocessed data are available online: https://osf.io/bnxjt/?view_only=64e5a13c91ad4eb7a98d6f338a46ccb9.

Table 1: Demographic and trait measures per experimental group

Variable	Placebo Group *N*	Hydrocortisone Group *N*	Yohimbine Group *N*	Hydrocortisone + Yohimbine Group *N*	BF_{10}
Sample	31	31	34	33	
Gender					< 0.01
Female	14	15	18	17	
Male	16	15	16	16	
Non-binary	1	1	0	0	
University Degree					0.59
Yes	9	16	7	10	
No	22	15	27	23	
Income Friend < €20,000					<0.01
Yes	14	14	20	23	
No	10	8	6	7	
SVO					0.06
competitive	0	1	0	3	
individualistic	16	6	10	5	
prosocial	14	20	21	18	
unclassified	1	4	3	7	
	M (SD)	*M (SD)*	*M (SD)*	*M (SD)*	
Age (years)	24.16 (3.09)	24.35 (4.1)	23.47 (3.41)	24.00 (3.67)	0.06

Income (€)	1338.71 (1600.14)	1725.81 (1862.07)	1370.59 (1781.31)	1093.94 (1130.80)	0.11
TICS	139.68 (33.87)	147.48 (28.43)	147.79 (27.28)	145.48 (32.08)	0.07
BIS / BAS					
Behavioral Inhibition	15.45 (4.75)	13.65 (3.31)	14.38 (3.95)	13.97 (4.64)	0.14
Fun Seeking	7.58 (2.13)	7.68 (1.99)	7.26 (1.78)	7.73 (2.04)	0.06
Reward Responsiveness	7.94 (1.75)	8.00 (1.73)	7.24 (1.94)	7.97 (2.32)	0.16
Drive	7.19 (2.15)	7.23 (1.69)	7.41 (2.05)	7.06 (2.34)	0.05
BFI-10					
Extraversion	3.02 (1.06)	3.34 (0.79)	2.99 (1.03)	3.06 (0.97)	0.11
Openness	3.94 (0.89)	3.53 (1.13)	3.66 (1.13)	3.44 (1.10)	0.18
Agreeableness	3.40 (0.89)	3.19 (0.90)	3.22 (0.75)	3.14 (0.85)	0.08
Conscientiousness	3.39 (0.86)	3.53 (0.90)	3.41 (0.82)	3.44 (0.82)	0.05
Neuroticism	2.84 (1.01)	3.00 (0.72)	2.87 (1.01)	2.88 (0.96)	0.05
BIS-15	36.65 (2.60)	36.45 (2.55)	36.62 (2.37)	37.00 (2.32)	0.06
CRT	2.07 (1.00)	1.65 (1.08)	1.74 (1.14)	2.06 (1.00)	0.20
E-Scale	77.58 (16.05)	79.35 (13.68)	81.62 (13.18)	80.58 (16.65)	0.07
MEQ	13.42 (3.91)	12.45 (3.44)	13.32 (3.35)	13.03 (3.36)	0.07
STAI					
General	39.68 (7.89)	41.45 (6.59)	43.85 (7.93)	42.24 (8.91)	0.25
Moment	35.45 (8.45)	36.94 (8.37)	37.18 (7.88)	37.03 (9.11)	0.06
SDS-17	10.90 (2.29)	10.23 (2.50)	10.21 (2.66)	10.03 (3.07)	0.09
Perspective Taking	-0.01 (0.14)	0.02 (0.15)	-0.11 (0.24)	-0.10 (0.32)	0.74

Testosterone (pg/ml)	54.67 (54.07)	47.33 (47.88)	51.59 (49.63)	53.74 (50.93)	0.05
Progesterone (pg/ml)	12.84 (29.73)	11.13 (22.50)	18.98 (45.13)	11.45 (33.49)	0.07
Estradiol (pg/ml)	5.80 (7.84)	3.68 (1.30)	3.38 (1.87)	3.67 (2.57)	0.53
Baseline					
Cortisol (nmol/L)	6.27 (5.86)	5.10 (4.73)	6.48 (6.80)	4.60 (3.85)	0.12
Alpha-Amylase (U/ml)	79.80 (70.21)	63.06 (59.45)	92.93 (110.66)	58.36 (57.73)	0.19
Heart rate (bpm)	73.74 (13.65)	71.06 (9.55)	75.47 (11.06)	70.61 (11.7)	0.18
Positive Affect	2.92 (0.63)	2.68 (0.72)	2.75 (0.60)	2.79 (0.72)	0.09
Negative Affect	1.27 (0.40)	1.35 (0.38)	1.26 (0.39)	1.29 (0.36)	0.06
Subjective Stress	20.29 (19.57)	20.55 (21.78)	23.62 (18.84)	14.06 (17.02)	0.22

Note. As described in Section 2.6, we used a Bayesian approach to our data analysis. Bayes factors (BF) were calculated using uninformative priors. BF_{10} represents evidence in favor of the alternative hypothesis: values of $BF_{10} \geq 3$ can be interpreted as moderate evidence for systematic group differences prior to pharmacological manipulation, while values of $BF_{10} < 1$ can be interpreted as evidence against systematic group differences. Abbreviations: BFI-10 = Big Five Inventory (10 item version), BIS-15 = Barratt Impulsiveness Scale, BIS/BAS = Behavioral Inhibition/Activation Scale, bpm = beats per minute, CRT = Cognitive Reflection Test, M = mean, MEQ = Morningness-Eveningness-Scale, nmol/L = nanomoles per liter, pg/ml = picograms per milliliter, SD = standard deviation, SDS-17 = Social Desirability Scale (17 item version), STAI = State-Trait-Anxiety Inventory, SVO = Social Value Orientation, TICS = Trier Inventory of Chronic Stress, U/ml = units per milliliter. For a complete list of the trait questionnaires and references, see Supplementary Materials

3 Results

3.1 Trait and baseline measures

Overall, our analysis showed no conclusive evidence of group differences across a range of trait, demographic, and baseline measures, including sex hormone levels, heart rate, subjective stress and mood, salivary cortisol, and salivary alpha-amylase (see Table 1). This indicates that our randomization protocol was effective in ensuring that there were no systematic differences between experimental conditions prior to the pharmacological manipulation.

3.2 Subjective stress measures

3.2.1 Positive affect

We found strong evidence for an effect of measurement block ($BF_{incl} > 100$) on positive affect in the PANAS, and moderate to strong evidence against an effect of drug condition ($BF_{excl} = 4.20$) or a condition by block interaction ($BF_{excl} > 100$). Post-hoc tests showed evidence of a decrease in positive affect between baseline and block 2 (adjusted posterior odds > 100), baseline and block 3 (adjusted posterior odds > 100), block 1 and block 2 (adjusted posterior odds > 100), and block 1 and block 3 (adjusted posterior odds > 100). Thus, positive affect decreased across the experiment regardless of drug condition (see Figure 2).

3.2.2 Negative affect

We found strong evidence for an effect of measurement block ($BF_{incl} > 100$) on negative affect in the PANAS, and moderate evidence against an effect of drug condition ($BF_{excl} = 6.12$). Additionally, we found no conclusive evidence supporting a condition by block interaction ($BF_{incl} = 0.70$). Post-hoc tests showed evidence of a decrease in negative affect from baseline to block 3 (adjusted posterior odds > 100), block 1 to block 3 (adjusted posterior odds > 100), and block 2 to block 3 (adjusted posterior odds = 21.74, see Figure 2). This means, negative affect remained relatively stable throughout the experiment until block 3, when it decreased across all drug conditions.

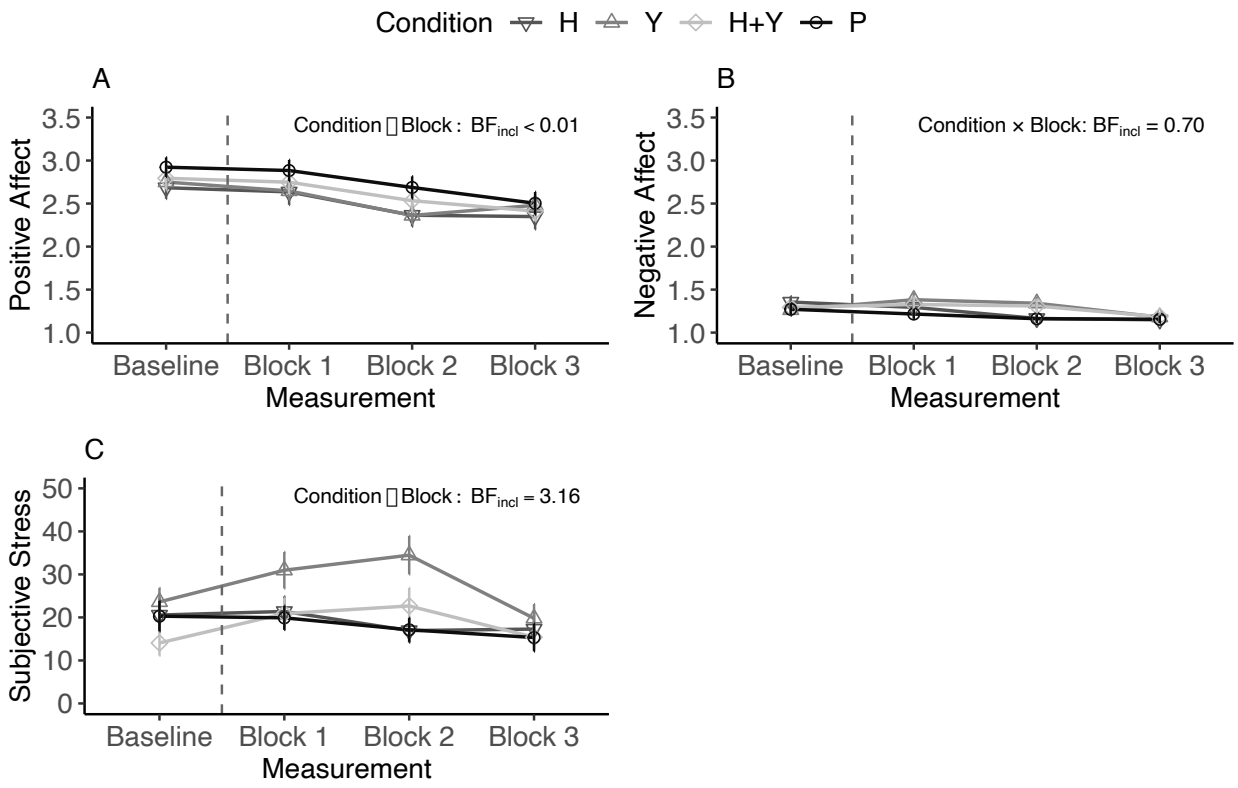

Figure 2. Subjective stress and affect measures. (A) Mean positive affect (± standard error of the mean, SEM), (B) negative affect (± SEM), and (C) subjective stress levels (± SEM) across measurement blocks by drug condition. Affect was measured using the Positive and Negative Affect Schedule and subjective stress was measured using a visual analogue scale ranging from 0 to 100. The vertical dashed line marks the moment of drug administration (after baseline and before block 1). Blocks correspond to the approximate time point post-intake (in minutes) of stress and affect measures: Block 1 ~ +25 min, Block 2 ~ +60 min, Block 3 ~ +190 min. Subjective stress levels were increased in the yohimbine group compared to the hydrocortisone and placebo groups in block 2 (adjusted posterior odds = 7.58 and 7.13, respectively). No group differences were observed at baseline, block 1, or block 3. Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone and yohimbine combined, P = placebo.

3.2.3 Subjective stress level

We found strong evidence for a main effect of measurement block ($BF_{incl} > 100$) on subjective stress levels, and moderate evidence for a block x drug condition interaction ($BF_{incl} = 3.16$), but no conclusive evidence for a main effect of drug condition alone ($BF_{incl} = 0.80$). To follow up on the interaction effect, we conducted block-wise analyses of drug effects. These revealed no evidence for drug effects in block 1 ($BF_{incl} = 0.46$) or in block 3 ($BF_{incl} = 0.07$). In block 2, there was strong evidence for a drug effect ($BF_{incl} = 13.33$), with participants in the yohimbine group reporting higher subjective stress

than those in the hydrocortisone (adjusted posterior odds = 7.58) or placebo groups (adjusted posterior odds = 7.13; all other adjusted posterior odds < 0.5).

3.3 Physiological stress measures

3.3.1 Heart rate

We found moderate evidence for an effect of time point (BF_{incl} = 5.56) on heart rate, and strong evidence against a time point by drug condition interaction (BF_{excl} > 100). There was no conclusive evidence in favor of an effect of condition (BF_{incl} = 0.57). Post-hoc tests revealed strong evidence for differences between time point 1 and all other time points (all adjusted posterior odds > 100), as well as between baseline and time point 3 (adjusted posterior odds = 13.48), and time point 4 (adjusted posterior odds = 35.33, see Figure 3). Descriptively, we observed an increase in heart rate during drug intake, followed by a decrease below baseline, after which it remained relatively stable.

3.3.2 Cortisol

We found strong evidence for a main effect of measurement block (BF_{incl} > 100), drug condition (BF_{incl} > 100), and a block x condition interaction (BF_{incl} > 100) on salivary cortisol levels. To follow up on the interaction effect, we conducted block-wise comparisons between drug groups. These revealed a drug effect in all blocks (BFincl > 100). Cortisol levels rose sharply from baseline in the hydrocortisone and combined groups and remained elevated throughout the experiment (blocks 1, 2, and 3; all adjusted posterior odds > 100). In contrast, cortisol levels in the yohimbine and placebo groups remained relatively stable across all blocks (all adjusted posterior odds < 0.89; see Figure 3). This confirms that hydrocortisone administration, either alone or in combination with yohimbine, effectively manipulated cortisol levels.

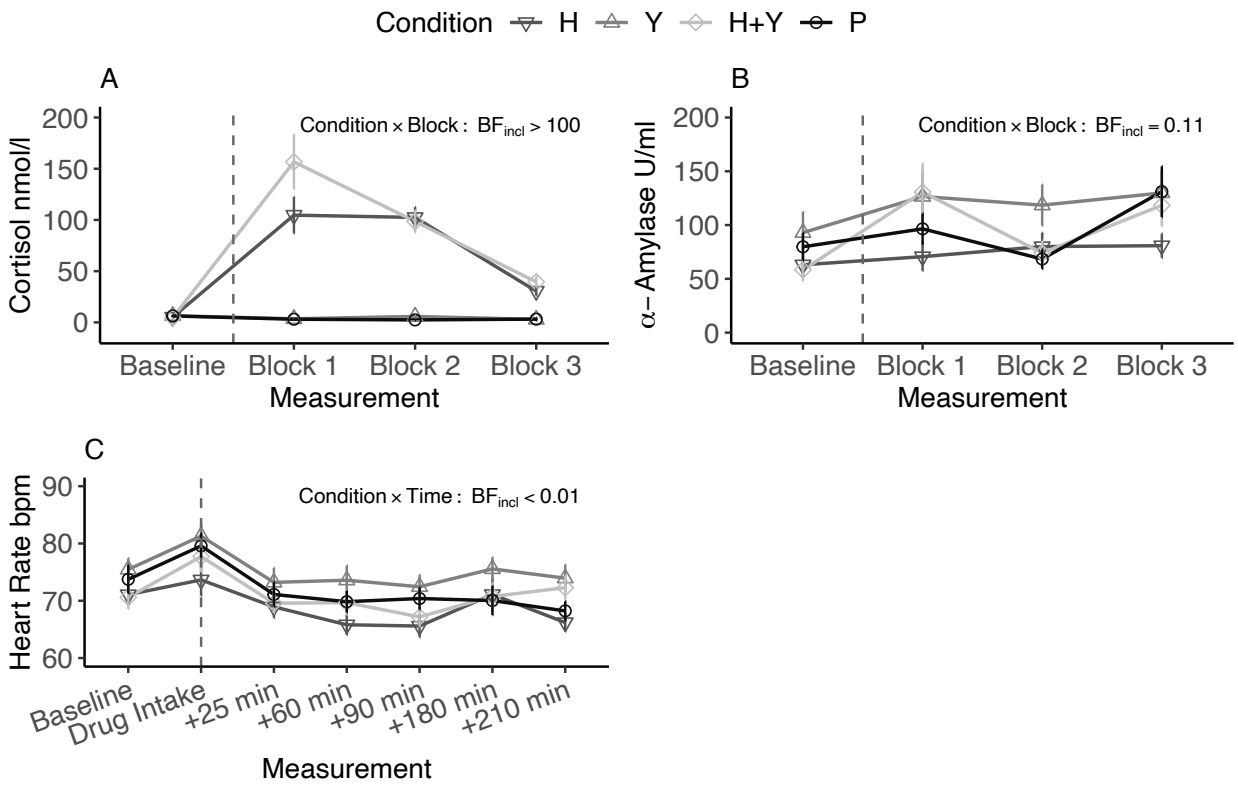

Figure 3. Physiological stress measures. (A) Mean salivary cortisol levels (± SEM), (B) mean salivary alpha-amylase activity (± SEM), and (C) mean heart rate (± SEM) across measurement blocks by drug condition. The vertical dashed line marks the moment of drug administration (after baseline and before block 1). Blocks correspond to the approximate time point post-intake (in minutes) of physiological stress measures: Block 1 ~ +24 min, Block 2 ~ +59 min, Block 3 ~ +180 min. Salivary cortisol levels were increased in the hydrocortisone and combined groups compared to the placebo and yohimbine groups at each post-baseline time point (blocks 1–3; all adjusted posterior odds > 100). They remained stable across blocks in the placebo and yohimbine groups (all adjusted posterior odds < 0.89). Salivary alpha-amylase activity increased in all participants, exploratory analyses suggest that is was more pronounced in participants receiving yohimbine alone, or combined with hydrocortisone. Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone and yohimbine combined, P = placebo, nmol/L = nanomoles per liter, U/ml = units per milliliter, bpm = beats per minute.

3.3.3 Alpha-Amylase

We found strong evidence for an effect of measurement block ($BF_{incl} > 100$), and moderate evidence against an effect of drug condition ($BF_{excl} = 3.52$) or a block by condition interaction ($BF_{excl} = 8.86$) on salivary alpha-amylase. Post-hoc tests showed evidence of increased salivary alpha-amylase in blocks 1 and 3 compared to baseline (all adjusted posterior odds > 100), as well as in block 3 compared to

block 2 (adjusted posterior odds = 19.60, see Figure 3). The block effect indicates that the autonomic activity of our participants changed over the course of the experiment.

Exploratory analyses of the area under the curve with respect to increase of salivary alpha-amylase activity (AUC_I; Pruessner et al., 2003) provide a somewhat more nuanced picture. Both the yohimbine and yohimbine + hydrocortisone groups showed AUC_I values clearly above zero (all $BF_{+0} > 10$), while the hydrocortisone and placebo groups did not ($BF_{+0} = 0.84$ and 1.08, respectively). This suggests that alpha-amylase activity increased more strongly in the groups that received yohimbine relative to a generally elevated alpha-amylase response across all conditions.

This somewhat unclear interaction effect between measurement block and drug condition on salivary alpha-amylase is not particularly surprising given that it is only an indirect and very noisy measure of central noradrenergic activity (Rohleder and Nater, 2009). For instance, it was demonstrated that alpha-amylase correlates with serum noradrenaline only to a limited extent, which is why alpha-amylase is only partially suitable as a marker for changes in noradrenergic activity (Nater et al., 2006). In addition, it is possible that the general autonomic activity of the participants in all conditions masked effects of increased noradrenergic activity due to bathroom breaks and general arousal and subjective nervousness, e.g., during drug intake (white coat effects).

3.3.4 Treatment belief

Consistent with previous studies (Margittai et al., 2018b), participants were unable to accurately identify which drug they had received. In fact, their guesses were systematically incorrect, with false guesses exceeding the 25% chance level ($BF_{+0} > 100$).

3.4 GARP task

3.4.1 Prosocial decision-making

To test if the drugs changed social preferences as their pharmacological effects unfolded, we calculated how much money the participants shared with their friend, or with a stranger, in each measurement block and drug condition. We found moderate to strong evidence against an effect of condition ($BF_{excl} = 3.89$) or interactions between condition and any other factor on the share score (x

distance: BF_{excl} = 2.38, x block: BF_{excl} = 11.12, x distance x block: BF_{excl} = 14.49), as well as strong evidence against a social distance by block interaction (BF_{excl} = 79.70). Additionally, we found strong evidence for an effect of distance (BF_{incl} > 100) and moderate evidence for an effect of block (BF_{incl} = 9.43). Post-hoc tests showed that there was a decrease in sharing from baseline to block 3 (adjusted posterior odds = 5.24) as well as from block 1 to block 3 (adjusted posterior odds = 6.68). Overall, participants shared less with socially distant than with socially close others, and they also shared less at the end of the experiment than in the beginning (see Figure 4). However, we found conclusive evidence against an effect of the drugs on sharing behavior, suggesting that the drugs did not change our participants' social preferences.

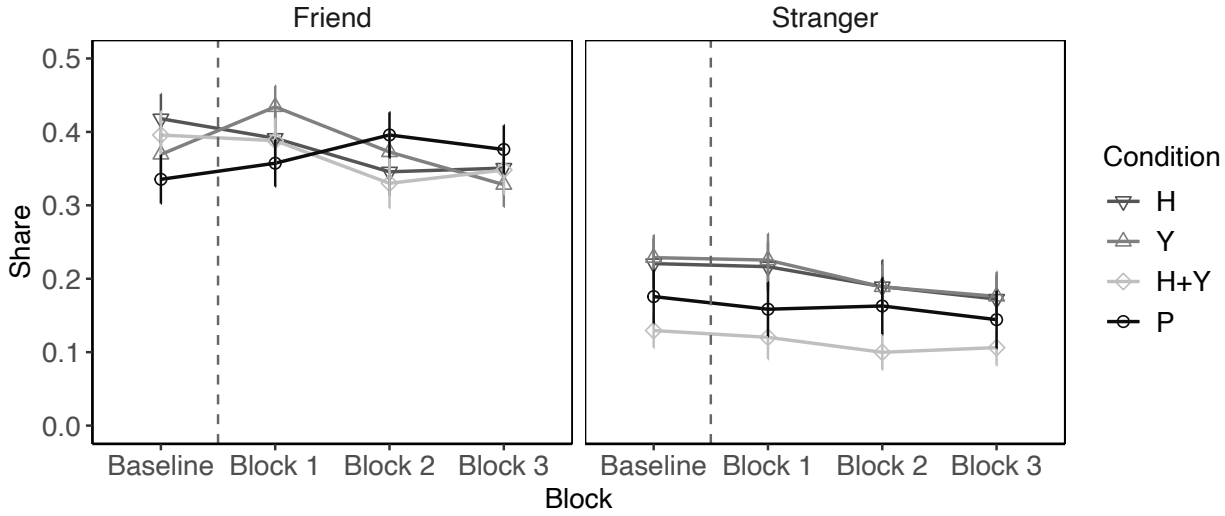

Figure 4. Prosocial behavior. Mean share score (± SEM) across measurement blocks by drug condition, separately for recipient type (friend or stranger). The vertical dashed line indicates the time of drug administration (after baseline and before block 1). Blocks correspond to approximate minutes post-intake: Block 1 ~ +25 min, Block 2 ~ +60 min, Block 3 ~ +190 min. Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone and yohimbine combined, P = placebo.

3.4.2 Choice consistency

As explained above, for each participant, we computed the CCEI across all trials and measurement blocks in the experiment. If the drugs indeed changed the participants' social preferences as their pharmacological effects unfolded, we would expect a systematic change in prosocial allocation

choices, which should manifest in a lowered CCEI when computed across all trials. However, we found moderate evidence against an effect of drug condition ($BF_{excl} = 7.52$), social distance ($BF_{excl} = 4.20$), or condition by social distance interaction ($BF_{excl} = 6.85$) on the CCEI. This means, participants' CCEI across all choices made in the experiment were unaffected by the pharmacological manipulation (see Figure 5).

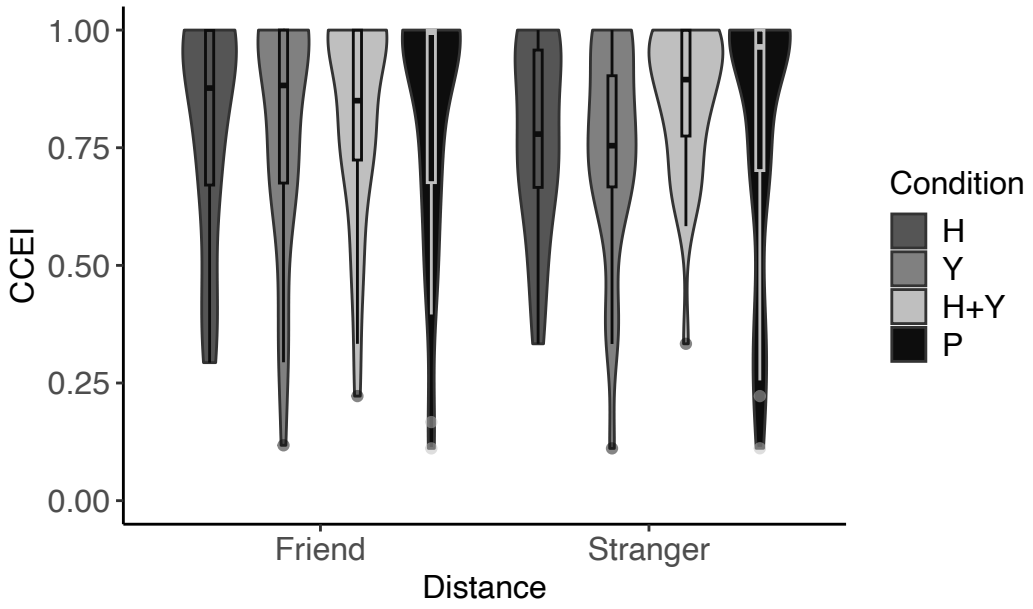

Figure 5. Choice consistency. Mean CCEI scores (± SEM) by drug condition, separately for recipient type (friend or stranger). Abbreviations: H = hydrocortisone, Y = yohimbine, H+Y = hydrocortisone and yohimbine combined, P = placebo.

4 Discussion

In our study, we used a psychopharmacological approach to test the stability of choice consistency and social preferences across varying levels of glucocorticoid and noradrenergic activity. To this end, we administered hydrocortisone, yohimbine, a combination of both hydrocortisone and yohimbine, or placebo to participants playing a modified dictator game. In this game, participants made repeated choices on money allocations between themselves and either a friend or a stranger. To be able to quantify choice consistency within the GARP framework, we manipulated the budget constraint as well as the prices of the money allocations (akin to transfer and transactions costs). We measured sharing

behavior at baseline and at several time points after drug administration and assessed choice consistency across all choices. We found moderate to strong evidence against drug effects on both sharing behavior and choice consistency.

Specifically, across all drug conditions, participants shared more with close others (best friends) than with distant others (strangers), replicating the well-documented social discounting phenomenon (Jones and Rachlin, 2006; Margittai et al., 2018b, 2015), but they shared less over time. Hence, contrary to our hypotheses, fluctuating levels of stress neuromodulators did not systematically alter social preferences or choice consistency.

These findings extend prior work on the robustness of choice consistency during altered cognitive or neurohormonal states such as stress, menstrual cycle phases, or cognitive load (Cettolin et al., 2020; Drichoutis and Nayga, 2020; Lazzaro et al., 2016; Nitsch et al., 2021). Importantly, these past studies have focused on within-state choice consistency, i.e. whether individuals make internally consistent choices during a specific internal state, such as specific time windows of the stress response (Nitsch et al., 2021). Our design instead assessed whether choices remained internally consistent across transitions in neurohormonal states. For this, we computed our consistency measure across the entire time course as the drugs unfolded their effects. Despite these dynamic shifts in cortisol and noradrenaline action, we found no drug effects on choice consistency, likely due to the stability of social preferences. Our results suggest that even under dynamic internal states, social preferences remain sufficiently stable to satisfy the core assumption of preference-based choice models, thus implying that it is not necessary to consider transient but unobservable stress states of individuals in the analysis of choices and preferences.

At the same time, we did not replicate previous findings that showed that hydrocortisone administration increased generosity toward close others and that concurrent yohimbine administration abolished this effect (Margittai et al., 2018b). Although we used an identical pharmacological protocol, our study design differed in several ways. Specifically, we used a more complex choice environment, where we introduced transaction costs (prices of sharing) to assess choice consistency, had repeated within-subject measurements, and employed a budget line as a response scale. These design differences

may have increased cognitive demands or masked subtle motivational shifts that can be observed in simpler choice paradigms, potentially contributing to our inability to replicate prior findings.

This discrepancy aligns with recent evidence showing that the effects of stress on social decision-making are not universal, but rather appear to be highly complex and context-dependent (Nitschke et al., 2022; Sarmiento et al., 2024). For example, minor methodological differences, such as different response scales, may influence the observed stress effects on prosocial choice (Nitschke et al., 2022). In this context, it has been suggested that stress does not uniformly increase or decrease prosocial behavior, but, instead, the effects may vary depending on the specific needs triggered and the contextual stimuli present (Dashti et al., 2025; Faber and Häusser, 2022). Taken together, these findings and recent theoretical advances suggest that stress and stress neuromodulators do influence social preferences, but in ways that are context-sensitive, goal-dependent, and shaped by the structure of the choice environment.

The manipulation checks provided strong evidence for the successful manipulation of cortisol levels by hydrocortisone administration. In contrast, yohimbine administration did not reliably produce elevated salivary alpha-amylase as an indirect proxy for central noradrenergic activity. However, this is not particularly surprising given that previous studies have shown that salivary alpha-amylase does not reliably correlate with serum noradrenaline, suggesting that it reflects general autonomic activity rather than specific noradrenergic effects in the brain (Nater et al., 2006). In addition, general autonomic activity in participants, such as arousal and physical activity, may have masked yohimbine-induced effects on salivary alpha-amylase. Since the mechanism of yohimbine's action on noradrenaline is well-established (Berlan et al., 1991; Charney et al., 1982; Goldberg et al., 1983), we are confident that our manipulation was successful, although, admittedly, our study lacks data to support this, highlighting the need for better readouts of central noradrenergic activity.

Choice consistency is often used to define economic rationality and treated as a trait or state characteristic of individuals. However, we have recently criticized the psychometric properties of contemporary measures of choice consistency, such as the CCEI (Nitsch et al., 2022). Specifically, we identified low inter-method and test-retest reliability in these measures, implying that they are not reliable

enough to qualify as psychometric indices of economic rationality as a characteristic of individuals (Nitsch et al., 2022). While this is a major problem for correlational studies (Nitsch et al., 2022), it is less of a problem for designs involving experimental manipulations and group comparisons, as we have done here. In addition, here, we explicitly refrain from making claims about economic rationality as an individual state or trait, thus avoiding psychometric statements and conclusions. We opted for the CCEI as a measure of choice consistency in the absence of a better measure. Yet, we continue to stress the clear need within economic modeling to develop alternative measures with improved psychometric properties. These new measures would not only enhance the accuracy and reliability of the assessment of choice consistency but would also contribute to a more nuanced understanding of how various factors, including neurobiological influences and, perhaps, stress, shape economic behavior.

4.1 Conclusion

In conclusion, our study provides evidence for consistency in social choice behavior across varying levels of glucocorticoid and noradrenergic activation. It extends previous findings showing that choice consistency is maintained during altered cognitive and neurohormonal states. We show that standard economic modelling and preference analyses are not affected by dynamically changing neurohormonal states. Furthermore, our results advance the ongoing controversy as to whether stress or stress neuromodulators affect decision-making, especially social decision-making. They indicate that the behavioral effects of stress neuromodulators may be more context-dependent than previously assumed. Rather than producing uniform shifts in prosociality, cortisol and noradrenaline may modulate behavior in distinct ways that depend on the choice environment, social context, and motivational salience. We advocate the need to develop more reliable measures of choice consistency and to explore additional factors that may affect the stability of social preferences.

Acknowledgements

We thank José Michele Dören and Maurice Zech for valuable comments on the study design, the statistical analyses and the manuscript. We also thank Damon Dashti, Helena El Kholy, Franziska Faust,

Julian Grefer, Sofia Guerreri, Ariane Quade, Luna Seume, Daniel Siman, Hannah Wahle, and Marie Wülfing for their invaluable assistance with data collection.

The work was supported by a grant from the German Research Foundation (Deutsche Forschungsgemeinschaft, Bonn, Germany) to Tobias Kalenscher (grant-ID: DFG-KA 2675/7-1).

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

During the preparation of this work the authors used ChatGPT 3.5 in order to improve readability and language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT author statement

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Supplementary Materials

Trait measures

Before participation in the experiment, participants completed an online questionnaire. The questionnaire took approximately 45 minutes to complete and included a list of the exclusion criteria as well as eleven questionnaires to measure the following traits: chronic stress (Trier Inventory of Chronic Stress, TICS; Petrowski et al., 2012), approach and avoidance (Behavioral Inhibition / Activation, BIS/BAS; Carver and White, 1994), Big Five personality traits (10 item version of the Big Five Inventory, BFI-10; Rammstedt and John, 2007), impulsivity (Barratt Impulsivity Scale, BIS-15; Meule et al., 2011), cognitive deliberation capacities (Cognitive Reflection Test, CRT; Frederick, 2005), empathy (E-Scale; Leibetseder et al., 2007), individual chronotype (reduced version of the Morningness-Eveningess Questionnaire, rMEQ; Griefahn et al., 2001), social value orientation (SVO; Van Lange et al., 1997), state and trait anxiety (State-Trait Anxiety Inventory, STAI, Spielberger et al., 1983), social desirability (Social Desirability Scale, SDS-17; Stöber, 1999), and perspective taking ability (Soutschek et al., 2016).

Power of GARP test

Dependent on the budget and price constraints used, the Generalized Axiom of Revealed Preferences (GARP; Houthakker, 1950; Samuelson, 1938) may be easy or difficult to satisfy (Bronars, 1987). To ensure that purely random choice behavior was not sufficient to satisfy GARP with our budget and price setup, we conducted a series of simulations. That is, we simulated random choice behavior and compared it with that of our participants to verify that our participants were indeed systematic in their choices and that consistent or inconsistent choices were thus interpretable.

First, we simulated choices of 1,000 uniformly random decision-makers for each trial that our participants faced. We then calculated the Critical Cost Efficiency Index (CCEI; Afriat, 1973, 1972; Varian, 1993) scores for these simulated choices in the same way as we did for our participants. The CCEI scores for all simulated decision-makers were below 1 (max = 0.55, M = 0.28, SD = 0.07), indicating a high power of our test (see Figure 1).

Next, we controlled for possible missed trials by simulating 100 uniformly random decision-makers for each participant, but only for the trials that the participant actually completed. Again, we calculated the CCEI scores for each simulated decision-maker and obtained comparable results, with all CCEI scores below 1 (max = 0.70, M = 0.29, SD = 0.07).

To further validate our test, we averaged the 100 simulated CCEI scores per participant and compared these averages to the actual CCEI scores of our participants using a Bayesian t-test. The results provided strong evidence that the simulated CCEI scores were lower than the actual CCEI scores (BF_{10} > 100).

Overall, this suggests that our GARP test was sufficiently powerful to detect violations of GARP.

Figure 1

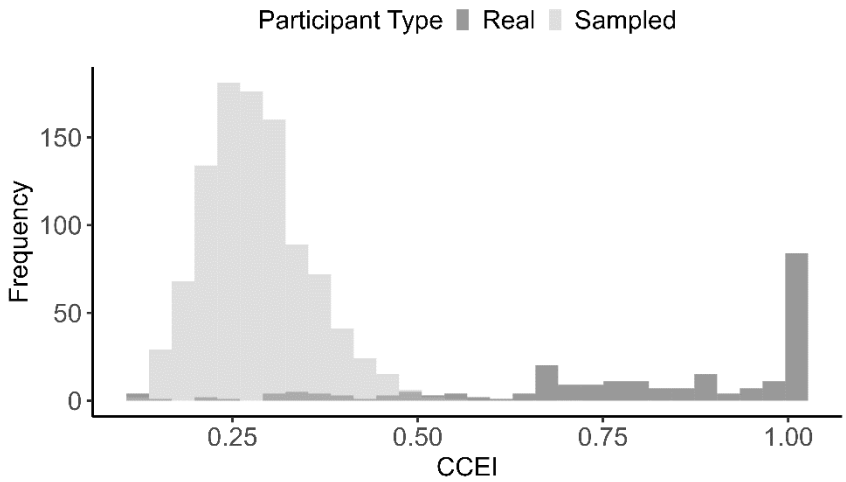

Figure 1. Frequency distribution of CCEI scores of both real participants (Real) as well as 1000 sampled participants (Sampled) who made uniform random choices across all trials faced by the real participants.

Robustness checks

Attention check exclusion criteria

To evaluate the robustness of our findings to stricter attention check criteria, we re-ran the main analyses on prosocial choice (sharing score) and choice consistency (CCEI), excluding participants who

failed at least one, two or three of the attention check trials embedded in the task. We also report results including all participants, regardless of attention check performance.

Table S1 reports the results from these re-analyses. Across all exclusion thresholds, the conclusions remain unchanged, suggesting that our main findings are not driven by participants who may have failed one or several attention checks.

Table S1: Robustness of Effects Across Different Attention Check Exclusion Criteria

Prosocial decision-making: share score	
Full sample (N = 129)	BF_{excl}
Distance	< 0.01
Block	0.09
Drug condition	2.52
Distance x block	93.38
Distance x drug condition	2.76
Block x drug condition	3.95
Distance x block x drug condition	14.01
At least 1 attention check failed (N = XXX)	
Distance	< 0.01
Block	0.04
Drug condition	1.90
Distance x block	43.74
Distance x drug condition	2.77
Block x drug condition	90.71
Distance x block x drug condition	4.93
At least 2 attention checks failed (N = XXX)	
Distance	< 0.01
Block	0.26
Drug condition	3.38
Distance x block	76.03
Distance x drug condition	2.99
Block x drug condition	4.25
Distance x block x drug condition	23.24
At least 3 attention checks failed (N = XXX)	
Distance	< 0.01
Block	0.21
Drug condition	3.76
Distance x block	77.76
Distance x drug condition	2.42
Block x drug condition	3.43
Distance x block x drug condition	19.05

Choice consistency: CCEI	
Full sample (N =129)	BF_{excl}
Distance	4.47
Drug condition	7.51
Distance x drug condition	5.87
At least 1 attention check failed (N = XXX)	
Distance	1.52
Drug condition	9.73
Distance x drug condition	5.74
At least 2 attention checks failed (N = XXX)	
Distance	5.19
Drug condition	7.67
Distance x drug condition	7.02
At least 3 attention checks failed (N = XXX)	
Distance	4.51
Drug condition	7.09
Distance x drug condition	7.24

Gender

To examine potential gender-specific effects, we conducted exploratory analyses including gender as an additional variable in our primary models. These analyses did not alter any of our main conclusions.

We found moderate evidence against an overall effect of gender on sharing ($BF_{excl} = 5.45$) and no conclusive evidence for interactions between gender and social distance, measurement block, or drug condition (all $BF_{incl} < 1$).

We found no evidence for interaction effects between gender and either social distance or drug condition on the CCEI (all $BF_{incl} < 0.5$), but we did find evidence for a main effect of gender ($BF_{incl} = 21.65$), with men showing higher CCEI scores than women. We interpret this finding with caution. The lower average CCEI scores in women may be due to greater heterogeneity in their responses, as reflected in wider interquartile ranges and higher variance. This pattern could potentially stem from contextual factors, such as social obligations or fairness concerns. However, without pre-specified hypotheses or targeted control measures, such interpretations remain speculative.

Recent research suggests that apparent gender differences in decision-making may partly reflect contextual influences, such as Prospect-theoretical reference points, rather than stable traits (Kettlewell et al., 2023; Levy et al., 2024). Meta-analyses further indicate that gender differences in behavior are often small (Hyde, 2005; Zell et al., 2015), and shaped by gender role expectations and socialization processes (Eagly and Wood, 1999; Endendijk et al., 2017; Spencer et al., 1999). Accordingly, we caution against interpreting gender as a fixed causal factor without theory-driven mechanisms that specify how, when, and why gendered behavioral differences might emerge.

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Study 2 – Original Paper

Nitsch, F.J.*, Lüpken, L.M., Lüschow, N., Kalenscher, T., 2022. On the reliability of individual economic rationality measurements. Proc. Natl. Acad. Sci. 119, e2202070119. https://doi.org/10.1073/pnas.2202070119

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Tobias Kalenscher: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

PNAS RESEARCH ARTICLE | PSYCHOLOGICAL AND COGNITIVE SCIENCES

On the reliability of individual economic rationality measurements

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Edited by Tobias Hauser, University College London, London, United Kingdom; received February 5, 2022; accepted June 23, 2022 by Editorial Board Member Michael S. Gazzaniga

A contemporary research agenda in behavioral economics and neuroeconomics aims to identify individual differences and (neuro)psychological correlates of rationality. This research has been widely received in important interdisciplinary and field outlets. However, the psychometric reliability of such measurements of rationality has been presumed without enough methodological scrutiny. Drawing from multiple original and published datasets (in total over 1,600 participants), we unequivocally show that contemporary measurements of rationality have moderate to poor reliability according to common standards. Further analyses of the variance components, as well as a allowing participants to revise previous choices, suggest that this is driven by low between-subject variance rather than high measurement error. As has been argued previously for other behavioral measurements, this poses a challenge to the predominant correlational research designs and the search for sociodemographic or neural predictors. While our results draw a sobering picture of the prospects of contemporary measurements of rationality, they are not necessarily surprising from a theoretical perspective, which we outline in our discussion.

rationality | reliability | econometrics | psychometrics | measurement

Significance

Identifying potential determinants of rationality—interpreted as a characteristic of decision makers—is of great relevance from an applied science perspective: both policy makers and industry have a pronounced interest in understanding which individuals make rational decisions, be it to design effective policies, enhance equity, or fine-tune talent selection processes. However, especially for research at the frontier of foundation to application, we must ensure that our measurements are precise and reliable. Here, we show that established empirical measurements of rationality are not reliable enough, implicating the urgent need for advances in measurement of rationality.

A common definition of economic rationality states that decision makers should consistently choose the subjectively best option according to their preferences as their budget allows. It can be shown that any collection of choices of such decision makers can be reconciled with a definite structure of wants, cost efficiency, and transitivity (1). Specifically, the generalized axiom of revealed preference (GARP) requires that if a decision maker accepts costs to choose one choice object over another (strict direct revealed preference), they may, *ceteris paribus,* in fact never choose the latter over the former choice object (no direct revealed preference) as long as it is not associated with higher costs (2–4). Rational choice theory is theoretically parsimonious and elegant and delivers tractable analytical results; therefore, it is widely used in economic applications. However, since its inception, this standard model has also received severe criticism on descriptive (e.g., 5), predictive (e.g., 6), and normative (e.g., 7) grounds.

Despite this criticism, a contemporary research agenda in psychology, behavioral economics, and neuroeconomics aims to identify individual differences and (neuro)psychological correlates of rationality [(8, 9) for an overview]. Here, indices of revealed preference consistency specifically are used as an ad hoc measurement tool for the supposedly latent concept of rationality that is often interpreted as a psychological construct (see *Discussion*). Importantly, this interpretation of revealed preference consistency as a characteristic of decision makers goes beyond the original intent of the founders of revealed preference theory, which was to provide a test of whether a specific set of choices allows for the construction of a preference ordering (e.g., 10). Empirical research on this topic has been widely received in important interdisciplinary and field outlets such as *Science* or the *American Economic Review* (e.g., 11, 12). However, the validity of such measurements of rationality has been, perhaps due to the strong economic-theoretical foundation, presumed without enough scrutiny.

In this article, we identify and discuss a core issue of the aforementioned research program: contemporary measurements of individual rationality have moderate to poor reliability according to common standards. As has been argued previously for other behavioral measurements (13), this poses a challenge for the predominant correlational research designs and the identification of individual differences.

Importantly, the empirical analyses reported in this paper draw from multiple original and published datasets that vary in the deployed choice domain (social choice, food choice, choice under risk, or choice under ambiguity), choice complexity (two or three goods), study context (laboratory or online), incentivization (incentive compatible or

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The authors declare no competing interest.

This article is a PNAS Direct Submission. T.H. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2202070119/-/DCSupplemental.

Published July 26, 2022.

hypothetical), study population, sample size, task structure, measurement length, and time gap between measurements (*SI Appendix*, Table S1). Hence, the large amount of data and methodological diversity allow us to draw conclusions with reasonable generality for contemporary research practice.* To support the robustness of our results, we collected data and replicated the low reliability of rationality measurements in eight datasets with, in total, over 1,600 participants, including a preregistered replication.

In comparison to previous related work on the reliability of choice consistency (e.g., 14, 15), the revealed preference methodology for the measurement of rationality is the standard in research practice (8) and is not only conceptually but also mathematically linked to utility theory (1). Another feature that distinguishes revealed preference consistency from choice consistency more generally is the consideration of consumer theory, specifically price effects on demand (16). Thus, our investigation specifically focuses on the measurements of economic rationality via revealed preferences.

A clear implication of our research is that the reliability of such rationality measurements cannot be assumed until shown otherwise. While few (perhaps none) of the relevant studies in the field report reliability coefficients, our results suggest that reliability is modest even for more conservative study designs. More broadly, however, we ask how valid rational choice theory is as a measurement model for differential-psychological applications.

Results

Analysis Approach. Following the standard approach appropriated from neoclassic economic theory, rationality was quantified via the two most prominent indices of rationality, namely, Afriat's critical cost efficiency index [CCEI (17)] and the Houtman-Maks index [HMI (18, 19)]. Broadly, the CCEI utilizes the fact that irrational choice behavior is not cost efficient. It denotes the minimal hypothetical waste of wealth that a decision maker accepts given their irrationality.† The HMI, on the other hand, does not consider the fraction of wealth wasted but instead determines the size of the largest subset of choices consistent with GARP. Hence, the HMI is possibly more robust to single outliers (e.g., mistake choices) but also more sensitive to multiple but practically negligible violations of rationality (see *Methods* for further details). To quantify the reliability of rationality measurements, we calculated the intraclass correlation coefficients (ICCs), which we report and interpret following the standards put forth by Koo and Li [(21); preregistered for study 2], where "[v]alues less than 0.5 are indicative of poor reliability, values between 0.5 and 0.75 indicate moderate reliability, values between 0.75 and 0.9 indicate good reliability, and values greater than 0.90 indicate excellent reliability."

Study 1: Initial Finding. In our first online study, we included 53 adult, English-speaking participants recruited via the online platform Prolific. Participants solved two measurements (test and retest) of a modified dictator game with 20 trials each (22). Briefly, in each trial, participants were granted a variable monetary endowment. Importantly, they could freely share a fraction of this endowment with their best friend at variable exchange rates (i.e., sometimes their friend could receive more or less money than given up by the participant). This design allowed us to determine the rationality of their revealed preferences in sharing.

Importantly, we manipulated the way the dictator game was presented: we used two common design versions (Fig. 1 A and B) and a novel version (Fig. 1C). Each participant solved all 2 (test vs. retest) × 3 (design) = 6 measurement-task version combinations.

The number and configuration of trials was confirmed to be sufficient to detect violations of rationality via a task-based power analysis (see *Rationality and reliability*). Between the two measurements, participants solved an unrelated filler task on reading comprehension (Fig. 1D and *SI Appendix*). At the end of the experiment, participants answered several questions regarding their decision strategies and experiences solving the tasks.

Rationality and reliability. To determine the statistical power of our GARP test, we bootstrapped 1,000 virtual participants from our dataset as a model of random choice (23). Results showed that Bronars power = 91.8% bootstrapped participants did not comply with GARP (see *Methods*, axiom), indicating that the task can accurately detect random behavior. Overall, the rationality of our actual participants (quantified by either CCEI or HMI) was relatively high for both measurements (*SI Appendix*, Table S1) and significantly higher than a bootstrapped random benchmark of equal sample size (all $P < 0.001$; *SI Appendix*, Fig. 13).

Intermethod reliability between task versions. The intermethod reliability (between task versions) for the CCEI was ICC (2, 1) = 0.071 ($-0.108 <$ ICC < 0.297) for the first measurement and ICC (2, 1) = 0.356 (95% CI: $0.176 <$ ICC < 0.539) for the second measurement (Fig. 2, *Top*). Similarly, the intermethod reliability (across task versions) for the HMI was ICC (2, 1) = 0.094 ($-0.089 <$ ICC < 0.320) for the first measurement and ICC (2, 1) = 0.309 (95% CI: $0.129 <$ ICC < 0.497) for the second measurement (Fig. 2, *Bottom*). Hence, the intermethod reliability of the CCEI and the HMI was poor for both measurements according to common standards.

Test-retest reliability per task version. The test-retest reliability (within task versions) for the CCEI was ICC (2, 1) = 0.626 (95% CI: $0.404 <$ ICC < 0.779) for the diagram task, ICC (2, 1) = 0.439 (95% CI: $0.180 <$ ICC < 0.641) for the bundles task, and ICC (2, 1) = 0.277 (95% CI: $-0.021 <$ ICC < 0.531) for the slider task. Overall, only the diagram task showed moderate test-retest reliability for the CCEI, while the two other tasks performed poorly (Fig. 3, *Left*). The test-retest reliability (within task versions) for the HMI was ICC (2, 1) = 0.345 (95% CI: $0.054 <$ ICC < 0.583) for the diagram task, ICC (2, 1) = 0.550 (95% CI: $0.317 <$ ICC < 0.720) for the bundles task, and ICC (2, 1) = 0.310 (95% CI: $0.014 <$ ICC < 0.556) for the slider task. Overall, only the bundles task showed moderate test-retest reliability for the HMI, while the two other tasks performed poorly (Fig. 3, *Right*).

Decision strategies. In order to gain a better understanding of the decision-making process and to further validate our conclusions, we conducted an inductive, qualitative content analysis (24) using the free-text responses about the decision strategies of our participants (*SI Appendix*, Fig. 1A). Our results indicated that most participants either tried to fairly share the payout (22 participants, 41.50%) or maximize the total payout (20 participants, 37.70%). Few participants decided with an egotistical bias (6 participants, 11.30%) or prosocial bias (2 participants, 3.77%). For 3 participants (5.66%), we could not determine a clear strategy from their response.

*We, however, acknowledge that this diversity also introduces heterogeneity, which limits the means of quantitative data aggregation.

†For our main analysis, we quantified this hypothetical waste in terms of percentages of the monetary expenditure. To test the robustness of our results, we used an alternative specification in terms of the absolute waste of expenditure (20). The results of this robustness check are aligned with our main analysis (*SI Appendix*).

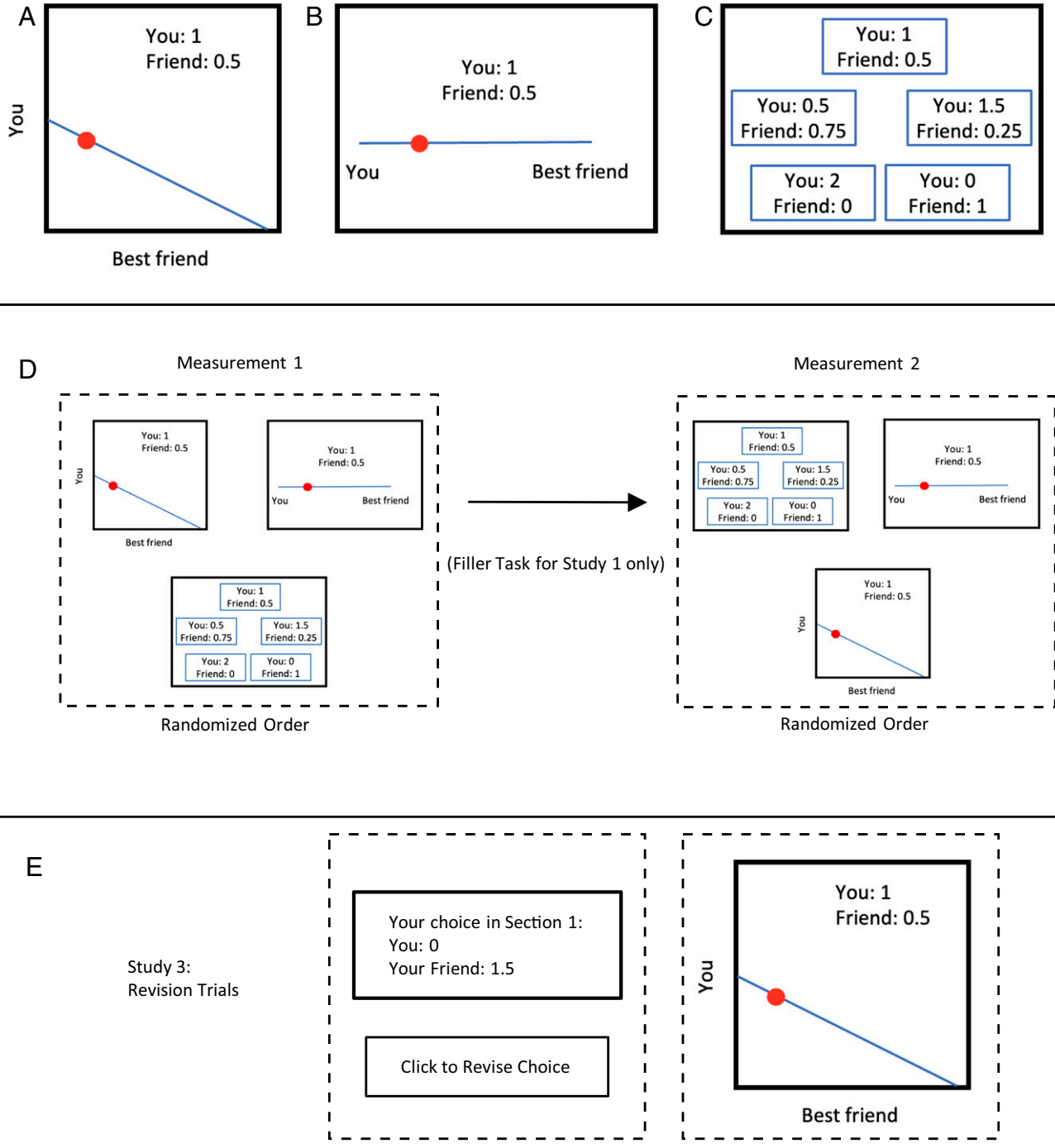

Fig. 1. Behavioral task versions used to measure rationality. Participants played a modified dictator game. In each trial, they could share a fraction of an endowment with their best friend at a variable exchange rate (i.e., sometimes their friend could receive more or less money than given up by the participant). We manipulated the way the decision problem was presented in three different task versions: (*A*) diagram, (*B*) slider, and (*C*) bundles. (*D*) Experimental structure of studies 1 and 2. All task version blocks were presented in randomized order for two measurements each. Intermethod reliability was calculated within measurements (across task versions). Test-retest reliability was calculated between measurements (per task version). (*E*) Sample trial of the choice revisions in study 3. Participants first were displayed their choice from the previous section and then had the opportunity to either remake or revise that decision.

Study 2: Preregistered Replication. A potential limitation of study 1 was the relatively small number of participants and trials,[‡] which could have led to unstable and biased reliability estimates (25). To address this concern, we conducted study 2, which was preregistered on the Open Science Framework (OSF, https://osf.io/wfd4z). Here, we tried to replicate the results of study 1 in a larger sample and with a higher number of trials. We included 148 adult, English-speaking Prolific participants who did not participate in study 1. Participants underwent the same procedure as in study 1 except for two differences. First, we increased the number of trials from 20 to 40. The number and configuration of trials were confirmed to be sufficient to detect violations of rationality via a task-based power analysis (see *Rationality and reliability*). Second, we omitted the filler task to compensate for the higher number of trials and thus longer experiment duration. At the end of the experiment, participants answered several questions regarding their decision strategies and experiences solving the tasks.

[‡]The number of trials for study 1 was confirmed to be sufficient via a Bronars power analysis and well within the range used in the literature.

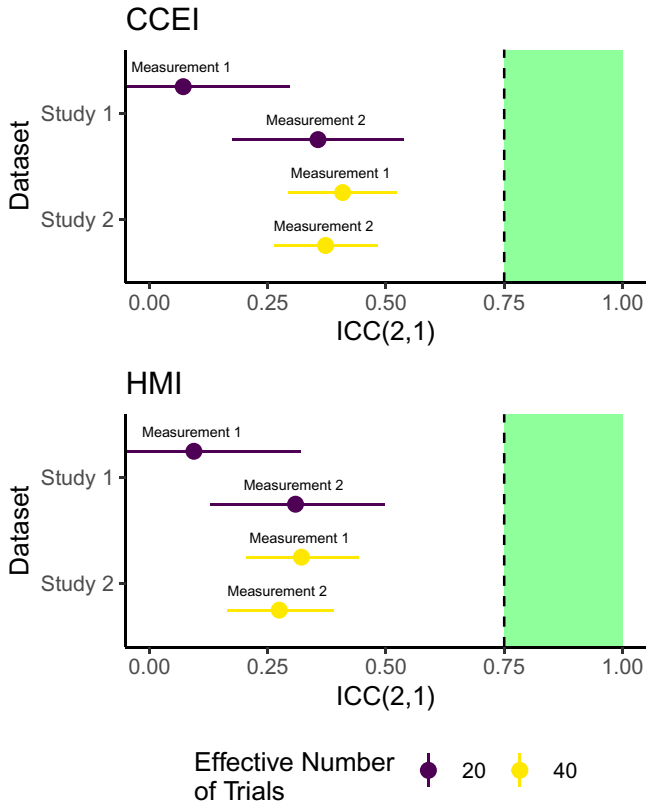

Fig. 2. Intermethod reliability of individual rationality measurements. Depicted are ICC estimates and 95% CI of the intermethod reliability of CCEI (*Top*) and HMI (*Bottom*). The dashed vertical line and subsequent green area indicate the range of acceptable, that is, good reliability according to common standards. The effective number of trials is the number of trials per measurement (test-retest reliability).

Rationality and reliability. As in study 1, to determine the statistical power of our GARP test, we bootstrapped 1,000 virtual participants from our dataset. Results showed that Bronars power > 99.9% bootstrapped participants did not pass GARP, indicating that the task can accurately detect random behavior. Again, the rationality of our participants (quantified by either CCEI or HMI) was relatively high for both measurements (*SI Appendix*, Table S1) and significantly higher than a bootstrapped random benchmark (all $P < 0.001$; *SI Appendix*, Fig. 14).

Intermethod reliability between task versions. The intermethod reliability (between task versions) for the CCEI was ICC (2, 1) = 0.408 (95% CI: 0.293 < ICC < 0.522) for the first measurement and ICC (2, 1) = 0.372 (95% CI: 0.263 < ICC < 0.482) for the second measurement. Hence, as in study 1, the intermethod reliability of the CCEI was poor for both measurements (Fig. 2, *Top*). The intermethod reliability (between task versions) for the HMI was ICC (2, 1) = 0.321 (95% CI: 0.204 < ICC < 0.442) for the first measurement and ICC (2, 1) = 0.275 (95% CI: 0.164 < ICC < 0.390) for the second measurement. Again, the intermethod reliability of the HMI was poor for both measurements (Fig. 2, *Bottom*).

Test-retest reliability per task version. The test-retest reliability (within task versions) for the CCEI was ICC (2, 1) = 0.515 (95% CI: 0.372 < ICC < 0.635) for the diagram task, ICC (2, 1) = 0.497 (95% CI: 0.354 < ICC < 0.617) for the bundles task, and ICC (2, 1) = 0.434 (95% CI: 0.283 < ICC < 0.564) for the slider task. Overall, test-retest reliability for the CCEI was moderate for the diagram and bundles tasks and poor for the slider task; therefore, it was not sufficient according to our preregistered criterion (at least good reliability; Fig. 3, *Left*). The test-retest reliability (within task versions) for the HMI was ICC (2, 1) = 0.505 (95% CI: 0.360 < ICC < 0.626) for the diagram task, ICC (2, 1) = 0.640 (95% CI: 0.525 < ICC < 0.732) for the bundles task, and ICC (2, 1) = 0.343 (95% CI: 0.182 < ICC < 0.487) for the slider task. Overall, test-retest reliability for the HMI was moderate for the diagram and bundles tasks and poor for the slider task following standards; therefore, it was not sufficient according to our preregistered criterion (at least good reliability; Fig. 3, *Right*).

Decision strategies. Free-text responses about participants' decision strategy were categorized via the same categories inducted in study 1 (*SI Appendix*, Fig. 1B). Again, our results showed that most participants either tried to fairly share the payout (63 participants, 42.6%) or maximize the total payout (43 participants, 29.1%). Few participants decided with an egotistical bias (25 participants, 16.9%) or prosocial bias (3 participants, 2.0%). For 14 participants (9.5%), we could not determine a clear strategy from their response. This number was expectedly higher than for study 1 as no new response categories were inducted.

Reliability of Rationality in Published Research. Next, to assess the reliability of contemporary rationality measurements more generally, we reanalyzed five published datasets for test-retest or split-half reliability: Choi et al. [(26), henceforth C07, and (11), henceforth C14], Kurtz-David et al. [(27), henceforth K19], the control group of Nitsch et al. [(28, 29), henceforth N21], and Ahn et al. [(30), henceforth A14]. *SI Appendix*, Table S1 shows key details about the datasets. The N21 dataset contained three measurements over about 3 h in total, which were jointly entered for the reliability estimation. Since the C07, C14, K19, and A14 datasets did not contain multiple measurements, we used the split-half method to estimate reliability.

Split-half/test-retest reliability. Results for all datasets are summarized in Fig. 3. The split-half/test-retest reliability for the CCEI was ICC (2, 1) = 0.256 (95% CI: 0.056 < ICC < 0.436) for the C07 dataset, ICC (2, 1) = 0.503 (95% CI: 0.402 < ICC < 0.591) for the C14 dataset, ICC (2, 1) = 0.183 (95% CI: −0.166 < ICC < 0.491) for the K19 dataset, ICC (2, 1) = 0.483 (95% CI: 0.340 < ICC < 0.619) for the N21 dataset, and ICC (2, 1) = 0.408 (95% CI: 0.268 < ICC < 0.532) for the A14 dataset (Fig. 3, *Left*, rows 6–10). Hence, split-half/test-retest reliability for the CCEI was poor in four of five datasets and moderate in one of five datasets. The split-half/test-retest reliability for the HMI was ICC (2, 1) = 0.442 (95% CI: 0.263 < ICC < 0.592) for the C07 dataset, ICC (2, 1) = 0.158 (95% CI: 0.032 < ICC < 0.279) for the C14 dataset, ICC (2, 1) = 0.685 (95% CI: 0.451 < ICC < 0.831) for the K19 dataset, and ICC (2, 1) = 0.497 (95% CI: 0.355 < ICC < 0.630) for the N21 dataset (Fig. 3, *Right*, rows 6–9).[§] Hence, split-half/test-retest reliability for the HMI was poor in three of four datasets and moderate in one of four datasets.

Study 3: Long-Term Reliability and the Role of Mistake Choices. Study 3 was a follow-up measurement within a subset of the participants of study 2 ∼5 mo later, which had three main goals. The first goal was to replicate our findings in participants who were already familiar with the task. This was important since we observed learning effects in studies 1 and 2, where participants became on average more rational in the second measurement [study 1: b = 0.023, SE = 0.017, $t(240.932) = 1.387$, $P = 0.167$; study 2: b = 0.037, SE = 0.02, $t(658.251) = 3.183$, $P = 0.002$]. The second goal was to explore how test-retest

[§]We failed to reproduce the HMI for the A14 dataset with our algorithm, presumably due to the presence of three different kinds of goods.

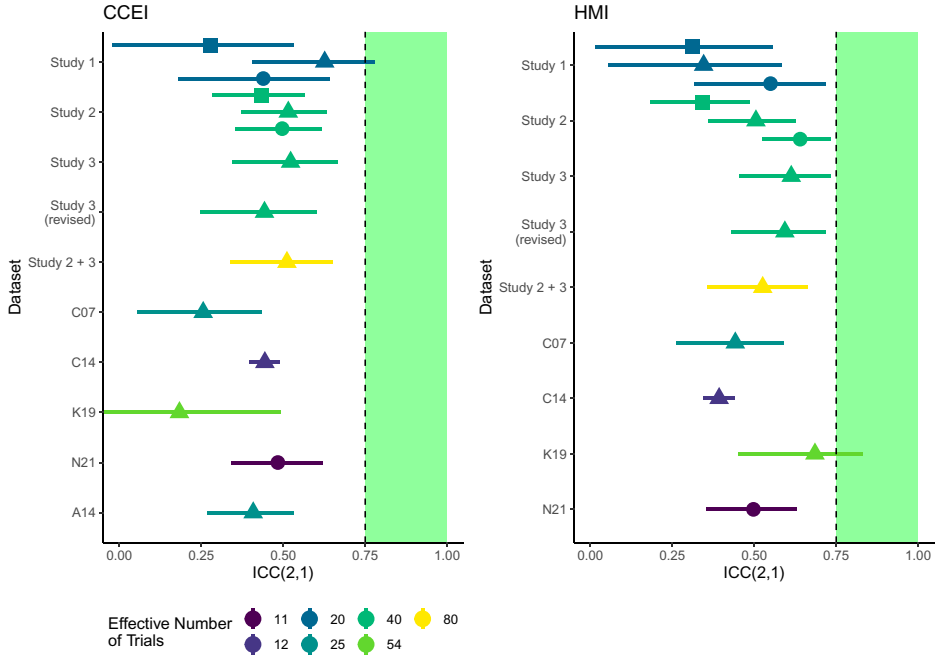

Fig. 3. Test-retest and split-half reliability of individual rationality measurements. Depicted are the ICC estimates and 95% CI of the test-retest/split-half reliability of CCEI (*Left*) and HMI (*Right*) across all eight datasets. Symbols indicate which task version was used: triangles indicate the diagram task, circles indicate the bundles task, and rectangles indicate the slider task. The dashed vertical line and subsequent green area indicate the range of acceptable, that is, good reliability according to common standards. The effective number of trials is the number of trials per measurement (test-retest reliability) or split (split-half reliability). Studies 2 and 3 were conducted ~5 mo apart in the same sample.

reliability was affected when the two tests were further apart (months rather than minutes). For this, we leveraged the fact that we recruited a subset of the sample of study 2 and the same diagram choice task. The third goal was to test whether low reliability was driven by the noisiness of participants' decisions (i.e., mistake choices). We were able to rerecruit 97 of the original 148 participants.[¶] Participants underwent the same procedure as in study 2 except for three differences. First, we omitted the slider and bundles tasks and only used the diagram task (for a total of 2 × 40 trials). Second, we omitted the free-text questions regarding participants' decision strategy (to limit both the length of the study and fatigue in participants; see *Discussion*). Third, following Breig and Feldman (31), we allowed participants to revise a random subset of their initial choices after the completion of the first two task blocks and undo potential mistake choices.

Rationality and reliability. Bronars power was equivalent to study 2, that is, >99.9% bootstrapped participants did not pass GARP, indicating that the task can accurately detect random behavior. Again, the rationality of our participants (quantified by either CCEI or HMI) was relatively high for both measurements (*SI Appendix*, Table S1) and significantly higher than a bootstrapped random benchmark (all $P < 0.001$; *SI Appendix*, Figs. 15 and 16).

Goal 1: Reliability of participants who are familiar with the task. The test-retest reliability for the CCEI was ICC (2, 1) = 0.522 (95% CI: 0.343 < ICC < 0.665), which was comparable to study 2 and can be considered moderate. The test-retest reliability for the HMI was ICC (2, 1) = 0.613 (95% CI: 0.455 < ICC < 0.733), which was slightly higher than for study 2 but still only moderate.

Goal 2: Long-term test-retest reliability. We collapsed the 2 × 40 trials of studies 2 and 3 each for an effective number of 80 trials per study. The 5-month test-retest reliability (across studies 2 and 3) for the CCEI was ICC (2, 1) = 0.511 (95% CI: 0.338 < ICC < 0.651), which can be considered moderate. The 5-month test-retest reliability (across studies 2 and 3) for the HMI was ICC (2, 1) = 0.526 (95% CI: 0.355 < ICC < 0.662), which can be considered moderate. Hence, overall the 5-month test-retest reliability of both indices was comparable to short-term reliability.

Goal 3: The role of mistake choices. Following Breig and Feldman (31), we allowed participants to revise a random subset of 10 choices per block of their initial choices after the completion of the first two task blocks and undo potential mistake choices. Surprisingly, this led to an increase neither of rationality (measurement 1: delta mean CCEI = −0.025, delta mean HMI = −0.262; measurement 2: delta mean CCEI = −0.013, delta mean HMI = −0.058) nor of test-retest reliability. The test-retest reliability for the CCEI was ICC (2, 1) = 0.443 (95% CI: 0.248 < ICC < 0.603), which can be considered poor. The test-retest reliability for the HMI was ICC (2, 1) = 0.593 (95% CI: 0.431 < ICC < 0.719), which can be considered moderate.

Explorative Analysis of Variance Components. Next, we tried to answer the question of what gives rise to the low reliability of the revealed preference indices. As explained above, the ICC represents the fraction of the total variance which is attributable to true differences (i.e., not attributable to error). Hence, the ICC could be small due to high measurement error (large denominator), small true differences (small numerator), or both. To identify the degree of measurement error, we calculated within-subject coefficient of variance (WSCV) using the repeated measures per the same instrument. The WSCV determines the degree of closeness of the repeated observations made on the same subject (32) (Fig. 4); the lower the WSCV, the lower the measurement error. Results indicated a drop of the WSCV for measurements with at least 20 trials for both CCEI and HMI (i.e., all datasets but C14 and N21). For such

[¶]Study 3 was an unplanned follow-up motivated by a reviewer comment. Hence, we had to rerecruit participants via Prolific who had not been informed about this follow-up in advance.

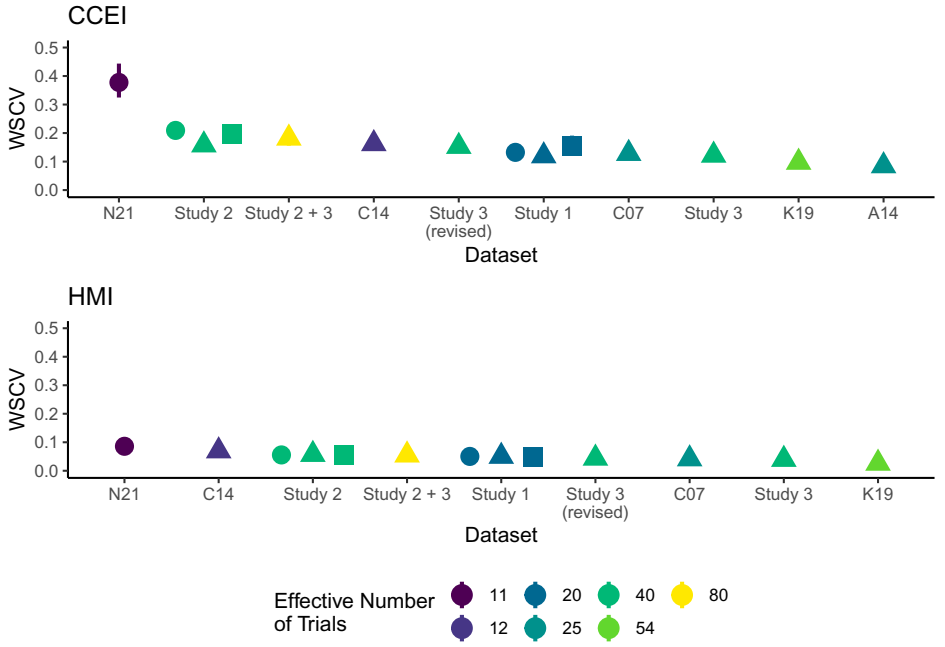

Fig. 4. WSCV. Depicted are the WSCV estimates and 95% CI of the test-retest/split-half reproducibility of CCEI (*Top*) and HMI (*Bottom*) across all eight datasets. Symbols indicate which task version was used: triangles indicate the diagram task, circles indicate the bundles task, and rectangles indicate the slider task. Studies 2 and 3 were conducted ~5 mo apart in the same sample. The effective number of trials is the number of trials per measurement (test-retest reliability) or split (split-half reliability).

measurements with at least 20 trials, the WSCV was relatively small (median = 15% for the CCEI and median = 5% for the HMI).

Discussion

In the present paper, we investigated the reliability of behavioral measurements of rationality as a characteristic of individual decision makers. Across multiple original and published datasets, we found that the reliability of the two most prominent rationality indices (and variations thereof) is moderate to poor. This result held independent of the choice domain (social choice, food choice, choice under risk, or choice under ambiguity), choice complexity (two or three goods), study context (laboratory or online), incentivization (incentive compatible or hypothetical), study population, sample size, task structure, measurement length, and time gap between measurements. Hence, given data from multiple datasets with sufficient methodological diversity, our conclusions not only apply to a specific configuration of rationality measurements but speak with reasonable generality for contemporary research practice. More broadly, our results align with recent work on the reliability of measurements of risk preferences, sensitivity to losses, and self-regulation (33–35).[#]

Reliability indicates how much of the total variance in the variable of interest is attributable to true difference and not caused by measurement error. Hence, one potential explanation of moderate to poor reliability could be the presence of high measurement error (large denominator in the fraction) in the revealed preference methodology (e.g., 38). Our data offer two arguments against this explanation. First, allowing participants to revise a subset of choices (i.e., fixing potential mistakes, a source of measurement error; see study 3) did not increase reliability. Second, an analysis of the variance components in the data tentatively suggested that within-subject variance, as a proxy for measurement error, was sufficiently low for measurements with at least 20 trials.

Another explanation for moderate to poor reliability is a lack of true differences between participants: it could be possible that it is difficult to distinguish between participants because they do differ enough with respect to economic rationality. In line with this explanation, most participants across all datasets descriptively behaved with high consistency, and taking individual measurements of CCEI and HMI yielded approximately two times worse predictive accuracy for another measurement within the same individual than simply assuming the population mean (*SI Appendix*). In conjunction with the absence of high measurement error, this tentatively suggests that the low reliability of contemporary measurements of individual rationality (that is, the inability to distinguish between individuals) was indeed driven by a lack of interindividual differences in rationality.[||]

As has been argued previously for other behavioral measurements, the lack of reliability poses a challenge to the contemporary search for sociodemographic or psychological correlates of economic rationality. Pragmatically speaking, our results show that a simple increase of trials or using a different task interface is not sufficient to fix this problem (unless the sample size is increased substantially); rather, individual differences must be increased. Possible avenues to explore here are, for instance, to ask participants to make decisions under stress or time pressure, increasing the difficulty of the decisions or using a manipulation (i.e., a between-groups design).

A more general point we want to raise here is the validity of economic rationality as a psychological construct, which is a prerequisite to valid measurements (39). Strictly speaking, economic rationality describes whether or to what extent a set of choices can be described by a utility function. In the recent literature,

[#]Interestingly, temporal discounting seems to be reliable (36, 37).

[||]It is important to point out that few individual differences in rationality pose a desirable result for economic theory: specifically, it means that most individuals' decisions can be closely approximated by utility theory.

however, economic rationality of a finite set of choices of an individual has been compared with decision quality (11, 29, 40), policy responsiveness (41), or variability in the neural computation of value (27) based on face validity and correlational evidence,** all of which are arguably related but not identical constructs. Given this lack of a clear definition of the psychological construct to be measured and lack of evidence of validity for widely used measures, advances in psychological theory and measurement appear necessary. A recent, particularly promising approach for the applications outlined here are generative models,†† which can serve to formalize psychological constructs and increase the reliability of behavioral measurements (43, 44). The theoretical basis to inspire the development of such models could be provided by cognitive science: past studies have shown that cognitive skills (e.g., executive control, working memory, and intelligence) pose a common factor of many aspects of decision making, including choice consistency (45–50).

Limitations. A limitation to our assessment might be that the upper limit of effective trials considered for our reliability assessments was 80, which is below that of a few particularly high-powered studies (e.g., [27] used up to 108 trials). Optimistically, it could be possible to improve the reliability of rationality measurements by increasing the number of trials in behavioral experiments to further reduce measurement error. However, a high number of trials (i.e., at least more than 80 trials) comes at the cost of practical feasibility in many studies and the risk of increasing fatigue due to prolonged measurement durations, which in itself might bias the measurement (ranging from relative changes in preference to qualitative changes of decision strategy). To give a benchmark, in study 2, the number of participants indicating that they were "very much fatigued" tripled from after 20 to after 40 trials (after measurement 1: $n = 10$; after measurement 2: $n = 29$; *SI Appendix*, Fig. 2).

Another potential limitation is that we could not replicate the finding of Breig and Feldman (31) that allowing participants to revise their choices leads to an increase of revealed preference consistency in the choice set. We acknowledge that, as the authors also demonstrate in their paper, the effectiveness of such an intervention depends on the specific configuration of the choice interface. Hence, due to the ineffectiveness of the intervention, we cannot rule out that a more effective intervention could increase the reliability of rationality measurements.

Lastly, we acknowledge that while the qualitative results for each dataset are similar, there is some variability in the quantitative reliability estimates, which could be driven by the heterogeneity of the included datasets.

Conclusions. We demonstrate that the reliability of individual rationality measurements cannot be assumed until shown otherwise. While few (perhaps none) of the relevant studies in the field report reliability coefficients, our results suggest that reliability is modest even for more conservative study designs. From the theoretical perspective outlined above, however, we might ask more broadly how useful a measurement model rational choice theory (or choice structure representations thereof) is for differential-psychological applications.

**A notable exception is Cohen et al. (42), who provide mechanistic and causal evidence for the link between neuronal constraints and economic rationality in nematodes.

††Generative models are models that formally specify "how behavior is generated within people and how generative processes vary across people" (43, p. 2).

Methods

All participants recruited for this research project gave their informed written consent before participation. The study protocol of the original studies 1 to 3 was approved by the ethical council of the medical faculty of Heinrich-Heine-University Düsseldorf (study 2020-910). Studies 1 to 3 were conducted in alignment with the Declaration of Helsinki. For ethical information regarding the literature data, see the corresponding references. Study 1 was conducted as part of the doctoral thesis of F.J.N. [51].

Study 1. Study 1 served as the initial investigation into the reliability of measures of revealed preference reliability and was embedded in a larger study on the malleability of rational choice.

Participants. For study 1, 101 adult, English-speaking participants completed our study. For the study, 48 participants were randomly assigned to an experimental manipulation group, which entailed a reading-based priming manipulation. As this manipulation was irrelevant to the presented research question, we only considered the control group (which only read a neutral text; *SI Appendix*) for the present analyses. No other participants were excluded, resulting in a final sample size of $n = 53$ participants. *SI Appendix*, Table S2 gives an overview of the demographics.

Procedure and design. Participants were recruited via the online platform Prolific (https://www.prolific.co), receiving compensation of 4.30 pounds. Prolific is a widely used online research subject pool that has been accredited for more transparency and research suitability than comparable platforms (52, 53). The online experiment was programmed in jsPsych (54) and hosted on Pavlovia. Before the start of the experiment, all participants were fully debriefed about the content and aim of the research project and provided informed consent via a checkbox. After providing consent, we asked for their demographic information. Next, participants underwent the first measurement of all three experimental tasks in randomized order. For the first measurement, each task entailed a detailed description and five practice trials. After completion of the first measurement, participants solved a filler task that consisted of reading three informational texts about unrelated topics and answering three quiz questions on the content of these texts (*SI Appendix*). Then participants underwent the second measurement of all three experimental tasks, again in randomized order. At the end of the experiment, participants answered several questions regarding their decision strategies and experiences solving the tasks. Then they were redirected back to Prolific to receive their compensation.

Our experimental design was completely within subject. Participants solved all three decision tasks for two measurements (3 × 2 within-subject design).

Experimental tasks. All decision tasks were based on a modified dictator game (22), consisting of $I = 20$ decisions per measurement. Participants had to hypothetically allocate a budget m_i between them and their best friend, resulting in a final monetary split of $x_i = (x_i^{Self}, x_i^{Friend})$. Importantly, the monetary endowment m_i and the "prices" of keeping and giving money $p_i = (p_i^{Self}, p_i^{Friend})$ varied per decision. Hence, $x_i^{Self} = \frac{share_i^{Self} m_i}{p_i^{Self}}$ and $x_i^{Friend} = \frac{share_i^{Friend} m_i}{p_i^{Friend}}$, with the share indicating the relative fraction of the budget (0–1) allocated to each account. Budgets and prices were randomly sampled per trial: $m_i \in [2, 3, 4, 5, 6, 7, 8, 9, 10]$ and $p_i^{Self}, p_i^{Friend} \in [1, 2, 3]$. For our analysis, we normalized prices and budgets so that $\sum p_i = 1$ and $m_i = x_i^{Self} p_i^{Self} + x_i^{Friend} p_i^{Friend}$.

For each task and measurement, we further included two attention check trials where participants were instructed to allocate the full budget to either themselves or their best friend. Those trials were not included in the analysis. If participants failed an attention check for a given measurement of a task, we excluded that measurement of the task from our analysis specifically (8% of measurements).

Contemporarily, experimental investigations of revealed preference rationality interchangeably utilize different ways to present the decision problems (task versions). One line of research uses a task introduced by Choi et al. (26). In their elaborate and widely used paradigm (here, diagram task), participants must allocate a budget between two dimensions (e.g., two investment accounts, oneself and a coplayer) using a cartesian coordinate display. The task is mostly applied in the investigation of choices under risk (11, 27, 55, 56) but also intertemporal choices (12, 57). It has the appeal that it transparently depicts all economic parameters (budget, prices, budget line, etc.) and even allows for a visual

identification of inconsistent choices. A potential drawback is that the task can be hard to understand for people without experience in the interpretation of diagrams and the theoretically large number of potential choice options.

Another line of research uses a more simplistic choice-bundles task that was first prominently used by Harbaugh and colleagues (58) and by many others since (40, 41, 59). In the choice-bundles task (here, bundles task), the budget line is divided into (equidistant) discrete points, which are subsequently presented as a discrete set of choice options to the participant. Conveniently, in this task, participants can ignore the underlying economic parameters and must only choose the most liked choice bundle in the set. This significantly reduces the cognitive demand of the task and is desirable for indivisible goods (e.g., food items), specific participant groups (e.g., children), and research questions (e.g., decisions under stress). A drawback of the task is that discrete choice options can only approximate optimal choices from a continuous budget line, which might introduce small inconsistencies by itself.

A compromise suggested by Garagnani (60), which so far has not been widely applied, however, would be to present participants with a slider (here, slider task) that allows for the continuous allocation of the budget while concealing economic parameters to a degree that allows for an intuitive approach to solving the task. Concretely, participants move a slider that controls the fraction of money allocated to each dimension (in our study, self and best friend). The effective payouts are shown in an infobox.

In study 1, we used all task variants in order to be able to draw inferences independent of the specific task design and evaluate intermethod reliability (Fig. 1).

Diagram task. For each decision, participants had to choose a point on a diagonal line in a coordinate system (Fig. 1A). The points on the diagonal line represented the possible money allocations between themselves and their best friend that they might choose. In each coordinate system, the vertical axis corresponded to the money chosen for themselves (you) and the horizontal axis corresponded to the money chosen for their best friend (friend). While they were making their decision, they could see which amount of money they had chosen for themselves and for their best friend in the upper right corner of the coordinate system. The flatter the lines, the more money their best friend could receive as a maximum compared to them. The steeper the lines, the more money they could receive as a maximum compared to their best friend.

Bundles task. For each decision, participants had a choice of five different money allocations and were instructed to simply choose the allocation that they thought was best (Fig. 1C).

Slider task. For each decision, participants had to choose a point on a horizontal line by moving a slider, which represented the possible allocations of money amounts between themselves and their best friend. While making their decision, they could see which amount of money they had chosen for themselves and their best friend in two boxes above the slider. The labeling of the endpoints and spatial presentation were randomized from round to round (Fig. 1B).

Task questionnaires. At the end of the experiment, participants were asked to answer how they reached their decisions ("How did you reach your decisions?") and what they considered particularly important in their decisions ("What was particularly important to you in your decisions?" in study 1 only) in open-text format. Further, they were asked multiple questions regarding their experiences with the specific task formats that will be reported elsewhere.

Study 2. Study 2 was preregistered on OSF (https://osf.io/wfd4z/). Here, we tried to replicate the results of study 1 in a larger sample and with a higher number of trials to address the issue of portability, as this theoretically could increase the reliability of the task.

Participants. We recorded complete data of 148 adult, English-speaking participants, none of which were excluded. Our sample size rationale was based on the maximum feasible sample size given our monetary budget and the second-largest and largest non–panel-based sample of all datasets considered [*SI Appendix*, Table S1, following Lakens (61)]. *SI Appendix*, Table S2 gives an overview of the demographics.

Procedure and design. Our procedure and design were similar to the control condition of study 1 except that we increased the number of trials from 20 to 40 and removed the filler task. Again, participants were recruited via Prolific, receiving compensation of 4.30 pounds. Participants underwent two measurements of all three experimental tasks, each measurement in randomized order. For the first measurement, each task entailed a detailed description and five practice trials. As study 2 took on average longer than study 1 to complete, we asked participants to indicate their fatigue once after the first measurement and once after the second measurement. The fatigue measurement was used to evaluate the extended experiment length after the recruitment of 10 initial participants, as indicated in our preregistration. Of these 10 participants, most participants were not or only a little fatigued throughout the experiment; therefore, we deemed the experimental length acceptable. At the end of the experiment, participants again answered several questions regarding their decision strategies and experiences solving the tasks. Our experimental design was completely within subject. Participants solved all three decision tasks for two measurements (3×2 within-subject design). Again, if participants failed an attention check for a given measurement of a task, we excluded that measurement of the task from our analysis specifically (10% of measurements).

Study 3. Study 3 was a follow-up measurement within a subset of the participants of study 2 ~5 months later, which served to replicate our findings in participants who were already sufficiently familiar with the task, explore how test-retest reliability was affected when the two tests were further apart (months rather than minutes), and test whether low reliability was driven by the noisiness of participants' decisions (i.e., mistake choices).

Participants. We were able to rerecruit and include 97 of the original 148 participants. *SI Appendix*, Table S2 gives an overview of the demographics.

Procedure and design. Participants underwent the same procedure as in study 2 except for three differences. First, we omitted the slider and bundles tasks and only used the diagram task (for a total of 2×40 trials). Second, we omitted the free-text questions regarding participants' decision strategy (to limit both the length of the study and fatigue in participants; see *Discussion*). Third, following Breig and Feldman (31), we allowed participants to revise a random subset of 10 choices each of their initial choices after the completion of the first two task blocks.

Again, participants were recruited via Prolific, receiving compensation of 3 pounds. Participants underwent two measurements of the diagram task. For the first measurement, we again displayed a detailed description and five practice trials. After the completion of the two first measurements, participants were informed that they now had the opportunity to revise a selection 10 of their decisions from the first (second) measurement (Fig. 1E). For each potential revision, the previous choice was displayed to the participants as a reminder. Then, participants could proceed to redo their choice in their own pace. Importantly, the starting point of the slider on the budget line was again randomized (transparently to the participants) to facilitate an active decision.

Again, if participants failed an attention check for a given measurement of a task, we excluded that measurement of the task from our analysis specifically (12% of measurements).

Analysis.

Revealed preference analysis. Let N be the number of different commodity types in a commodity bundle. Let X be the nonnegative, N-dimensional space of commodity bundles. Let P be the strictly positive, N-dimensional space of prices of commodities. Let M be the nonnegative, one-dimensional space of budgets. Let $I = i, j, \ldots, n$ denote observations of choice. Let x_i be the chosen commodity bundle of an observation i. Each bundle x_i is a N-dimensional vector of the shape $x_i = (x_i^1, x_i^2 \ldots, x_i^n)$, with each scalar component x_i^n representing the quantity of commodity type n within bundle x_i. Let p_i be the given prices of commodities of an observation i. Each prices p are a N-dimensional vector of the shape $p_i = (p_i^1, p_i^2, \ldots p_i^n)$, with each scalar component p_i^n representing the price of commodity type n per unit size. Then the scalar product $x_i \cdot p_i$ represents the total price of a commodity bundle x_i at some prices p_i. Let m_i be the given budget of an observation i. We assume that decision makers spend all their budget so that $x_i \cdot p_i = m_i$.

Definition 1 (Direct Revealed Preference): A bundle x_i is directly revealed preferred to another bundle x_j if and only if $x_j \cdot p_i \leq m_i$. Then we denote $x_i R_D\, x_j$.

Definition 2 (Revealed Preference): A bundle x_i is revealed preferred to another bundle x_k if there exists a transitive preference relation $x_i R_D\, x_j\, R_D\, x_k$ between both bundles. We denote $x_i R x_k$.

Definition 3 (Strict Direct Revealed Preference): A bundle x_i is strictly directly revealed preferred to another bundle x_j if and only if $x_j \cdot p_i < m_i$. Then we denote $x_i P_D\, x_j$.

Axiom (GARP). $x_i R x_j \Leftrightarrow \neg\, x_j P_D\, x_i$.

In this framework, the CCEI presents a relaxation of definition 3 so that only $x_i P_D\, x_j \leftarrow x_j \cdot p_i < CCEI \cdot m_i$ is required.[‡‡] The CCEI is then the highest possible value so that the axiom holds for all observations. The HMI, on the other hand, denotes the largest number of observations $HMI \leq I$ for which the axiom holds.

Statistical analysis. To quantify the reliability of measurements of rationality, we calculated the ICCs of type consistency between the variables of interest to account for potential learning effects [62]. Reliability indicates how much of the total variance in the variable of interest is not caused by measurement error. A reliability of 1 indicates a perfect measurement: all variance in the measurement is caused by true differences in the variable of interest. As reliability approaches 0, the measurement is becoming less precise and a higher fraction of variance is due to measurement error [63]. Specifically, we calculated the ICC of consistency measures among tasks for each measurement to assess intermethod reliability. Further, we calculated the ICC of consistency measures within tasks across measurements to assess test-retest reliability. For qualitative interpretation of reliability, we followed the standards by Koo and Li (21): an ICC estimate lower than 0.50 is considered poor, one between 0.50 and 0.75 is considered moderate, one between 0.75 and 0.90 is considered good, and lastly one greater than 0.90 is considered excellent.

Qualitative content analysis. In order to gain a better understanding of the decision-making process and to further validate our data, we conducted an inductive, qualitative content analysis (24) using the free-text responses about the decision strategies of our participants. For study 1, we concatenated the answers of our participants to both questions. Using an ad hoc inductive approach on the material from study 1, five exhaustive and mutually exclusive categories were generated. Subsequently, three raters (of which one was blind to the objective of the study) coded all answers independently for studies 1 and 2 using these categories without further revisions. On their first try, our raters reached good interrater reliability for study 1 [ICC (2, 1) = 0.831; 95% CI: 0.750 < ICC < 0.892] and moderate interrater reliability study 2 [ICC (2, 1) = 0.740; 95% CI: 0.676 < ICC < 0.796]. The final categorization was then decided via majority rule where possible or labeled "unclear" otherwise.

Data Availability. Processed data and anonymized raw data and analysis scripts have been deposited in OSF (https://osf.io/KD4HW/). Previously published data were used for this work (11,26–30,64). All other study data are included in the article and/or *SI Appendix*.

ACKNOWLEDGMENTS. Portions of this work were developed from the doctoral thesis of F.J.N. We thank Paul Kramer for support with the qualitative content analysis, as well as Paula Klug and Hannah Wahle for help with piloting the experiment. We thank Yue Hu for insightful discussion on earlier versions of this paper. We thank Syngyoo Choi and Shachar Kariv for generously providing their data and analysis code, as well as helpful pointers to other datasets. We thank for Matthew Polisson, John Quah, and Ludovic Renou for compiling and publishing a wide range of datasets. We thank the four anonymous reviewers for critical comments and comments that substantially increased the quality of this paper. The research was supported by a grant from the Deutsche Forschungsgemeinschaft (Bonn, Germany) to T.K. (grant DFG-KA 2675/4-3). Study 2 was preregistered (https://osf.io/wfd4z/).

[‡‡]Choi et al. and Kurtz-David et al. use a slightly different definition of the CCEI. In addition to the relaxation of definition 3, they apply a similar relaxation to definition 1. Further, Kurtz-David et al. [27], report 1 - CCEI. However, all nuances yield strongly related CCEI values. Our results hold independent of which definition of the CCEI is used (*SI Appendix*).

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Study 3 – Original Paper

Dashti, D.[1], Lüpken, L.M.[*1], Seidisarouei, M., Forbes, P.A., Schnitzler, A., Kalenscher, T., 2025. Dissociable Glucocorticoid and Noradrenergic Effects on Parochial Cooperation and Competition in Intergroup Conflict. Proc. Natl. Acad. Sci. 122(29), e2502257122. https://doi.org/10.1073/pnas.2502257122

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PNAS RESEARCH ARTICLE | NEUROSCIENCE
PSYCHOLOGICAL AND COGNITIVE SCIENCES

Dissociable glucocorticoid and noradrenergic effects on parochial cooperation and competition in intergroup conflict

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Edited by Susan Fiske, Princeton University, Jamaica, VT; received January 29, 2025; accepted May 30, 2025

Stress changes social behavior, yet its effects remain contradictory. Traditionally, stress was thought to trigger an antagonistic fight-or-flight response aimed at eliminating the stressor. However, recent studies have revealed the opposite response, tend-and-befriend, where individuals prosocially invest in their social network in exchange for support and mutual protection. We hypothesize that stress does not promote one response over the other; instead, it stimulates both behaviors, dissociable on the neuropharmacological level and moderated by social context. In a placebo-controlled, double-blind psychopharmacological study, we administered hydrocortisone and yohimbine—alone or in combination—to manipulate the actions of the main stress hormone cortisol and the arousal transmitter noradrenaline. Participants then made decisions in an intergroup conflict task. They teamed up with others to form an in-group and played against multiple out-groups. Notably, out-group members initiated financial harm to in-group participants before these responded. Participants then chose either to 1) maximize their own payoff, 2) cooperatively increase the payoff of their in-group, or 3) increase the in-group's payoff while competitively decreasing that of the out-group. Consistent with our hypotheses, glucocorticoid activation increased generosity toward the in-group, whereas noradrenergic activation increased parochial competition, i.e., prosocial in-group support combined with hostility toward the out-group. These findings challenge the dichotomy between fight-or-flight and tend-and-befriend, suggesting stress-related behavior is neither static nor one-directional, but shaped by the relative dominance of cortisol versus noradrenaline in the neurohormonal stress response and by intergroup dynamics. We highlight broader societal implications, offering a potential biological mechanism underlying the self-perpetuating cycle of intergroup conflict.

cortisol | norepinephrine | stress | social preferences | parochial altruism

Significance

There is a longstanding debate in the stress field whether stress promotes antagonistic fight-or-flight or altruistic tend-and-befriend responses. We argue that these responses are not mutually exclusive but instead reflect different facets of the stress-adaptive process. In a placebo-controlled psychopharmacological study, using an intergroup conflict task, we show that the primary stress hormone cortisol enhances cooperative in-group support, while the arousal transmitter noradrenaline fosters competitive behavior toward out-groups. Hence, stress effects on social behavior are shaped by intergroup dynamics and the relative dominance of cortisol versus noradrenaline in the neurophysiological stress response. This dual effect of stress—simultaneously promoting in-group support and out-group aggression—provides insights into the neurobiological mechanisms underlying the self-perpetuating cycle of violent intergroup conflicts.

Stress changes social behavior, yet its effects remain contradictory. Nearly a century ago, Cannon described the "fight-or-flight" response, identifying stress as a trigger for antagonistic tendencies to either confront a threat, or escape from it (1). Next to ample evidence for fight-or-flight responses in animals (2), humans also show antagonistic social behavior after stress, such as increased violence (3, 4), selfishness (5), and competitiveness (6), and reduced sharing (7–9) and trust (10).

In contrast, the universality of fight-or-flight in humans has been substantially challenged over the past 25 y: Evidence has emerged for a "tend-and-befriend" response, which is characterized by affiliative and prosocial behaviors aimed at strengthening social bonds with close-knit group members and securing mutual protection (11). In support of this, generosity and prosocial behavior have been shown to increase in stressed individuals (12–16).

Thus, although stress appears to affect social decision-making, it remains unclear when, how, and if (17) it increases antagonistic or affiliative responses (see ref. 18 for a review). To reconcile these inconsistent findings, we propose that stress does not promote one response over the other; instead, it stimulates both behaviors simultaneously, dissociable on the neuropharmacological level and moderated by the particular nature of the social group dynamics (15, 19).

The stress response involves both the rapid response of the sympathetic-adrenal-medullary (SAM) system, whose central neuromodulator is noradrenaline, and a slower and more prolonged response of the hypothalamic–pituitary–adrenal (HPA) axis, whose main neuromodulator is cortisol (20, 21).

Glucocorticoid action by cortisol has tentatively been implicated in promoting affiliative and prosocial behaviors (22), such as increased social bonds (23) and sharing (15, 19), especially toward socially close others (15, 16). In contrast, some evidence has associated SAM activation, or the action of noradrenaline, respectively, with aggressive fight-or-flight responses in animals and humans (24–26) as well as inhibiting the prosocial effects of cortisol in humans (15).

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2502257122/-/DCSupplemental.

Published July 14, 2025.

Critically, whether an individual prioritizes cooperation and social bonding or adopts more defensive and aggressive strategies also depends on whether they perceive their interaction partners as in-group or out-group members (27). For example, intensely stressful experiences, such as those faced by combatants in actual conflicts (28), have been shown to foster strong bonding with in-group members and, simultaneously, aggression against the enemy—a tendency termed parochial competition (27, 29).

Hence, we hypothesize that cortisol promotes prosocial behavior aimed at improving the well-being of the in-group [i.e., parochial cooperation (27)], while noradrenaline fosters costly parochial competition. To address this, we manipulated cortisol and noradrenaline action in a placebo-controlled double-blind psychopharmacological study and measured social decision-making using the Intergroup Prisoner's Dilemma–Maximizing Difference (IPD–MD), an intergroup conflict task designed to measure both parochial cooperation and competition (30).

In this task, participants are randomly assigned to a group consisting of three members, and allocate an endowment across three options (Fig. 1): 1) keeping money for themselves (maximizing individual payoff), 2) contributing to a within-group pool that benefited all in-group members, including themselves, but could be individually costly (parochial cooperation), and 3) contributing to a between-group pool that provided the same in-group benefit while simultaneously reducing the out-group's payoff (parochial competition). The in-group benefits from the within- and between-group pools were identical, but only the between-group pool imposed harm on the out-group. Importantly, we included an element of initial aggression by the out-group: Out-group members first reduced the in-group's initial endowment. In-group participants were then informed about the extent to which their group had been targeted by the out-group (none, moderate, or strong). Allocation decisions were subsequently made based on the remaining endowment.

We found support for our prediction that two dissociable components of the neurobiological stress response boost either parochial cooperation (generosity toward the in-group) or parochial competition (generosity toward the in-group and hostility toward the out-group). Our study contributes to our understanding of the biological mechanisms underlying the self-perpetuating cycle of intergroup conflict (29, 31).

Results

Increases in Salivary Alpha-Amylase and Cortisol Following Drug Administration. To test the effectiveness of our pharmacological manipulation, we analyzed the changes in salivary alpha-amylase activity and cortisol levels following drug administration. The area under the curve with respect to increase (AUC_I, ref. 32) of salivary alpha-amylase was significantly increased by yohimbine, $F(1, 74) = 11.05$, $P = 0.001$, $\eta_p^2 = 0.13$, while there was no main effect of hydrocortisone, $F(1, 74) = 0.13$, $P = 0.717$, $\eta_p^2 < 0.01$ and no interaction, $F(1, 74) < 0.01$, $P = 0.957$, $\eta_p^2 < 0.01$. Conversely, the AUC_I of cortisol was significantly increased by hydrocortisone, $F(1, 78) = 14.09$, $P < 0.001$, $\eta_p^2 = 0.15$, while there was no main effect of yohimbine, $F(1, 78) = 2.05$, $P = 0.156$, $\eta_p^2 = 0.03$ and no interaction, $F(1, 78) = 2.85$, $P = 0.095$, $\eta_p^2 = 0.04$ (Fig. 2).

These results confirm that yohimbine and hydrocortisone effectively manipulated noradrenergic and glucocorticoid activity, respectively.

Hydrocortisone Promotes Parochial Cooperation. Using a linear mixed-effects model (LMEM) on within-group pool allocations (*Materials and Methods*), we tested the effects of drug administration and aggression by the out-group on cooperative monetary allocations. The model revealed a main effect of drug on cooperative allocation decisions (Fig. 3). After controlling for the main effect of aggression by the out-group, hydrocortisone increased allocations to the within-group pool by 22.41% of the budget compared to placebo ($SE = 8.20$, $t(86) = 2.73$, $P = 0.008$, $d = 0.59$), indicating that cortisol promoted nonaggressive parochial cooperation with team members. Notably, this effect of hydrocortisone was offset by simultaneous yohimbine administration (no significant effect of combined administration of hydrocortisone and yohimbine compared to placebo, $P = 0.217$). Yohimbine administered alone also had no significant effect on parochial cooperation ($P = 0.185$) compared to placebo.

In addition, the model provided evidence for an effect of aggression by the out-group on cooperative allocations (Fig. 3). Compared to no out-group aggression, participants allocated 7.75% less to the within-group pool at moderate out-group aggression ($SE = 3.83$, $t(178) = -2.02$, $P = 0.044$, $d = -0.30$) and 8.35% less at strong out-group aggression ($SE = 3.83$, $t(178) = -2.18$, $P = 0.030$, $d = -0.33$), when controlling for the main effect of drug. None of the effects of drugs and out-group aggression on within-group pool allocations were moderated by gender (*SI Appendix*).

Yohimbine Promotes Parochial Competition. Next, to test the effects of drug administration and aggression by the out-group on competitive monetary allocations, we used a LMEM on between-group pool allocations (*Materials and Methods*). The model revealed a main effect of drug on competitive allocation decisions (Fig. 3). After controlling for the main effect of aggression by the out-group, yohimbine increased allocations to the between-group pool by 11.03% of the budget compared to placebo ($SE = 5.39$, $t(86) = 2.05$, $P = 0.044$, $d = 0.44$), suggesting that noradrenergic activity promoted parochial competition in participants. This effect was offset by simultaneous hydrocortisone administration, as no other comparisons with placebo reached significance (hydrocortisone: $P = 0.277$; combined: $P = 0.557$).

Furthermore, the model showed a significant effect of aggression by the out-group on competitive allocations (Fig. 3). Compared to no out-group aggression, participants allocated 13.30% more to the between-group pool in response to moderate out-group aggression ($SE = 3.30$, $t(178) = 4.03$, $P < 0.001$, $d = 0.60$) and 18.07% more in response to strong out-group aggression ($SE = 3.30$, $t(178) = 5.48$, $P < 0.001$, $d = 0.82$), after controlling for the main effect of drug administration. Hence, as aggression by the out-group increased, so did tendencies of parochial competition, reminiscent of a retaliation response. Again, none of these effects on between-group pool allocations were moderated by gender (*SI Appendix*).

Discussion

We investigated the effects of a pharmacological manipulation of noradrenaline and cortisol on intergroup conflict behavior using the IPD-MD. Consistent with our hypotheses, glucocorticoid activation increased parochial cooperation, i.e., generosity toward the in-group, whereas noradrenergic activation increased parochial competition, i.e., generosity toward the in-group combined with hostility toward the out-group. Hence, glucocorticoid and noradrenergic systems adaptively modulate social decision-making under stress in dissociable ways. Additionally, out-group behavior matters: Regardless of the administered drug, aggression by the out-group redirected resource allocation from in-group-focused cooperation to parochial competition, reminiscent of a retaliation response and in line with previous research (33). Notably, gender

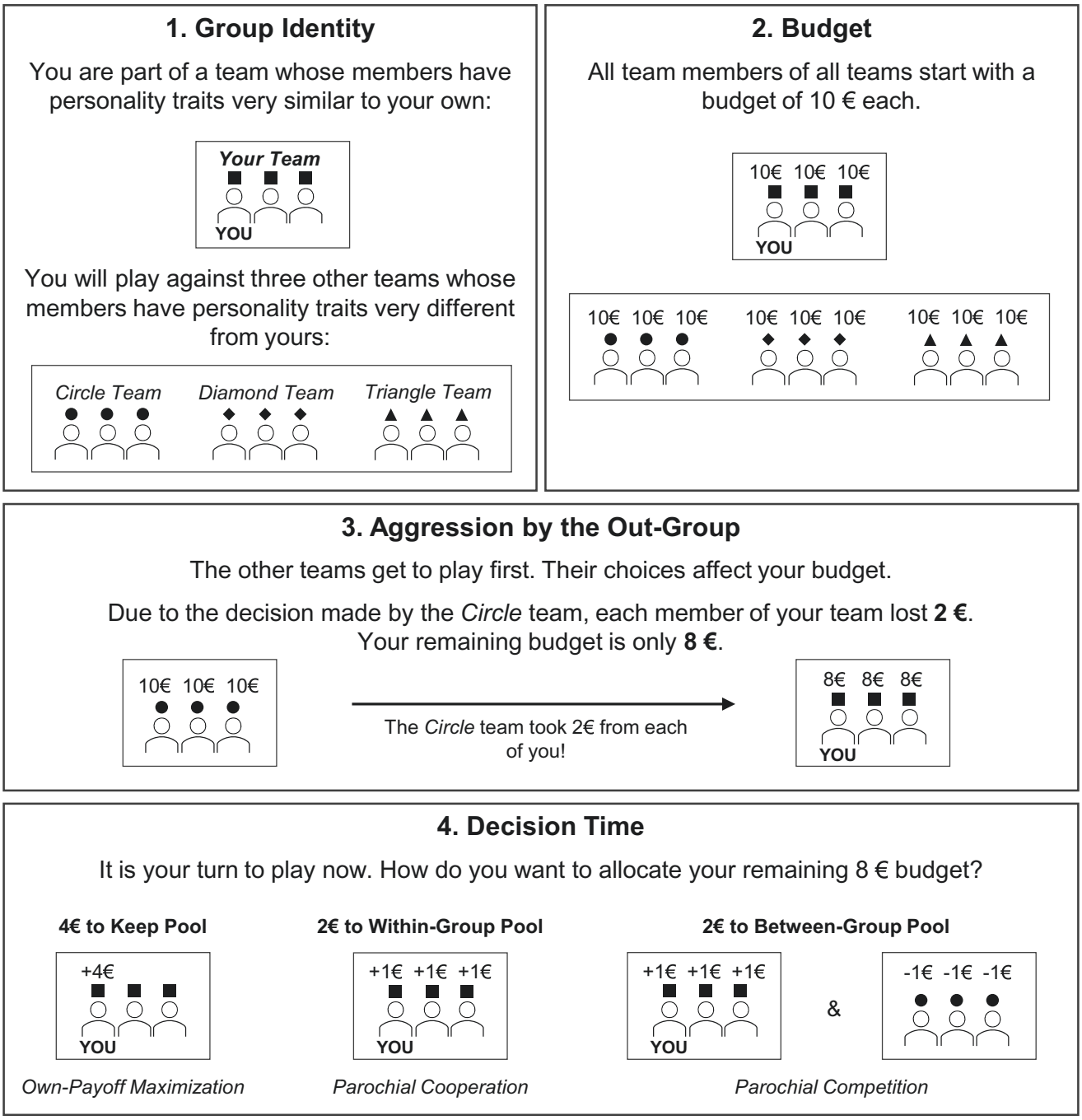

Fig. 1. Logic and example trial of the Intergroup Prisoner's Dilemma—Maximizing Difference task. Each participant was first assigned to a team (Panel 1) and told that they would have a budget of 10€ (Panel 2). Next, each participant learned whether, and how much money, the out-group (here: the circle team) had deducted from them and the other in-group members (Panel 3). They then allocated their remaining budget across three options (Panel 4). Any Euro allocated to the "keep pool" was kept by the participant (maximizing individual payoff). For every Euro allocated to the "within-group pool", each in-group member, including the participant, received half of the amount (parochial cooperation). The "between-group pool" provided the same in-group benefits as the within-group pool, but, additionally, half of the allocated amount was deducted from each out-group member's payoff (parochial competition).

did not moderate any of these effects on allocation decisions, as in ref. 17).

The neurohormonal response to stress follows a particular time pattern. Immediately after the onset of the stressor, catecholamines, including noradrenaline, are released through activation of the SAM system, followed by the slower but longer-lasting release of cortisol via the HPA axis (20, 21). These temporal dynamics of the stress response may give rise to distinct social-behavioral tendencies.

The initial rapid noradrenaline release prepares the organism to either aggressively confront or escape from the stressor (1, 18), potentially shifting behavioral patterns toward more competitive tendencies (25, 26, 34). Indeed, under elevated noradrenaline action, we observed increased hostility toward aggressive out-groups. Notably, participants in the yohimbine condition kept less money for themselves than those in the placebo condition. This pattern suggests that their motivation was not purely self-serving or competitive. Instead, they appeared to prioritize their in-group while simultaneously directing resources toward harming the out-group. Thus, extending traditional fight-or-flight predictions, we found that SAM activity did not exclusively promote self-serving aggression. Rather, we argue that noradrenaline

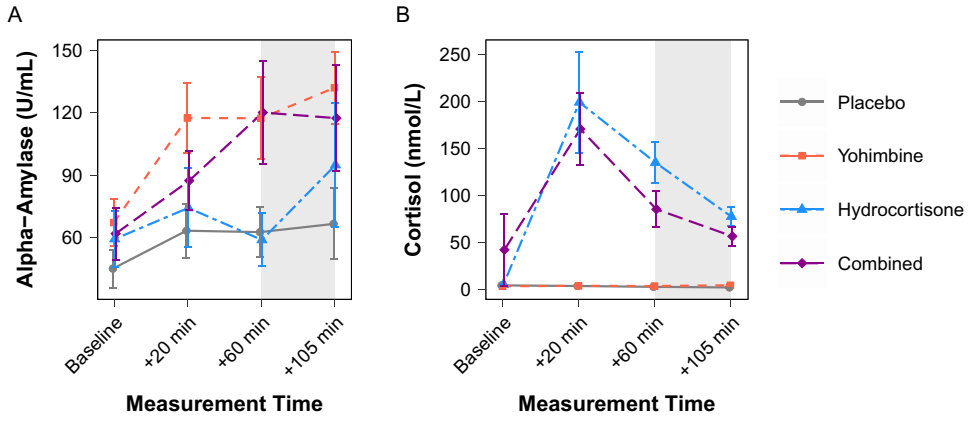

Fig. 2. Manipulation check. Mean (± *SEM*) salivary alpha-amylase activity (*A*) and salivary cortisol levels (*B*) across the experimental timeline for each drug condition. The timing of the experimental tasks is indicated by gray shaded bars. Participants who received yohimbine showed an increase in salivary alpha-amylase activity ($P = 0.001$). Participants who received hydrocortisone showed an increase in salivary cortisol levels ($P < 0.001$).

promotes parochial competition—favoring the in-group at the expense of the out-group.

Previous research has shown that resource inequality between in-group and out-group as well as environmental unpredictability increased out-group harm (33, 35). This suggests that threat perception as a potential source of stress and arousal may increase competitive tendencies, in line with our results. Further, the descriptive trend in our findings—that yohimbine increased competitive resource allocations more strongly when initial aggression by the out-group was higher—suggests that noradrenaline action during acute stress may exacerbate competitive drives, potentially by increasing sensitivity to threat.

By contrast, when the slower HPA response takes over, the focus shifts toward coping with postacute stress vulnerability (11). To buffer against the negative effects of stress, individuals tend to seek support from their in-group by investing in social relationships (11, 15). Consequently, cortisol likely facilitates prosocial behavior within the group, fostering cohesion and maintaining supportive social bonds (15, 19, 23). Consistent with this, after hydrocortisone administration, we observed increased generosity toward the in-group. Effective poststress coping also implies reducing conflict to avoid additional threats during periods of vulnerability, which may be facilitated by cortisol as well. This could explain reduced altruistic punishment after hydrocortisone (36) and reduced rejection rates of unfair offers in the late aftermath of acute stress (8), suggesting that cortisol fosters an "accept what you get and avoid conflict" mentality.

Together, these findings confirm that cortisol and noradrenaline promote different forms of social behavior (29, 37): Noradrenaline appears to promote more hostile parochial competition in early phases of stress (29, 38, 39), whereas cortisol effects involve peaceful in-group-focused cooperation in the aftermath of stress. Hence, our findings are in line with the idea that cortisol and noradrenaline regulate a temporal transition from early competitiveness to later cooperation.

Our results also resolve a long-standing debate in stress research as to whether stress primarily triggers fight-or-flight or tend-and-befriend behaviors (1, 11). We show that fight-or-flight and tend-and-befriend responses to stress are not mutually exclusive, but rather are part of a more complex, dynamic process that helps to adapt social behavior to social demands during and after stress, possibly in concert with other neuromodulators, such as oxytocin (40).

Finally, our findings offer a solution to another puzzle in the social stress field: Stress effects on prosocial preferences are notoriously inconsistent (17). Here, we propose that these inconsistencies arise because stress influences social behavior not in a simple, one-directional way; instead, its effects dynamically depend on intergroup relationships and the relative dominance of cortisol versus noradrenaline in the neurophysiological stress response. Crucially, previous research rarely controlled for the time window after stress, for group membership, or for the particular neurohormonal cocktail composition. In light of our findings that stress can promote prosocial as well as hostile behavior, the inconsistent results of recent years are not surprising (17, 18, 41). Therefore, it is essential to expand from testing whether stress promotes prosocial or antagonistic behavior (1, 11) to testing when, toward whom, and why it does so (17, 41).

To conclude, we show that activation of stress-related physiological pathways can induce in-group support as well as out-group aggression, especially in situations where the out-group is perceived as aggressive to begin with. Specifically, noradrenaline and cortisol distinctly influence social behavior in intergroup conflicts, with noradrenaline driving parochial competition and cortisol enhancing parochial cooperation. This challenges the dichotomy between fight-or-flight and tend-and-befriend responses, showing they are not mutually exclusive, but instead reflect two sides of the same coin. This suggests that social stress responses are dynamic, involving an interplay between neuroendocrine systems, to adapt social behavior to immediate and postacute demands. Beyond this, our findings have broader societal implications. They resonate with a recently proposed neurobiological model of war, which posits that neurobiological processes direct group behavior in war toward in-group protection and out-group harm, promoting an us-versus-them mentality (31). Thus, the stress-boosted parochial competition, suggested here, is likely to maintain the self-perpetuating vicious cycle of strike and counterstrike typical for intergroup conflict. Our study provides a foundation for future research exploring how neuroendocrine stress systems shape social decision-making in real-world settings.

Materials and Methods

Participants. A total of 91 participants were initially included in the experiment. One participant had to be excluded for taking medication prior to testing. This left a final sample of 90 participants (male: $n = 39$, female: $n = 49$, nonbinary: $n = 2$), ranging in age from 18 to 37 (see *SI Appendix* for exclusion criteria).

Participants received a fixed compensation of 15€ and could earn up to 40€ additionally during the experiment, which depended both on chance and on the choices participants made during the experimental tasks.

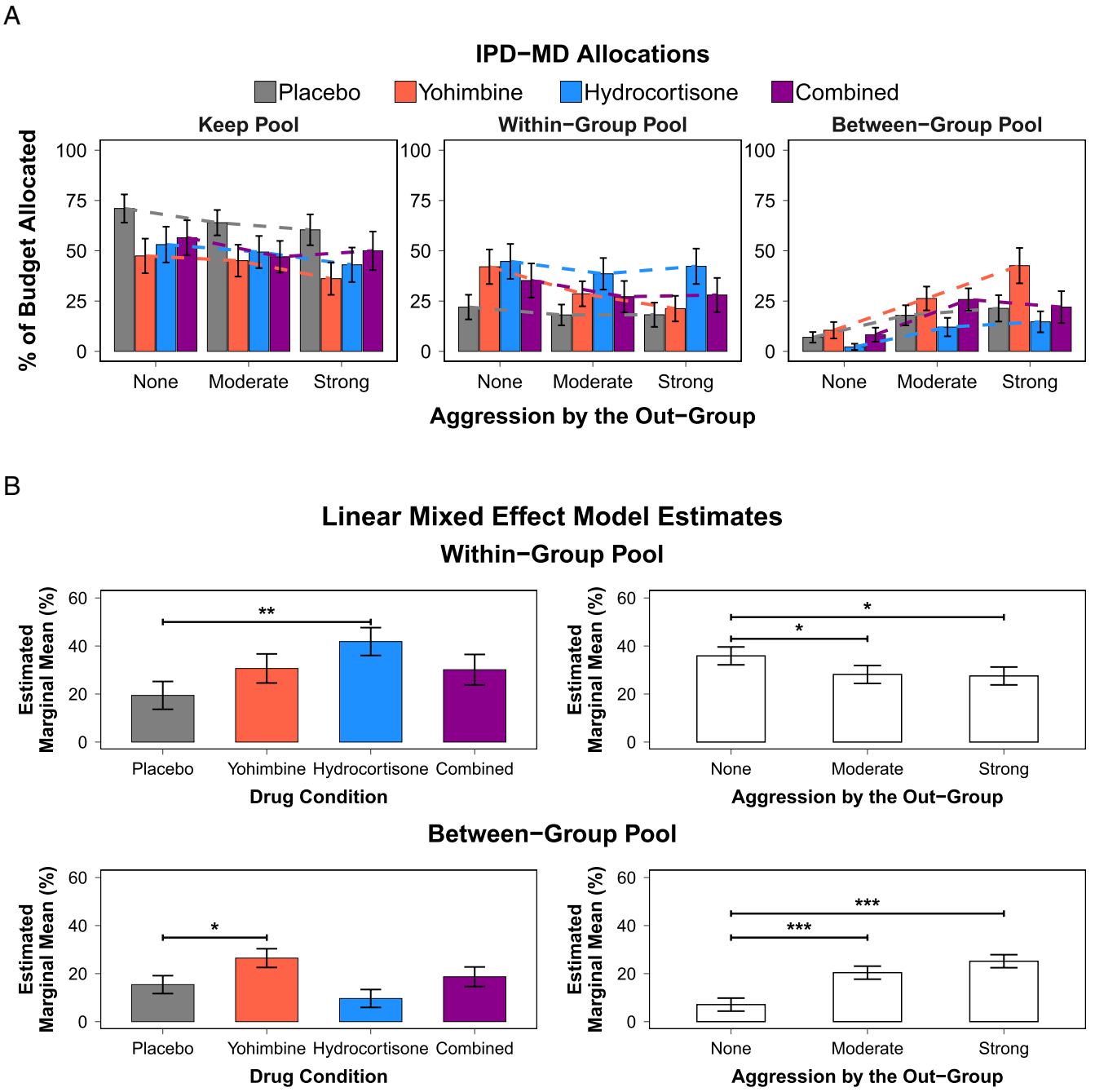

Fig. 3. Hydrocortisone and yohimbine differentially affect parochial cooperation and competition. (*A*) Mean percentage (± *SEM*) of the budget allocated to the keep-, within-group, and between-group pools in the IPD-MD at different levels of aggression by the out-group, shown separately for the four drug conditions. Compared to placebo, participants receiving hydrocortisone allocated more money to the within-group pool, independent of the level of aggression by the out-group. Participants receiving yohimbine allocated more money to the between-group pool compared to placebo. Participants in all drug conditions increased their allocation to the between-group pool across levels of aggression by the out-group. (*B*) Estimated marginal means (± *SEM*) of allocations to the within-group pool and between-group pool shown separately for the different drug conditions and levels of aggression by the out-group. *$P < 0.05$, **$P < 0.01$ and ** $P < 0.001$.

The study was approved by the ethics committee of the University Hospital Düsseldorf (study numbers 4920 and 2020-910) and complied with the Declaration of Helsinki.

Trait Measures. Prior to the experimental session, participants completed an online questionnaire assessing several trait measures to identify potential confounds between experimental conditions and to check for exclusion criteria (*SI Appendix*).

Pharmacological Manipulation. In a double-blind procedure, we pharmacologically manipulated cortisol and noradrenaline action by oral, exogenous administration of hydrocortisone, a synthetic form of cortisol, or yohimbine, an alpha-2 adrenergic receptor antagonist that stimulates the release of noradrenaline (i.e., norepinephrine). Participants were pseudorandomly assigned to one of four experimental conditions: hydrocortisone (20 mg; Jenapharm, mibe GmbH; $n = 24$), yohimbine (20 mg; Yocon-Glenwood, Cheplapharm Arzneimittel GmbH; $n = 22$), hydrocortisone + yohimbine (combined; 20 mg each; $n = 20$), or placebo ($n = 24$). The dosage was consistent with previous studies (15, 42). The number of pills was equal across conditions, so participants could not use it as a guide to which drug they had received.

Physiological Stress Measures. To monitor changes in cortisol and noradrenergic activation throughout the experiment, saliva samples (Salivettes; Sarstedt AG & Co. KG) were collected at four time points (Fig. 4). The samples were frozen at −20 °C until analysis by Dresden Lab Services GmbH. Salivary cortisol concentrations were determined by immunoassay, and salivary alpha-amylase activity [an

indirect marker of noradrenergic activation; (43)] was determined by an enzyme kinetic method as described in ref. 44. Thirty-two out of 720 samples could not be analyzed due to insufficient saliva or sample contamination. Heart rate was measured at four time points (Fig. 4) with a wrist-worn heart rate monitor (Polar A370, Polar Electro Oy).

Additional Control Measures. We additionally assessed baseline sex hormone levels to control for their potentially confounding effects (45) and repeatedly assessed subjective stress and mood ratings (Fig. 4 and see *SI Appendix* for more details).

Procedure. Three participants were invited for each experimental session. If less than three people were available for a session, the vacancies were filled by confidants of the experimenter who acted as real participants. All sessions began at 2:30 pm to control for circadian fluctuations in stress neuromodulators. After providing informed consent and completing a screening questionnaire to further check for exclusion criteria, participants were pseudorandomly assigned to one of four pharmacological conditions as mentioned before (hydrocortisone, yohimbine, hydrocortisone + yohimbine, and placebo; see above). They then provided baseline saliva samples and subjective stress and mood ratings and subsequently took the drugs.

After a 60-min break during which participants could do a jigsaw puzzle, they completed three experimental tasks in randomized order: the IPD-MD task reported here, as well as an Implicit Association Test and a Social Discounting Task (results will be reported elsewhere). Neither during the break nor during the experimental tasks were participants allowed to talk to each other or use their phones. While they could see each other, partitions separating them prevented them from seeing each other's screens.

Following the experimental tasks, participants provided information about their demographics, beliefs about the drug effects, and guessed which drug they had received.

IPD–MD Task. We used an adapted version of the IPD–MD paradigm (30), a money allocation task assessing individual decisions in an intergroup context. In this task, participants were assigned to a three-member group and told they would play a total of three one-shot rounds against different opposing teams. To create group cohesion (46), they were told that they were grouped with the other two participants in the session based on similar personality traits identified in the online questionnaire, whereas the opposing groups, allegedly participating in separate rooms simultaneously, were said to have significantly different personality traits. In reality, group assignment was pseudorandom, and decisions of the opposing groups were simulated.

In each round, participants allocated an initial endowment of 10 Euro (or less, see below) among three options ("pools"): 1) the "keep pool", where allocations were retained by the participant, reflecting a motive to maximize own payoff, 2) the "within-group pool", where each in-group member, including the participant, received half of the allocated amount, thus reflecting cooperative in-group support, 3) the "between-group pool", which yielded the same in-group benefit, but additionally, half of the allocated amount was deducted from each out-group member's payoff, indicating competitive motivation (see Fig. 1 and *SI Appendix*, Table S1).

For example, allocating 4 Euros to the keep pool increased the participant's final payoff by 4 Euros, without affecting the payoffs of the in-group or out-group members. Allocating 4 Euros to the within-group pool increased each in-group member's payoff by 2 Euro, including the participant. This creates a cooperative problem: if only the participant, and no other in-group member, contributed 4 Euros to the within-group pool, the participant would obtain a net loss of $4 - 2 = 2$ Euros. But if all three in-group members contributed 4 Euros to the within-group pool, they would obtain a net gain of $3 \times \frac{4}{2} = 6$ Euros, thus making cooperation mutually beneficial. Allocating 4 Euros to the between-group pool likewise increased each in-group member's payoff by 2 Euros, as with the within-group pool, but it also deducted 2 Euros from each out-group member's payoff. Thus, allocations to the between-group pool maximized in-group benefits at the out-group's expense. In line with ref. 27, we interpret within-group pool allocations as parochial cooperation and between-group pool allocations as parochial competition.

A key aspect of our design was incorporating an element of initial aggression by the out-group: The out-group moved first in each round, i.e., participants learned how much money the out-group had deducted from their in-group before they could make their choice. We manipulated the amount of money deducted from the in-group by the out-groups, ranging from no aggression (no money deducted) to moderate aggression (2 Euro deducted) to strong aggression (5 Euro deducted). Thus, depending on the extent of aggression by the out-group, participants began each round with a potentially reduced budget. They then had to decide how to allocate this remaining budget. The order of rounds was pseudorandomized across participants.

Participants were told that one round would be randomly selected at the end of the experiment and that the money they allocated in that round would be added to their final payoff. To avoid order and carry-over effects across rounds, participants were not told how their in-group members had allocated the available budget in each round (see *SI Appendix* for more task details).

Data Analysis. We ran separate LMEMs for the two dependent variables, "percentage of budget allocated to the within-group pool" and "percentage of budget allocated to the between-group pool", using the lme4 package in R (47). Allocations to the keep pool were excluded from analysis to ensure that the remaining dependent variables were independent of each other, as was done in ref. 19.

The models included the predictors "aggression by the out-group" [three levels: none (reference) vs. moderate vs. strong] and "drug" [four levels: placebo (reference) vs. hydrocortisone vs. yohimbine vs. combined]. Random intercepts for participants were included in the models.

We compared null models to models including the main effect of aggression by the out-group, the main effect of drug, the main effects of both predictors, and their interaction. If multiple models provided a better fit than the null model, we chose the simplest model that was not outperformed by a more complex one in a pairwise comparison. For both dependent variables [budget allocated to 1) the within-group pool and 2) the between-group pool], this model selection procedure resulted in the model that included the two main effects of aggression by the out-group and drug (see *SI Appendix* for detailed information). Thus, we report the models including the main effects of both predictors. Notably, when considering "gender" as an additional predictor,

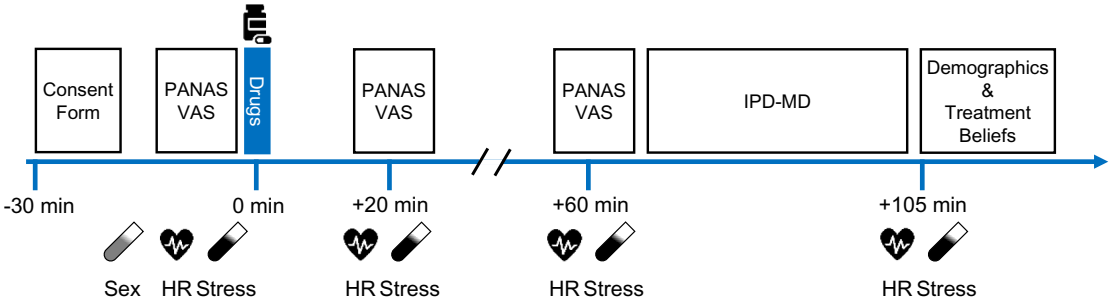

Fig. 4. Experimental procedure. Saliva samples were collected to measure sex hormone levels (Sex; testosterone, estradiol, and progesterone) and cortisol and alpha-amylase (Stress). Heart rate (HR) was recorded using a wrist-worn monitor. Mood was evaluated with the Positive and Negative Affect Schedule (PANAS), and subjective stress levels were rated on a visual analog scale (VAS) ranging from 0 to 100. Drug administration depended on group assignment: Participants received either hydrocortisone, yohimbine, hydrocortisone and yohimbine combined, or placebo.

we found no main or interaction effects on any of the outcome variables (*SI Appendix*).

We also tested for group differences in each demographic, trait, and baseline measure, using a series of ANOVAs for continuous variables and chi-squared tests for categorical variables. Additionally, we assessed whether participants could correctly guess which drug they had received using binomial tests. If group differences were found in any of these variables, we ran separate models with that variable as the predictor instead of drug and compared these models with the original models as a robustness check (*SI Appendix*). This was the case for the variables "egocentricity bias", "baseline negative affect", and "treatment belief" (*SI Appendix,* Table S2). However, none of these significantly predicted the dependent variables. Thus, overall, these checks confirmed the robustness of our results to potential confounds.

To assess changes in biomarkers (cortisol, and alpha-amylase) following yohimbine and hydrocortisone administration, we conducted separate ANOVAs on the AUC_I, with "yohimbine" (yes vs. no) and "hydrocortisone" (yes vs. no) as between-subject factors. We also compared AUC_I for heart rate as well as subjective stress and mood ratings as detailed in the *SI Appendix*.

Cohen's d effect sizes (48) were determined using the t-to-d transformation and calculated with the custom R package "reportMLM". The data and code for the analyses are available online: https://osf.io/e2pz6/?view_only=ce94b021e1c3463b99b8e742457ab581 (49).

Data, Materials, and Software Availability. Anonymized data and code data have been deposited in Open Science Framework (https://osf.io/e2pz6/?view_only=ce94b021e1c3463b99b8e742457ab581) (49).

ACKNOWLEDGMENTS. We thank Recep Dogan, Helena El Kholy, Sofia Guerreri, Alina Hansen, Hannah Herweg, Paul Kramer, Amanda Michalik, Pia Paschmann, Saroj Phuyal, Madalena Sophia Tavares, and Veronika Wild for their invaluable assistance with data collection. The work was supported by a grant from the German Research Foundation (Deutsche Forschungsgemeinschaft, Bonn, Germany) to Tobias Kalenscher (Grant-ID: DFG-KA 2675/7-1). Paul Forbes is supported by a Marie Skłodowska-Curie Postdoctoral Fellowship from the European Commission (101107160).

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Study 4 – Original Paper

Kalenscher, T.*, Lüpken, L.M., Stoop, R., Terburg, D, van Honk, J., 2025. Steeper social discounting after human basolateral amygdala damage. Proc. Natl. Acad. Sci. 122, e2500692122. https://doi.org/10.1073/pnas.2500692122

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David Terburg: Resources, Writing - Review & Editing.

Jack van Honk: Investigation, Resources, Writing - Review & Editing.

PNAS BRIEF REPORT | NEUROSCIENCE
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Steeper social discounting after human basolateral amygdala damage

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Edited by Susan Fiske, Princeton University, Jamaica, VT; received January 10, 2025; accepted March 24, 2025

Translational research suggests that the basolateral part of the amygdala (BLA) computes some of the core processes underlying social preferences, but its precise role in prosocial choice remains unclear. We hypothesize that the human BLA is not necessary for prosocial behavior per se, but fine-tunes the degree of prosociality as a function of the social distance between actor and recipient of a prosocial act. We tested five participants with Urbach–Wiethe disease (UWD) who had isolated, bilateral damage to BLA and compared their behavior in a modified dictator game to that of 16 healthy control participants matched for (neuro-) psychological traits and cultural and socioeconomic background. In this game, participants selected eight people from their social environment and assigned them to variable social distance levels ranging from 1 (emotionally closest person) to 100 (random stranger on the street). They decided how much of a monetary endowment they would share with each person at each social distance. Compared to controls, UWD participants were less generous overall and showed steeper social discounting, that is, their willingness to share declined more sharply with increasing social distance. This difference in social discounting could not be explained by empathy, personality, or social network size. Our data suggest that BLA is critical for resolving the conflict between selfish and altruistic motives during social discounting. This finding underlines the BLA's role in model-based social cognition, calibrating prosocial behavior based on the social-emotional distance between individuals.

basolateral amygdala | altruism | prosocial | social discounting | brain lesion

The basolateral subregion of the amygdala (BLA) is an important neural hub for prosocial behavior in humans and animals: In rodents and monkeys, neurons in BLA correlate with own- and other rewards, their activity predicts the propensity for prosocial decisions (1–3), and BLA lesions reduce prosocial choices (4). In humans, amygdala activity explains extraordinary generosity toward strangers (5), and it predicts the degree of inequity aversion and social value orientation (6). Also, amygdala malfunction has been implicated in psychopathy and aggression (7). This body of evidence suggests that the amygdala, in particular BLA, computes some of the core processes underlying prosocial decision-making, and that BLA impairment compromises prosocial behavior.

This conclusion stands in contrast to recent findings with South African participants with Urbach–Wiethe disease (UWD). The disease in this population is characterized by selective lesions of BLA while other brain areas, including other parts of the amygdala, remain intact (8–11). UWD subjects show hyperaltruistic behavior in the trust game (8, 9) that can neither be explained by atypical risk attitudes nor by altered fairness ratings and abnormal expectations about reciprocal backtransfers. UWD patients make hypermoral decisions in moral dilemmas; they strictly adhere to the deontological rule not to kill anyone under any circumstances (10). They also reveal enhanced altruistic punishment in the ultimatum game (12) as well as dissociable deficits in cognitive versus emotional empathy (13). Hence, while extant evidence across species indicates that BLA *does* play a role in regulating social behavior, it is apparent from research with human participants with BLA lesions that the story is more complicated than the simple equation that BLA integrity is necessary for prosociality. Here, we propose that BLA does not promote altruistic or selfish behavior per se, but supports social-cognitive mechanisms that compute the balance between selfish and altruistic motives (3, 5).

Individuals altruistically help others but are usually more inclined to support people they feel emotionally close to than unknown strangers—a bias called social discounting (5, 14). We recently argued (14) that social discounting involves the very tradeoff between selfish and altruistic motives attributed to BLA. We therefore hypothesize that human BLA would not be necessary for prosocial behavior as such, but would fine-tune the degree of prosociality as a function of how emotionally close or distant a participant feels to the recipient of help.

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Author contributions: T.K. designed research; T.K. performed research; T.K. analyzed data; L.M.L., R.S., D.T., and J.v.H. edited the paper; T.K. and J.v.H. collected data; D.T. and J.v.H. provided participant access; T.K. and R.S. provided funding; and T.K. wrote the paper.

The authors declare no competing interest.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2500692122/-/DCSupplemental.

Published April 15, 2025.

Results

Five UWD participants and 16 matched healthy controls played multiple rounds of an incentive-compatible monetary sharing game, based on a modified social discounting task (5, 14). In each round, participants were endowed with 200 South African Rands (approx. 11 US$) and they decided how much to share with other individuals varying in social-emotional distance, presented in pseudorandom order. Social-emotional distance was elicited beforehand by asking participants to assign real individuals from their social network to eight social distance levels on a scale ranging from 1 (their very best friend) to 100 (an anonymous stranger), based on how much, or little, they cared about the other individuals.

In all participants, generosity, measured as the amount of money shared with the other person, decreased hyperbolically across social distance. Descriptively, while UWD participants shared an equivalent amount of money with people at social distance 1, compared to controls, their generosity decayed much more steeply across social distance (Fig. 1*A*). The comparison of the area-under-the-curve (AUC; the normalized integral of the money shared with others; see *SI Appendix*) as a model-agnostic measure of social discounting revealed, accordingly, that UWD participants had significantly smaller AUC values than controls (Fisher's Exact Test for Medians, $P < 0.05$; results confirmed by an additional bootstrap test, $\alpha = 0.01$, Fig. 1*C* and *SI Appendix*).

To examine the individual differences in social discounting between UWD participants and controls, we fitted a hyperbolic discount function to the amount of money shared across social distance (*SI Appendix*). For each participant, we estimated the parameters log(k) and V that represent the degree of social discounting (discount rate) and the intercept with the y-axis at social distance 0 (often interpreted as generosity toward socially close others; *SI Appendix*). We assessed whether the individual parameter estimates for UWD subjects fell within the 95% percentile-based confidence interval (CI) established for the control group with a bootstrap procedure (*SI Appendix*). The log(k)-parameters of all UWD participants fell outside of the controls' CI (Fig. 1*D*). The log(k)-parameter of four out of five UWD participants exceeded the upper bound of the CI, indicating steeper discounting than controls, and the log(k)-parameter fell below the CI's lower bound in one case, suggesting flatter discounting. While the V-parameters of the four UWD participants with steeper discounting were within the control's CI bounds (*SI Appendix*), indicating no evidence for diverging generosity toward close friends, the V-parameter of the UWD participant with flatter discounting (subject UWD2) fell below the controls' CI, indicating less generosity toward socially close others. This was confirmed by visual inspection of the individual discount function of participant UWD2 (Fig. 1*B*), revealing that she shared almost no money with others, not even with her best friend. We observed no differences in empathy, personality traits, or social network size between UWD participants and controls (*SI Appendix*).

Discussion

We found reduced generosity after human BLA-lesions. Compared to controls, four UWD participants exhibited a markedly steeper decline in generosity across social distance, and one UWD participant

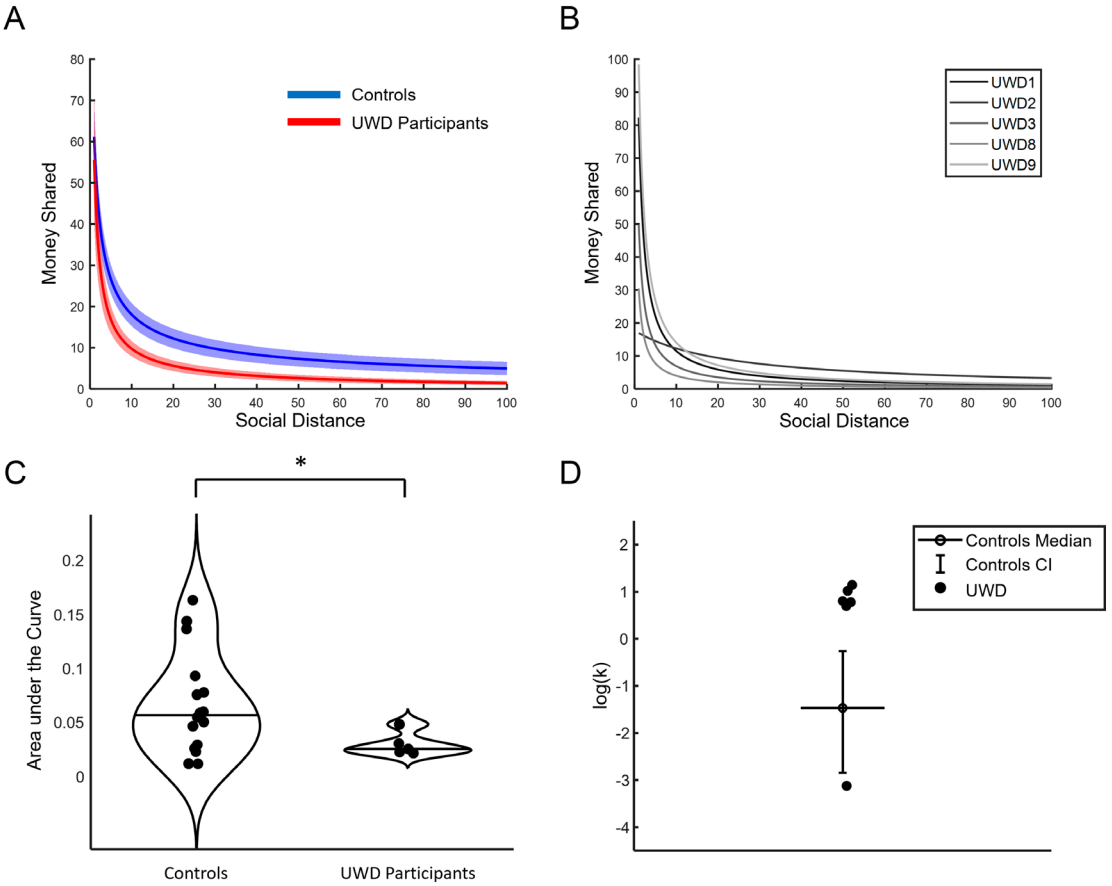

Fig. 1. Social discounting in UWD participants. (*A*) Mean best-fitting hyperbolic social discount functions (solid lines; ±SEM; shaded areas) of control (blue) and UWD participants (red). (*B*) Best-fitting individual social discount functions of the five UWD participants. (*C*) Violin plots of the normalized AUC of the proportion of money shared across social distance. Horizontal lines: median areas-under-the-curve; dots: data from individual participants. (*D*) log-transformed k-values [log(k)]. Controls' median of the bootstrap distribution (horizontal line) and 95% CI (vertical line). The dots indicate the log(k)-values of the five UWD participants. *$P < 0.05$

consistently showed very low generosity at all social distance levels. Thus, UWD participants were more selfish than controls, particularly toward socially more remote individuals. This difference in social discounting between UWD participants and controls could not be explained by empathy, personality traits, or social network size. Hence, BLA seems to fine-tune the degree of prosociality based on the social distance between individuals.

The finding that amygdala integrity is essential for prosocial choices toward socially more distant individuals aligns with recent neuroimaging evidence, linking amygdala activation to extraordinary altruism, particularly toward strangers (5). In addition, research with primates has shown that BLA contains neurons encoding the value of both own-rewards and, vicariously, rewards received by conspecifics (1, 3). It has therefore been proposed that prosocial and self-directed behaviors might be regulated in an antagonistic, competing manner within BLA (3). Lesions of BLA can consequently be expected to disrupt the computations underlying the tradeoff between maximizing own-rewards and considering reward for others.

We argue (14) that social discounting captures precisely this process; that is, it reflects the resolution of the internal conflict between self-regarding and other-regarding motives. Sharing resources with close others involves minimal conflict because their welfare is valued nearly as highly as one's own. In contrast, the vicarious value placed on others' outcomes decreases with social distance. Consequently, the tradeoff between motives is increasingly resolved in favor of self-interest as social distance increases. A plausible explanation for our current data, therefore, is that, without BLA, the social-distance-dependent conflict between selfishness and generosity cannot be amply processed or resolved. As a result, participants rely on neural reward systems that bypass BLA, adopting a default strategy to maximize their own payoff—except when it comes to socially very close relationships, where the internal conflict is minimal and helping instead becomes the default response.

Crucially, our results reconcile previous contradictory findings that, while BLA-integrity seems necessary for prosocial behavior (1–4), lesions increase, rather than decrease altruistic choice (8–10). We recently proposed that BLA is a crucial node in a network supporting model-based social motivation—the selection of social actions based on an internal representation of the state and structure of the world (10), such as flexibly down-regulating generosity in response to others' selfishness (8), or shifting between calculative, utilitarian, and noncalculative, rule-based moral reasoning (10). Trading-off self-directed and other-regarding motives during social discounting can also be viewed as a model-based process. Disruption of model-based computations following BLA-lesions can therefore be expected to favor selfish behavior as the predominant default response in social discounting, as argued above, especially when the target is socially distant. Conversely, the same model-free bias after BLA damage would result in more generous behavior in contexts like the trust game and moral dilemmas, where the once-acquired default response is trustful behavior (9), or the reluctance to be responsible for someone else's death (10). It is, hence, plausible that the disruption of a higher-level process—model-based social cognition—explains both the observed increase *and* decrease in prosociality following BLA lesions.

Previous studies on the amygdala's role in social preferences often overlooked the influence of social distance between individuals (6, 8–10, 12, 13). The lack of experimental control over whom participants have in mind may further help explain the discrepancies between studies, as thinking of a close friend versus a distant stranger is undoubtedly associated with different levels of trust, generosity, and moral behavior. Our results, which show that social distance matters for BLA, underscore the need to control for social distance in future experiments.

One obvious limitation of the present study is the small sample size. While this is unavoidable due to the extreme rarity of UWD, we emphasize that the focality and bilateral symmetry of brain lesion in this UWD sample (11) are unprecedented in human brain damage research, which has typically relied on single-case and twin UWD studies (13, 15). Also, note that our participants were instructed to exclude spouses, household members, and relatives from the target list (*SI Appendix*). Since individuals typically share more with these groups, their exclusion may have led to steeper social discounting in all participants, including controls.

In conclusion, our results offer an explanation for the incongruent evidence about the role of BLA in prosocial behavior: We show that BLA integrity is not necessary for altruistic behavior per se, but it fine-tunes the degree of prosociality based on the social-emotional distance between individuals, underlining its critical role in model-based social cognition.

Materials and Methods

All participants were female; they were matched for age, income, socio-economic and cultural-ethnic status, religion, and IQ (*SI Appendix*). The study was approved by the institutional review board of Cape Town University (Human Research Ethics Committee UCT, protocol no. 639/2016). All participants gave written informed consent in accordance with the Declaration of Helsinki. All data were pseudonymized and are publicly available on OSF (https://osf.io/hpw5t/). For further methodological details, see *SI Appendix*.

Data, Materials, and Software Availability. Choice and questionnaire data data have been deposited in OSF (https://osf.io/hpw5t/) (16).

ACKNOWLEDGMENTS. This project was funded by grants to T.K. (DFG KA-2675/7-1) and R.S. (SNSF IZLCZ0_206045). We thank Victoria Cloete and Mara Brandt for their invaluable fieldwork.

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