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Lexical access to experience-dependent representations in semantic memory

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“The only source of knowledge is experience.”

Albert Einstein

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Contents

List of abbreviations

ATL	anterior temporal lobe
DMN	default mode network
EEG	electroencephalography
ERD	event-related desynchronization
ERP	event-related potential
fMRI	functional magnetic resonance imaging
LDT	lexical decision task
LPC	late positive component

Summary

The semantic memory system contains the knowledge we acquire through experience in form of highly integrative conceptual representations. These are fundamental for higher cognitive functions such as language. In how far conceptual processing recruits the same brain areas, which were involved during the initial experience with the concept's referent is a matter of ongoing debate. The most recent theoretical approaches assume experience-specific brain areas and higher order semantic hubs to interact hierarchically. The studies presented in this dissertation investigated the role of experience in processing recently formed object representations as well as of consolidated abstract mathematical concepts. The first three studies employed a training paradigm to examine experience-dependent processing of the names of novel objects. These studies suggest that processing the novel objects representations recruits the same brain areas involved in the experience gained during a short training period. In Study 4, accumulated mathematical experience specifically affected the processing of mathematical words. This study supports the generalizability of experience-dependent semantic processes from concrete to abstract knowledge. Altogether, the current findings provide evidence for an experience-dependent formation and processing of conceptual representations. Importantly, the presented results reflect conceptual processing untainted of any perceptual influences, as we accessed the conceptual representation via lexical stimuli. This dissertation delivers important insights into the dynamics of conceptual processing at different stages of consolidation as well as across concrete and abstract knowledge, contributing to a comprehensive understanding of semantic memory.

1 Introduction

1.1 Semantic Memory

Semantic memory, also referred to as *conceptual knowledge,* contains information we gained about the world (i.e., facts, features, processes). The semantic memory system combines this information to highly integrative conceptual representations, which allow us to quickly interpret our constantly changing environment and react to it adequately (Kiefer & Pulvermuller, 2012). Higher cognitive functions like categorization, contextual evaluation and language strongly rely on conceptual knowledge (Binder, 2016; Binder & Desai, 2011). Classical theories consider our semantic memory separate from knowledge of our personal experience stored in episodic memory (i.e., when and where we gained certain experiences, see Tulving, 1972). In forming conceptual representations however, semantic and episodic memory processes are interwoven (Binder & Desai, 2011; Greenberg & Verfaellie, 2010). While semantic knowledge is derived from initial episodic information through abstraction from time and place (*decontextualization*; Baddeley, 1988), interpreting and integrating new episodic information relies on existing semantic knowledge (Irish & Piguet, 2013; Tulving, 1972). While at the stage of concept formation, perceptual experience plays an undeniably crucial role, the role of modality-specific experiential brain areas in conceptual processing is the matter of an ongoing debate (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012).

1.1.1 Theories on Semantic Memory

Theories on the architecture of semantic memory differ in the level of dependence on perceptual brain areas they assume (for a review, see Meteyard et al., 2012). The one extreme are disembodied theories like amodal symbolic theories (e.g., Fodor, 1975) or domain-specific theories (Caramazza & Shelton, 1998; Mahon & Caramazza, 2009, 2011). Both classes of theories postulate that semantic processing operates independently of experiential brain areas. The former emerged early from philosophical and philological/linguistic views as well as from computational models (e.g., Collins & Loftus, 1975). The latter assume that evolutionary pressure led to the formation of distinct brain networks involved in the processing of conceptual categories. The other extreme are modality-specific, strongly *embodied* theories (e.g., Fischer & Zwaan, 2008; Gallese & Lakoff, 2005; Glenberg, 1997; Glenberg & Kaschak, 2003), which claim that conceptual processing relies on a reactivation of primary sensorimotor brain areas involved in the initial experience with the concept's referent. These theories are also referred to as 'distributed-only' (Patterson, Nestor, & Rogers, 2007), because they assume that conceptual knowledge is independent of higher-order brain areas integrating modality-specific information. Embodied theories emerged from neuroscientific evidence on sensorimotor activations during conceptual processing (Barsalou, 2010), which led to a downright 'embodiment revolution' (Binder, 2016, p. 1096), a countermovement to classical amodal views on semantic memory.

The growing body of empiric evidence led to serious objections against either of these two extreme approaches. On the one hand, the involvement of distributed, modality-specific areas in conceptual processing (e.g., for action concepts; van Elk, van Schie, & Bekkering, 2014) challenges amodal and domain-specific theories. It has been shown, e.g., that processing visual, functional, motor and manipulation properties of object concepts draws on those sensorimotor brain areas specifically involved in the underlying type of experience (Martin, 2007). Further, the local, rigid neural representations assumed by disembodied theories are irreconcilable with contextual flexibility of meaning (Barsalou, 2016). Thus, disembodied theories fail to explain empiric evidence for task- and context-dependent reactivations of, e.g., motor areas in processing the motor features of action verbs (Kemmerer, 2015) or object names (Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008).

On the other hand, distributed-only embodied theories cannot explain the severe, modality-independent semantic impairments characterizing the clinical pattern of *semantic dementia* (Hodges & Patterson, 2007). This disease is caused by bilateral atrophy of the anterior temporal lobe (ATL), leaving modality-specific areas intact. Patients suffering from semantic dementia show highly correlated impairments between semantic tasks with different input and output modalities (i.e., picture naming, word-/sound-picture matching, association judgments on pictures and words), suggesting a degradation of amodal semantic representations (Jefferies & Lambon Ralph, 2006). Semantic dementia patients further show an impaired language comprehension and production, while phonology, visuospatial processing and executive functions remain intact (Reilly & Peelle, 2008). These impairments suggest that many semantic processes, including language comprehension, rely on a central, integrative mechanism, which is irreconcilable with the idea of a semantic system, which is distributed(-only) over modality-specific areas (Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Patterson et al., 2007). Strongly embodied approaches further cannot explain higher integrative functions of human cognition like detecting semantic similarities, retrieving typical contexts and generating predictions, for which modality-specific areas alone can hardly provide a basis (Barsalou, 2016; Binder, 2016; Reilly, Peelle, Garcia, & Crutch, 2016). The representation of abstract knowledge further challenges embodied theories, as abstract concepts do not refer to physical entities in the world and therefore cannot be directly grounded in sensorimotor perceptual areas (Desai, Reilly, & van Dam, 2018; Galetzka, 2017).

Recently, these objections against both extremes of the embodiment continuum led to the development of hybrid models of semantic memory (Barsalou, 2016; Lambon Ralph et al., 2017; Man, Kaplan, Damasio, & Damasio, 2013; Patterson et al., 2007; Reilly & Peelle, 2008), which assume modality-specific, distributed brain areas and higher order *semantic hubs* or *convergence zones* to interact in a hierarchical way. These hierarchical, hybrid models, however, differ in the number of higher-order areas they include (e.g., one amodal vs. multiple cross- and multimodal; compare Patterson et al., 2007; Xu, Lin, Han, He, & Bi, 2016) as well as in the hierarchical organization of the hubs and modality-specific areas. The (graded) hub-and-spokes model (Lambon Ralph et al., 2017; Patterson et al., 2007) assumes semantic processing to be generally amodal, crucially relying on the ventrolateral ATL with an amodal core. The grounded cognition approach (Barsalou, 2010, 2016) as well as the convergence zones model (Damasio & Damasio, 1994; Man et al., 2013; Meyer & Damasio, 2009), assume a more constitutive role of modality-specific areas in conceptual processing, which increasingly converges to higher-order areas. Functional magnetic resonance imaging (fMRI) studies in support of these hierarchical approaches could show that object identification in the ATL depends on converging information from early visual areas involved in shape and color processing (Chiou, Humphreys, Jung, & Lambon Ralph, 2018; Coutanche & Thompson-Schill, 2015).

1.1.2 Neural Correlates of Conceptual Processing

In order to investigate, which brain areas contribute to conceptual processing, many studies in cognitive neuroscience focused on lexical-semantic processing (Binder, Desai, Graves, & Conant, 2009). Studies on pictorial stimuli often face the critique of measuring stimulus-driven processes, which are driven by the pictures' perceptual features and are not constitutive of conceptual processing (Mahon & Caramazza, 2008). Word form, in contrast, is arbitrary and not systematically connected to semantic information. Given the arbitrary form of words, paradigms based on lexical-semantic processing eliminate perceptual influences potentially leading to stimulus-driven, epiphenomenal sensorimotor activations. For this reason, the studies comprised in this dissertation focused exclusively on lexical-semantic processing.

Studies on lexical-semantic processing often compared either semantic and non-semantic stimuli (e.g., tasks with words and pseudowords) or tasks (e.g., semantic vs. phonological tasks; see Binder et al., 2009). Research showed that even an implicit lexical decision task (LDT) on words and pseudowords robustly induces semantic processing of the words (Binder et al., 2003). Studies contrasting semantic with non-semantic lexical processing found a reliable activation of areas of the default mode network (DMN; Binder et al., 2009; Murphy et al., 2018). This network is known to underlie internal mentation processes and is active at rest, when no sensory input is given (Buckner, Andrews-Hanna, & Schacter, 2008; Raichle et al., 2001). It contains posterior association cortices (i.e., inferior parietal lobule and lateral temporal cortex), heteromodal frontal areas (i.e., inferior frontal gyrus, prefrontal cortex) and medial limbic regions (i.e., parahippocampal and fusiform gyrus), which receive highly multimodal input (Binder et al., 2016; Xu et al., 2016). It further shows a strong connectivity with the ventral ATL (Murphy et al., 2017). Activation in the DMN suggests a relative decoupling of perceptual brain areas during general conceptual processing (Smallwood et al., 2013). However, specific concept categories have been shown to elicit distinguishable activation patterns within the DMN (Binder et al., 2009). Action knowledge, for example, elicited activation in left supramarginal gyrus and posterior middle temporal gyrus, which are involved in executing and processing complex object-directed movement (Buxbaum, Kyle, & Menon, 2005; Buxbaum, Kyle, Tang, & Detre, 2006; Buxbaum, Shapiro, & Coslett, 2014).

Neuroimaging research on healthy participants (Murphy et al., 2017) inducing transient lesions (Pobric, Jefferies, & Lambon Ralph, 2010) discovered an involvement of the ventrolateral ATL in semantic processing independent of conceptual content. This is in line with general impairments in semantic dementia following lesions in this area (Jefferies & Lambon Ralph, 2006; Patterson et al., 2006). Recent neuroimaging research suggests that apart from a modality-independent, ventrolateral core, the ATL shows a graded functional specialization based on its connectivity with and proximity to modality-specific regions (Hoffman, Binney, & Lambon Ralph, 2015; Lambon Ralph et al., 2017). Medial portions have been shown to be more strongly involved in processing pictorial stimuli (Clarke & Tyler, 2015) and concrete concepts (Hoffman et al., 2015). The anterior superior temporal sulcus and gyrus, on the other hand, were more strongly involved in processing auditory/verbal material (Murphy et al., 2017; Scott, Blank, Rosen, & Wise, 2000; Visser & Lambon Ralph, 2011) and abstract concepts (Hoffman et al., 2015).

While fMRI delivers important insights into the brain areas underlying conceptual processing, event-related potentials (ERPs) obtained via electroencephalography (EEG) recording allow a closer examination of the temporal orchestration of conceptual processes (Hauk, 2016). The temporal precision of the EEG allows to disentangle early, (lexical-)semantic and later, strategical or imagery-based processes (Hauk, Shtyrov, & Pulvermuller, 2008).

The *N400*, a negative deflection 300 ms to 500 ms after stimulus-onset, has been identified as a robust marker of semantic processing independent of input modality (Kutas & Federmeier, 2011). It is thought to reflect semantic integration processes of contextual and conceptual information (Lau, Phillips, & Poeppel, 2008). Source localization and simultaneous EEG/fMRI acquisition (Lau, Weber, Gramfort, Hamalainen, & Kuperberg, 2016) as well as EEG acquisition with depth electrodes during surgery (Klaver et al., 2005) identified the ATL as the underlying generator. The N400 has been shown to be sensitive to the concreteness of words with higher amplitudes for concrete than abstract words (Barber, Otten, Kousta, & Vigliocco, 2013; Holcomb, Kounios, Anderson, & West, 1999; Kounios & Holcomb, 1994; Lee & Federmeier, 2008). This concreteness effect possibly mirrors the aforementioned graded functional specialization of the ATL.

At later processing stages, a frontal N700 and parietal late positive component (LPC) temporally support semantic processing. Gullick, Mitra, and Coch (2013) found that stimulus- and task-driven imagery processes modulate the N700 amplitude in interaction. Concrete (thus highly imaginable) words commonly elicit a larger N700 (Barber et al., 2013; West & Holcomb, 2000). In old-new recognition paradigms on single words, the LPC was consistently found to be higher for successfully recognized words as well as concrete words (Curran, 2000; Kandhadai & Federmeier, 2010a, 2010b; Strozak, Bird, Corby, Frishkoff, & Curran, 2016). Former research interpreted the N700 to reflect mental imagery (Gullick et al., 2013; West & Holcomb, 2000) and the LPC to reflect episodic retrieval (Kandhadai & Federmeier, 2010a; Strozak et al., 2016) in the service of conceptual processing.

1.2 Experience-Dependent Processing of Tool Concepts

The category of tools, i.e., man-made objects with a distinct function, attracted considerable interest in research on conceptual representations in the concrete domain (Beauchamp & Martin, 2007; Ishibashi, Pobric, Saito, & Lambon Ralph, 2016; Martin, 2007; van Elk et al., 2014). While tools share many perceptual qualities with other man-made objects, we gain additional functional and sensorimotor experience with them (Beauchamp & Martin, 2007). Research on tool-use has identified an extensive left-hemispheric fronto-parietal tool-network including action-related areas on manipulation and functional knowledge involved in actual and imagined as well as observed tool-use

(Canessa et al., 2008; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Ishibashi et al., 2016). Conceptual processing of tool pictures and, importantly, tool names partly reactivates this network (Cappa, 2008; Martin, 2007; Noppeney, 2008). While there is evidence that this conceptual reactivation during lexical-semantic processing is comparable to the one elicited by pictures (Chao et al., 1999), some evidence suggests that the reactivation during lexical-semantic processing might depend on task demands (Devlin, Rushworth, & Matthews, 2005) and the quantity of experience with the tool concepts (Dekker, Mareschal, Johnson, & Sereno, 2014).

Lesions in this network led to impairments not only in tool-related actions (i.e., imitation gestures; Buxbaum et al., 2014) but also in conceptual processing of, e.g., manipulation-related features in tool pictures (Lee, Mirman, & Buxbaum, 2014) as well as the recognition of tool words (Dreyer et al., 2015). In healthy participants, a concurrent motor-task (but not a control mental rotation task) interfered with spoken word processing in a semantic categorization as well as a picture-naming task (Yee, Chrysikou, Hoffman, & Thompson-Schill, 2013). This interference effect positively correlated with the amount of former manipulation experience the participants had gained.

In EEG studies, object-category-specific effects of tools vs. non-manipulable objects emerged as early as 110 ms to 250 ms after the onset of pictorial as well as verbal stimuli (Hoenig et al., 2008; Proverbio, Adorni, & D'Aniello, 2011). An event-related desynchronization (ERD) of the mu rhythm, reflecting activation of sensorimotor cortices (Pfurtscheller, 2000; Pfurtscheller & Neuper, 1997), has been found as early as 140 ms after the onset of tool pictures (Proverbio, 2012).

The early emergence of these effects supports of a rather constitutive than epiphenomenal role of sensorimotor brain areas in the processing of conceptual representations of tools.

A line of research investigated the role of sensorimotor experience in the conceptual representations of tools more directly by controlling the experiential information available during concept formation. Studies employing a training paradigm with novel, tool-like objects found that after manipulation training, processing pictures of these objects activated regions of the left-hemispheric tool-network (Weisberg, van Turennout, & Martin, 2007). Following studies showed that the involvement of areas of this network was stronger for objects after active as well as observational manipulation training than merely visual training (Bellebaum et al., 2013; Ruther, Tettamanti, Cappa, & Bellebaum, 2014b). While these studies used fMRI to explore the spatial characteristics of the underlying neuronal network, Ruther, Brown, Klepp, and Bellebaum (2014a) used the high temporal resolution of the EEG to explore the temporal dynamics of these reactivations. They found an ERD of the mu rhythm for manipulated than visually explored novel objects within the first 200 ms after stimulus onset. This line of research, however, has to face the criticism that the perceptual features of tool pictures used in the post-training fMRI and EEG acquisition might prime the actions afforded by the objects (Tucker & Ellis, 2004; van Elk et al., 2014).

1.2.1 Research Objectives Studies 1, 2 and 3

Studies 1 to 3 included in this dissertation pursued and extended the above-described line of research. These three studies introduced novel names to novel objects in a visual (Study 1) and manipulation (Study 2 and 3) training paradigm, which allowed to measure experience-dependent conceptual processing untainted of perceptual influences (Binder et al., 2009). Study 1 focused on the influence of merely visual experience with pictures of the novel objects on ERP correlates of subsequent object name processing. Studies 2 and 3 directly connect to the above-described line of research employing the manipulation vs. visual training paradigm (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b). Studies 2 and 3 extend this line of research by measuring conceptual reactivation during lexical-semantic processing of newly introduced novel object names (as opposed to pictorial stimuli). Study 2 investigated the temporal dynamics of early, experience-specific conceptual reactivations via EEG. Study 3 aimed to explore not only the spatial characteristics of the network underlying experience-specific reactivations but also the involvement of the previously identified semantic network (Binder et al., 2009) in processing newly formed conceptual representations. In a more fine-grained examination of manipulation experience, Study 3 further included not only active but also observational manipulation training, as studies delivering a direct comparison of these types of learning are scarce.

1.3 Experience-Dependent Processing of Mathematical Concepts

While Studies 1 to 3 in this dissertation focused on the role of experience in forming concrete object representations of novel tools, Study 4 investigated experience-dependent conceptual processing in the abstract domain. The abstract domain includes amongst others mental, emotional, social and mathematical concepts (Ghio, Vaghi, & Tettamanti, 2013; Troche, Crutch, & Reilly, 2014). Referents of concrete concepts like, e.g., objects, are directly perceivable via the senses and we can act upon them. Abstract concepts, however, lack such a direct link to perceptual and action experience (Hoffman, 2016; Troche et al., 2014). The tangibility of concrete concepts (e.g., the sensorimotor systems as well-defined underlying experiential channels) makes it convenient to develop paradigms to examine their experience-dependence. This led to a clear imbalance in favor of concrete concepts concerning not only the empiric basis available but also the theoretical approaches derived from it (Binder, 2016; Binder et al., 2016; Reilly et al., 2016). This imbalance gives reason to focus on whether and how far the mechanisms underlying concrete conceptual processing can be generalized to the abstract domain.

Rating studies suggest that mathematical concepts form a cohesive sub-category (Ghio et al., 2013; Troche et al., 2014), which makes them a promising candidate to examine conceptual processing in the abstract domain. Theoretical approaches of the underlying experiential information assume basic magnitude-based information (Dehaene, Molko, Cohen, & Wilson, 2004) or embodied spatial information (Fischer, 2012; Fischer & Shaki, 2018) to be especially relevant for mathematical and numerical concepts. Research has identified a prefrontal-intraparietal network to underlie basic magnitude processing, e.g., in number perception and calculation tasks (Dehaene et al., 2004; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). A lesion restricted to the intraparietal sulcus led to acalculia in an infarct patient (Ashkenazi, Henik, Ifergane, & Shelef, 2008) and reduced grey matter of this region played a role in developmental dyscalculia (Isaacs, Edmonds, Lucas, & Gadian, 2001). In healthy subjects, transient lesions induced in the inferior parietal sulcus via transcranial magnetic stimulation impaired the performance in solving subtraction and multiplication problems (Andres, Pelgrims, Michaux, Olivier, & Pesenti, 2011).

In order to investigate, whether this network involved in actual mathematical experience also serves the processing of mathematical concepts, research only began to explore lexical-semantic processing of mathematical terms. Recent neuroimaging studies revealed a selective reactivation of the prefrontal-intraparietal network during processing of the word *arithmetic* (Wilson-Mendenhall, Simmons, Martin, & Barsalou, 2013) and the processing of advanced mathematical statements in mathematicians (Amalric & Dehaene, 2016).

1.3.1 Research Objective Study 4

Study 4 included in this dissertation aimed to extend this recently emerging line of research and investigated experience-dependent mathematical conceptual processing. In Study 4, we tested subjects with high and low level of mathematical expertise, who processed mathematical and non-mathematical abstract words during EEG recording. A comparable approach with proficient athletes and novices revealed that experience in the action domain leads to more efficient conceptual processing of action concepts (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008). Study 4 thus aimed to contribute to the goal of examining the extent and limitations of the generalizability of semantic processes from the concrete to the abstract domain.

2 Overview of Studies

This dissertation comprises four studies on experience-dependent lexical-semantic processing of single words in young, healthy adults. All participants gave their written informed consent and voluntarily participated in these studies, which were in line with the ethical standards defined in the Declaration of Helsinki. The following sections include conceptual summaries of the four studies. Full details are provided in the original research articles in Appendix B.

2.1 Study 1

2.1.1 Research Question and Hypotheses

Differences in experience with concrete and abstract words are thought to lead to the *concreteness effect* with processing advantages for concrete over abstract words (Hoffman, 2016; Levy-Drori & Henik, 2006). This effect has been found to manifest in faster and more accurate reactions to concrete words in comprehension, memory and production tasks (Hoffman, 2016; Jessen et al., 2000; Paivio, 1991; Schwanenflugel & Shoben, 1983). Further, concrete words elicit higher amplitudes of the N400 and N700 ERP components (Barber et al., 2013; Holcomb et al., 1999; Huang & Federmeier, 2015; Kounios & Holcomb, 1994). One factor possibly influencing this concreteness effect is the higher imageability of concrete words (Gullick et al., 2013; Huang & Federmeier, 2015). Imageability results from visual perceptual features incorporated into concrete words' conceptual representations through visual experience with their referents, which is lacking for abstract words (Paivio, 1991). Concreteness and imageability, however, seem to result in at least partially dissociable mechanisms reflected by N400 and N700 effects (Barber et al., 2013; Gullick et al., 2013). While the N400 is thought to reflect processes of semantic feature integration (Kutas & Federmeier, 2011), the N700 is more clearly modulated by stand-alone imagery processes triggered by an interaction of stimulus-inherent imageability and task demands (Gullick et al., 2013; West & Holcomb, 2000). This study investigated the effect of training-induced, visual experience with novel object concepts on the electrophysiological correlates of lexical-semantic processing of novel object names via EEG.

For this purpose, Study 1 employed a two-day training paradigm to associate formerly meaningless pseudowords with two qualitatively different kinds of pictorial stimuli (i.e., objects and structures), which should induce different levels of imageability for the novel words. As a baseline control condition, we further familiarized participants with pseudowords without any picture association. In the EEG session after training, we presented the trained novel words intermixed with real concrete and abstract words. Participants had to classify the words as either concrete (i.e., referring to something perceivable, including novel names associated to pictures during the training) or abstract (i.e., not referring to anything perceivable, including familiarized pseudowords without picture association from the training).

If the N400 concreteness effect depends on the integration of multiple semantic features, we would not expect an effect of our training-induced merely visual imageability on the N400. We however expected effects of the training-induced imageability on the N700, as in studies employing real concrete words, this later component has been shown to be modulated by stimulus-inherent imageability (Gullick et al., 2013; Welcome, Paivio, McRae, & Joanisse, 2011; West & Holcomb, 2000).

2.1.2 Methods

We tested 21 healthy, right-handed participants aged between 19 and 34 years. They all underwent two days of training, in which each novel word was presented eight times, either together with the associated object or structure pictures, or without any picture in the control condition. Photographs of 15 novel tool-like objects employed in former training studies (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b) and electron-microscopical images of 15 living and non-living structures served as pictorial stimuli. The depicted objects on the photographs formed a coherent entity. The electron-microscopical images showed living and non-living things (e.g. asbestos, skin), which also included coherent parts but were clearly less tangible. The novel words were unfamiliar, meaningless pseudowords, matched for letter and syllable length between conditions. We generated them from real German words by exchanging two to three letters according to German phonological rules. The chosen visual and verbal stimuli made sure that none of the participants had any previous real-life experience with them. Participants were asked to learn the words and - where appropriate - their associated pictures. Learning performance assessments for the novel words (free reproduction, multiple-choice assignment to the training condition and assignment to the pictorial stimuli) were announced before the first training and carried out after both training sessions (all three tests) and the subsequent EEG session (multiple-choice and picture assignment).

The EEG acquisition after the training consisted of three runs. In each run, the 15 novel object words and 15 novel structure words, together with 15 additional untrained novel filler words as well as 30 real concrete and 30 real abstract words, were presented once in randomized order. The participants' task was a concreteness judgment in which they had to classify words as concrete or as abstract as described above.

2.1.3 Results and Discussion

We analyzed the learning performance in form of the percentage of correct free reproductions as well as correct assignments in the multiple-choice test. Analyses revealed that learning performance increased significantly from the first to the second training. The performance in both assignment tests did not change significantly after the second training. A significant Category x Session interaction for the free reproduction performance suggests that a higher imageability might have led to a learning advantage for novel names referring to object pictures. Taken together, the behavioral results show that the training paradigm successfully made the participants learn the novel names and their associated pictures.

EEG data were analyzed after a standard preprocessing procedure. Time windows for the N400 (300-500 ms) and an early (500-700 ms) and late N700 (700-900 ms) were chosen based on previous research and were validated by visual inspection of the grand averages of our data. For the real concrete and abstract words, all artifact-free trials were averaged per condition. Results on the real words showed a concreteness effect with higher amplitudes in the N400 and both N700 time windows, in line with the literature (Barber et al., 2013; Holcomb et al., 1999; Kounios & Holcomb, 1994). In the early N700 window, the effect was reversed at parietal electrode sites in comparison to frontal and central sites, possibly depicting an LPC involved in the recollection of individual experience (Strozak et al., 2016; Van Petten & Luka, 2012). In the late N700 window, the concreteness effect only showed at midline and right side electrodes, but not over left side electrodes. Overall, these results on the concreteness effect show that the chosen task was suitable to elicit imagery processes reflected in the N700 amplitude (Gullick et al., 2013).

For the analyses of the novel object names, we applied a learning criterion and only included the artifact-free trials with novel words, which the respective participant correctly assigned to their training condition in the multiple-choice test after the EEG session. We did not find any effects of training-induced imageability on N400 and early N700 amplitudes. In the late N700 time window, however, the Category significantly interacted with the electrode Frontality as well as Laterality. The topographical patterns mirrored the patterns found for the real word concreteness effect. At frontal electrode sites, novel object words elicited higher N700 amplitudes than novel words without picture association. At parietal sites, novel object words elicited the highest positive amplitudes. This LPC has been found to be involved in recollection of individual experiences also for novel words (Palmer, Havelka, & van Hooff, 2013). Further, novel object words elicited higher N700 amplitudes than novel structure words and novel words without picture association over right side electrodes.

This training-induced visual imageability did not affect the N400, supporting the hypothesis that the N400 reflects semantic feature integration processes beyond the processing of mere visual imageability. However, the training-induced visual imageability of especially novel object words led to late N700 effects mirroring the N700 effects for real words. Alternatively, during the training, the novel object's inherent affordance (i.e., an object-inherent graspability or even manipulability; Borghi & Riggio, 2015; van Elk et al., 2014), might have led to an integration of more than merely visual information into the conceptual representations.

2.1.4 Conclusion

The training-induced late N700 modulation suggests that mere visual experience leads to an altered processing of novel words probably by inducing imagery processes. Merely visual experience, however, does not seem to affect the N400 amplitude, an ERP correlate of rather automatic semantic feature integration processes. Our study was not designed to answer the question, on which additional information the N400 concreteness effect may rely. Former research suggests that the concreteness effect might rely on the dominance (Connell & Lynott, 2012) or multimodality (Barber et al., 2013) of conceptual features derived from experiential channels. Further research is necessary to test these possibilities.

2.2 Study 2

2.2.1 Research Question and Hypotheses

This study investigated the temporal dynamics of conceptual reactivation of sensorimotor areas during the processing of names of novel tool-like objects in form of an ERD of the mu and beta frequency band via EEG. This study directly followed the line of research on conceptual processing of pictures of novel tool-like objects after manipulation and visual training (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b). Study 2 applied a modified version of this paradigm by introducing novel names for the objects and measuring their lexical-semantic processing in an EEG acquisition after training. The chosen measures of mu and beta ERD over fronto-central areas are thought to reflect an activation of sensorimotor (Kuhlman, 1978) and primary/supplementary motor areas (Jasper & Penfield, 1949), respectively.

The main aim of this study was to investigate, whether stronger sensorimotor reactivations of sensorimotor area after manipulation than visual training (as found for tool picture processing; see Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b) would also be elicited by lexical stimuli. As in previous studies, we compared a manipulation and visual training condition. We further included a control condition with familiarized pseudowords. The second aim of the study was to examine the timing of this conceptual reactivation. While embodied theories postulate an early and thus automatic reactivation of experiential brain areas within the first 150 ms to 200 ms after stimulus onset (Kiefer & Pulvermuller, 2012), theories assuming a secondary kind of embodiment rather expect a reactivation at later, post-conceptual stages (Mahon & Caramazza, 2008). We expected a stronger early reactivation of sensorimotor and motor areas during the processing of names of novel objects after manipulation than visual training. Further, the exact temporal dynamics of ERD of the mu and beta band was of particular interest, as previous literature delivered mixed results (Niccolai et al., 2014; van Elk, van Schie, Zwaan, & Bekkering, 2010) and suggests a dissociation of the processes reflected by the different frequency bands (Sebastiani et al., 2014).

2.2.2 Methods

We tested 22 healthy, young adults. They underwent three training sessions and a subsequent EEG session. The three training sessions consisted of an active manipulation training and a visual exploration training with 12 novel tool-like objects each and pseudowords introduced as their names. Additionally, we included a lexical pseudoword familiarization training with pseudowords without an associated novel object. We used the pseudowords from Study 1, matched for letter and syllable length between conditions. The three sets of 12 novel objects each were taken from previous training studies (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b), matched between conditions for visual complexity, their resemblance to real objects and how much they stood out from the rest of the objects. We further counterbalanced the assignment of the object sets to the training conditions (active, visual, lexical).

The manipulation training included a non-verbal manipulation instruction in form of a video showing one full manipulation of each object, followed by a 90 s period, in which the participants manipulated the objects themselves. All objects had a certain function (e.g., transport, destroy or separate) performed on object-specific items (e.g., paper cups, table tennis balls). The visual exploration training consisted of a static picture of the novel object, followed by a 90 s exploration period. Features appearing on the screen, which participants should look for (e.g., colors or forms), guided the visual exploration of the novel objects. Importantly, any haptic experience with the objects was prevented in the visual training. During the lexical pseudoword familiarization training, the pseudowords from the third, unused object set were presented four times with varying durations. We assessed the participants' learning performance via an announced multiple-choice test, in which they had to assign the lexical stimuli to their training condition (comparable to Study 1).

During the EEG acquisition after the trainings, participants were presented with two lexical stimuli (novel object name or pseudoword) in each trial in randomized order. After presentation of the second stimulus, participants had to indicate whether the two stimuli were from the same or two different training conditions.

2.2.3 Results and Discussion

Like in Study 1, we measured the participants' learning performance as the percentage of correct multiple-choice training-condition assignments. Results showed that learning performance increased significantly from the first to the second Session, and subsequently remained constant. Further, pseudowords from the lexical training showed a higher learning performance throughout all sessions. The reaction times and accuracy in the training-condition-matching task were analyzed only for those trials, in which both stimuli came from the same training condition. The accuracy was generally high (M = 84.6%, SD = 10.8%) and did not differ significantly between training Categories. Reaction times, however, were significantly slower in response to novel object names from the manipulation training than for pseudowords from the lexical training. The behavioral measures thus suggest a learning advantage for pseudowords without object association, which might arise from the higher frequency of occurrence during the trainings (four times instead of once for the manipulation and visual training) as well as from their distinctiveness, as they were the only pseudowords not associated with any object.

EEG data underwent a standard preprocessing procedure aimed at detecting and excluding artifacts. We analyzed only the ERPs elicited the first stimulus in each trial, to exclude any task-related decision processes. Comparably to Study 1, we applied a learning criterion and only included the artifact-free trials with novel object names, which the respective participant correctly assigned to their training condition in the multiple-choice test after the EEG session. Segments of these trials were bandpass filtered in the three frequency bands of the lower (8-10 Hz) and upper mu rhythm (10-12 Hz) and beta band (18-25 Hz). Subsequently, the ERD was calculated as percentage change in relation to a 1s prestimulus reference interval (Pfurtscheller, 2001). The ERD data were then analyzed with a non-parametric cluster randomization approach, which allows to detect temporo-spatial clusters of significant differences between two conditions without a priori selection of electrodes or fixed time windows and simultaneously controls for multiple comparisons (Maris & Oostenveld, 2007).

The results of the comparison of ERD values elicited by the processing of novel object names yielded an early cluster (140-260 ms) over bilateral frontocentral electrodes in the beta frequency band, followed by a cluster (320-440 ms) over bilateral frontal to centro-parietal electrodes in the lower mu rhythm. In both clusters, names of manipulated objects elicited a stronger desynchronization and thus sensorimotor and motor activation than names of visually explored objects. We did not detect any clusters with significant differences between manipulation and visual training in the upper mu rhythm. The upper mu rhythm is thought to be more movement-type specific (Pfurtscheller, Neuper, & Krausz, 2000) and as the objects required different kinds of manipulation, this null-finding is not surprising. It is further in line with previous findings (Ruther et al., 2014a). The desynchronization of the lower mu and beta rhythm can be interpreted as a reactivation of primary and supplementary motor (beta; Jasper & Penfield, 1949) followed by sensorimotor brain areas (mu; Kuhlman, 1978) involved in the manipulation experience gained with the objects during training.

The chosen paradigm with the formerly unfamiliar pseudowords and objects, as well as the counterbalanced assignment of the object sets to the training conditions made sure that the learning experience was the only difference between the novel object names of the two training conditions (see also Fargier et al., 2014). Further, the use of the novel objects' names instead of pictures in the EEG acquisition after training allows to interpret the sensorimotor activation as conceptual reactivation uncorrupted by any perceptual features like affordances that former studies on object picture processing could not rule out (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b).

The early beta desynchronization can be interpreted to reflect automatic, conceptual processing (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006; Hauk et al., 2008). The temporally later mu rhythm desynchronization might also still reflect conceptual processing, as a slight delay of language compared to picture processing is known from the literature (Hauk et al., 2008), but its timing does not allow strong inferences in terms of an early conceptual reactivation process (Kiefer & Pulvermuller, 2012). The temporal dynamics of beta and mu desynchronization in close chronological sequence are an important finding of Study 2. They may suggest that during the processing of object names, the recruitment of primary motor and sensorimotor areas mirrors actual action execution from motor commands to sensorimotor feedback (Niccolai et al., 2014; Sebastiani et al., 2014).

Study 2 yielded unexpected findings of a cluster (360-520 ms) of lower and upper mu rhythm desynchronization elicited by pseudowords from the lexical training, which was significantly stronger than the desynchronization elicited by visually explored object names and comparable in magnitude to the one elicited by manipulated object names. Motor activations triggered by pseudowords are known from the literature and have been interpreted as compensatory articulatory processes (Carreiras, Mechelli, Estevez, & Price, 2007; Mechelli et al., 2005). Another explanation would be that the visual training led to a relative suppression of sensorimotor activations inherent to pseudowords (Rey, Roche, Versace, & Chainay, 2015), while the manipulation training led to a qualitatively different kind of sensorimotor activation comparable in magnitude. This interpretation would be in line with findings of Ruther et al. (2014a) but further research has is required to clarify this point.

2.2.4 Conclusion

The results on the stronger mu and beta desynchronization elicited by manipulated than by visually explored object names in Study 2 can be interpreted as an experience-specific reactivation of motor and sensorimotor information integrated into the manipulated objects' conceptual representation during concept formation. Whether these desynchronizations can be interpreted as early, conceptual reactivations, or whether the mu ERD reflects post-conceptual processing, cannot be answered at this point. The chosen paradigm and stimuli, however, allow attributing the differences in motor and sensorimotor activation during novel object name processing to the experience gained during the trainings.

2.3 STUDY 3

2.3.1 Research Question and Hypotheses

In this study, we applied the same training paradigm as in Study 2 with minor methodological changes. Additionally, we included an observational manipulation training, which we kept parallel to the active manipulation training, in a between groups design. Literature on experience-dependent conceptual processing hardly provides direct comparisons of active and observational experience. The few studies including both types of learning with tool-like objects seem to suggest a stronger involvement of the same experiential brain areas after active than observational experience (Cannon et al., 2014; Macuga & Frey, 2012). Further, we used fMRI instead of EEG to explore the spatial characteristics of experience-dependent processing of novel object names more deeply. FMRI does not allow judgments about the time course of processing and thus no distinction between early conceptual and late post-conceptual effects, as it lacks the high temporal resolution of EEG (Hauk et al., 2008). In order to measure automatic conceptual reactivations independent of explicit task demands, we chose an implicit LDT broadly used in research on semantic processing (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Binder et al., 2003).

The examination of novel word processing via fMRI allowed us to investigate not only experience-specific differences between words from the two training conditions, but also a successful training-induced lexicalization of the words as a prerequisite of conceptual processing. Thus, the first aim of this study was to provide evidence for a training-induced lexicality of the novel object names in comparison to unfamiliar, meaningless pseudowords. We hypothesized to find a word-like activation pattern for novel object names in a left-hemispheric network known to underlie lexical-semantic processing (Binder et al., 2009). The second aim was to provide evidence for experience-specific effects in the direct comparison of novel object names from the manipulation and visual training, like in Study 2. These experience-specific effects should manifest in a stronger reactivation of the left-hemispheric fronto-parietal tool-network after manipulation experience, possibly more strongly after active than observational learning.

2.3.2 Methods

We tested 20 and 21 healthy, young adults in the active and observational learning group, respectively. Participants of both groups underwent three training sessions and a subsequent fMRI acquisition session. The manipulation and visual trainings of the active group were the same as described in Study 2, with the minor change that the 36 novel objects from former studies (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b) were distributed into two sets with 18 (instead of three sets with 12) objects per set. We further used a pseudoword generator software to generate closely matched pseudowords serving as the novel object names as well as untrained lexical stimuli in the LDTs during the fMRI acquisition. For the observational training, we replaced the 90 s active manipulation period with two times 15 s visual exploration of the real object and 60 s observation of a video showing a continuous manipulation of the respective object. Both groups underwent the visual training as described in Study 2 with a different set of 18 objects. In this way, both groups received merely visual as well as functional manipulation information about the novel objects, while one group learned about the latter actively and the other observationally. Again, a multiple-choice test after each session assessed the participants' learning performance

During the fMRI acquisition session after the trainings, participants underwent two runs of an LDT on the novel object names. In each of the two runs, 36 novel object names intermixed with 36 meaningless pseudowords appeared once in randomized order. Participants should indicate whether the lexical stimulus was an object name known from the training or a pseudoword. An LDT with names of 18 manipulable and 18 non-manipulable real objects, intermixed with a different set of 36 meaningless pseudowords, served as functional localizer to identify regions specifically involved in processing names of real manipulable objects. These regions served as regions of interest to further explore experience-specific effects on novel object name processing.

2.3.3 Results and Discussion

We analyzed the learning performance in the multiple-choice test as described for Study 2. Again, learning performance increased significantly from the first to the second training session, and then stayed constant. In this study, however, learning performance dropped significantly after the fMRI session. One reason may have been that participants were exhausted after the 60 min fMRI acquisitions, which always took place in the evenings. Indeed, some participants reported being tired after the acquisition, but this factor was not systematically assessed. For this reason, we did not base the criterion to include novel object names in the fMRI analyses on the correct assignments in the post-acquisition session, but on the performance after the third training session.

Further, learning results show that, independent of the type of experience (manipulation vs. visual) and learning (active vs. observational), participants successfully associated the novel names with their training condition. This result was supported by the high accuracy (> 97 %) in the LDT, which again was neither affected by the training condition, nor the learning group. The reaction times in the LDT in response to pseudowords were significantly delayed, which mirrored the results from the localizer LDT on real words.

FMRI data were preprocessed and statistically analyzed with a two-stage random-effects approach, modelling the regressors of interest: novel object names from the manipulation training, novel object names from the visual training, and pseudowords. Novel object names not correctly assigned to their training condition after the third training as well as those for which participants made LDT errors were not included.

We analyzed training-induced lexicality effects by comparing the processing of novel object names, irrespective of their training condition, with pseudowords. As hypothesized, results revealed an extensive left-hemispheric word-like activation pattern known to underlie lexical-semantic processing (Binder et al., 2009) for novel object names. The significant activation clusters included important multi-modal semantic hub areas previously identified (Xu et al., 2016) and largely overlapping with the DMN (Buckner et al., 2008; Raichle et al., 2001). The word-like activation pattern also comprised areas known to be involved in tool-related cognition (i.e., the left inferior frontal and parietal regions and left middle temporal gyrus; for a review see Ishibashi et al., 2016). These areas overlap with areas involved in processing training-induced tool representations (Bellebaum et al., 2013; Malone, Glezer, Kim, Jiang, &

Riesenhuber, 2016; Weisberg et al., 2007). A comparable pattern was found for the real object names vs. pseudowords in the localizer task. However, activation of the medial temporal lobe (including dentate and parahippocampal gyri) exclusively arose for novel object names vs. pseudowords. This activation may reflect additional episodic resources (Bird, Capponi, King, Doeller, & Burgess, 2010; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Yonelinas, 2013) strategically involved in processing novel object names, whose conceptual representations rely on very recent, unconsolidated experience and might thus be more effortful (Smith & Squire, 2009).

Contrarily, pseudowords activated premotor and sensorimotor areas more strongly than novel object names. This pattern further validates the interpretation of a training-induced lexicality of the novel object names, as it is well-known from previous research (Binder et al., 2003; Carreiras et al., 2007). It was interpreted to reflect phonological and articulatory processing of meaningless pseudowords (Carreiras et al., 2007; Mechelli et al., 2005). We neither found general group differences in lexical processing between active and observational learners nor in interaction with the described pattern of the lexicality effect.

We examined experience-specific effects by directly comparing novel object names from the active and observational manipulation training and the visual training. Neither the type of information experienced in the training (manipulation vs. visual) nor the type of learning (active vs. observational), nor their interaction had significant effects on the hemodynamic responses in the univariate analysis. We neither found any effects on the whole brain level, nor with frontal and parietal regions of interest defined by the functional localizer. Within the short training period (compare, e.g., Kiefer, Sim, Liebich, Hauk, &

Tanaka, 2007), the newly formed conceptual representations might not have become sufficiently consolidated to elicit experience-specific reactivations during lexical-semantic processing in an implicit task. A study on proficient children and adult readers suggests that it takes years of experience until lexical stimuli elicit sensorimotor reactivations to a comparable degree as pictorial stimuli do (Dekker et al., 2014).

Based on the finding that the training induced a strikingly word-like activation pattern, but no effects distinguishing between the types of experience involved, we assumed the training might have caused more subtle experience-specific effects not detectable with standard univariate analysis methods. We formulated the post-hoc hypothesis that experience-specific effects might arise in form of an enhanced functional connectivity between the multi-modal hub areas of the semantic network and neuronal assemblies in areas involved in object-related information. This hypothesis, although introduced to cope with the unexpected null-findings, is in line with previous research in the embodiment framework (Chow et al., 2014; Malone et al., 2016).

We conducted a seed-to-voxel functional connectivity analysis with the clusters involved in the lexicality pattern as seeds. This analysis revealed a selectively enhanced functional connectivity of nearly all areas of the semantic network with experience-specific cortical, striatal and cerebellar brain areas. The functional connectivity pattern differentiated between manipulation and visual training, as well as active and observational learning and their interaction. Actively learned manipulation information selectively enhanced the connectivity of areas involved in episodic retrieval during semantic processing and areas involved in the processing of (egocentric) visuo-spatial manipulation information.

These results suggest that the lexicalization of novel object names shows a certain degree of grounding in experience-specific networks.

2.3.4 Conclusion

The results suggest that a short training period is sufficient to induce novel word meaning by associating newly formed conceptual object representations to novel object names. This training-induced lexicality of the novel object names led to a word-like activation pattern mirroring lexical-semantic processing of the formerly meaningless lexical stimuli with additional activation of areas involved in episodic retrieval. The short training in combination with an implicit task induced experience-specific effects in form of a functional coupling between multimodal areas involved in novel object name processing and neuronal assemblies in brain areas coding for object manipulation-related information. The semantic processing discovered in this study might represent an early stage of grounded word meaning acquisition. Further research is necessary to clarify the requirements for regional (re-)activations of experience-specific brain areas during conceptual processing.

2.4 Study 4

2.4.1 Research Question and Hypotheses

Study 4 aimed at extending findings on experience-dependent conceptual processing differences known from concrete concepts to the abstract domain. Embodied theories postulate that experience and conceptual processing of experience-specific features would recruit the same neural resources (Kiefer & Pulvermuller, 2012; Meteyard et al., 2012). Accumulative experience in a certain domain should lead to lasting changes of experience-specific brain areas, which serve as a resource for conceptual processing. Evidence for accumulative experience-induced changes in lexical-semantic processing stems from studies in the action domain with e.g., expert hockey players (Beilock et al., 2008) and extensive fine motor skill training (Locatelli, Gatti, & Tettamanti, 2012).

In the abstract domain, mathematical concepts seem a promising starting point to test whether processes assumed for such experience-dependent effects can be generalized from the concrete to the abstract domain. Research on mathematical cognition suggests that mathematical concepts form a coherent abstract sub-category, based on the involved experiential channels (e.g., magnitude estimation and visuo-spatial information, Ghio et al., 2013). A previous fMRI study by Amalric and Dehaene (2016) with mathematical experts and novices performing semantic judgments on advanced mathematical statements showed that mathematicians' processing of mathematical statements recruits a prefrontal-intraparietal network, underlying numerical and magnitude processing (Dehaene et al., 2004; Dehaene et al., 1999). The study by Amalric and Dehaene (2016) had the drawback, that the mathematical statements caused comprehension problems in the novices. Further, an early rise in activity in the mathematical network in the expert group suggested that its recruitment occurs already at early stages of conceptual processing. This would be important to show from a theoretical point of view, but was impossible to confirm with the poor temporal resolution of the method.

In Study 4, we employed mathematical and non-mathematical abstract words. To assure effective comprehension of these words in experts and novices, we matched the mathematical and non-mathematical words' subjective familiarity based on ratings by non-mathematicians. In a between-groups design, we included two levels of mathematical expertise (high vs. low), based on an administered math test. We expected the level of mathematical expertise to specifically affect the semantic processing of mathematical abstract words reflected by N400 and LPC amplitudes. Both, the N400 and the LPC showed experience-dependent effect for, e.g., concrete vs. abstract words (Adorni & Proverbio, 2012; Kanske & Kotz, 2007), and both proved sensitive to the level of effort involved in mathematical cognition (Dickson & Federmeier, 2017; Niedeggen & Rösler, 1999).

2.4.2 Methods

By means of a cutoff criterion in a math test, we subdivided our young, healthy participants into 23 mathematical experts and 20 novices. During EEG acquisition, participants performed two runs of an LDT on 31 mathematical and non-mathematical words, intermixed with word-like pseudowords presented in randomized order. Based on a pre-experimental rating, the mathematical and non-mathematical words were matched for important psycholinguistic variables (i.e., concreteness, abstractness, valence and familiarity) known to affect electrophysiological correlates of semantic processing. Further, a subsample of the EEG study (14 experts and 13 novices) took part in a post-experimental rating, delivering insights into the subjective rating differences between mathematical and non-mathematical words in our sample.

2.4.3 Results and Discussion

A significantly higher math test score in the expert than the novice group validated our group assignment. Accuracy in the LDT was very high with an average value above 97%. Driven by a performance decrease for mathematical words in the novice group, mathematical words showed a slightly diminished accuracy. This suggests that even though we carefully matched mathematical and non-mathematical words for the frequency of occurrence as well as subjective familiarity as rated by novices in a pre-experimental rating, we could not fully avoid comprehension problems with single mathematical stimuli. As the accuracy drop added up to less than 2%, this effect seems negligible.

In both ERP components, we found an interaction of the type of word and the experience level of our participants. Differences between the groups specifically arose for mathematical word processing, while the groups did not show any significant differences in N400 or LPC amplitudes for non-mathematical word processing. Mathematical word processing elicited a relatively reduced fronto-central N400 amplitude and enhanced centro-parietal LPC in experts compared to novices. The difference in N400 and LPC amplitudes for mathematical and non-mathematical words correlated significantly with the participants' math test score, but not with the familiarity and abstractness ratings obtained in the post-experimental rating. Those two ratings showed a significant interaction of word type and group, too, and could thus be considered as potential confounding factors, which we could partially exclude by means of the correlation analyses.

Therefore, the results seem to suggest that the specific effect of mathematical expertise on the processing of mathematical words originated from the experiential background of the mathematical experts. The relatively reduced N400 might reflect a less effortful processing of mathematical words in experts (Lau et al., 2008). At the same time, it could hint at a reduced reliance on superficial sensorimotor information like spatial number mapping and finger counting habits (Domahs, Moeller, Huber, Willmes, & Nuerk, 2010). These may play a bigger role for mathematical novices as suggested by the literature (Cipora et al., 2016). The enhanced LPC in experts' processing of mathematical words might reflect a stronger recollection of information derived from individual experience (Kandhadai & Federmeier, 2010a; Strozak et al., 2016). As the LPC has been shown to depend on explicit task demands (Kandhadai & Federmeier, 2010b), mathematical expertise might have motivated this recollection of extraordinarily consolidated knowledge. The topography of the LPC further suggests an involvement of parietal areas known to underlie mathematical cognition like, e.g., the intraparietal sulcus (Kiefer & Dehaene, 1997; Suarez-Pellicioni & Booth, 2018). This interpretation, however, has to be taken with caution, given the poor spatial resolution of surface EEG.

2.4.4 Conclusion

Study 4 delivers important insights into the temporal dynamics of experience-dependent changes in conceptual processing in the abstract domain. The results suggest that mathematical experience leads to lasting neural changes in resources recruited for the lexical-semantic processing of mathematical concepts. This processing is affected at stages of automatic (N400) as well as strategic (LPC) conceptual processing. Therefore, experience-dependent conceptual processes known from the concrete domain seem to be generalizable to mathematical conceptual processing in the abstract domain.

3 GENERAL DISCUSSION

The studies in this dissertation investigated the role of experience in lexical-semantic processing of recently formed object representations as well as of consolidated mathematical concepts. Studies 1 to 3 extended previous research in a training paradigm with novel tool-like objects (Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b; Weisberg et al., 2007). By measuring the lexical-semantic processing of the novel object names instead of pictures after training, these studies measured conceptual processing independent the perceptual features of object pictures. Study 1 showed that mere visual experience with novel object pictures during concept formation leads to visual imagery-based effects conceptual processing. Study 2 showed that conceptual processing of novel object names after manipulation training elicits experience-specific reactivations of sensorimotor brain areas. Study 3 revealed that processing novel object names, irrespective of the training experience, relies on a core semantic network. This network further recruited experience-specific brain areas. Taken together, Studies 1 to 3 suggest that the experience gained in a short training period is integrated to form new conceptual representations, which can be accessed via newly associated lexical stimuli. Finally, Study 4 focused on experience-dependent processing of abstract concepts. In this study, expertise specifically affected the electrophysiological correlates of automatic and strategical semantic processing of mathematical words. This study supports the generalizability of experience-dependent conceptual processes from the concrete to the abstract domain.

3.1 Experience-Dependence vs. Experience-Specificity

The training paradigm with unfamiliar stimuli applied in Studies 1 to 3 allows us to trace back any effects in conceptual processing directly to the experience gained during the trainings. This experience likely induced new conceptual object representations, which the lexical stimuli accessed via established word-referent associations, as was shown in other training studies (Fargier et al., 2012; Fargier et al., 2014). Opposed to studies on real words, it was important to ensure a successfully established word-referent association as a prerequisite to measuring lexical-semantic processing. We therefore only included lexical stimuli into the analyses, which the participants had learned. Further, the comparison with familiarized pseudowords in Studies 1 and 2 allows us to rule out familiarity effects as alternative explanation. Even though Study 3 did not include familiarized pseudowords, familiarity effects seem improbable here, too, given the word-like activation pattern mirroring findings from previous research on word vs. pseudoword processing (Binder et al., 2009; Carreiras et al., 2007; Mechelli et al., 2005; Mechelli, Gorno-Tempini, & Price, 2003; Mechelli, Josephs, Lambon Ralph, McClelland, & Price, 2007). We thus interpret the results of the training Studies 1 to 3 to reflect a lexical-semantic access to newly established conceptual representations.

The experience-dependent lexical-semantic processing in Studies 1 to 3, however, varies strongly in its experience-specificity. In Study 1, the mere visual experience involved in concept formation modulated the N700. Given the role of the N700 in visual imagery processes (Gullick et al., 2013; West &

Holcomb, 2000), this result reflects at least a certain degree of specificity for experience in the visual modality. However, Study 1 did not include a different quality of experience, like the visual vs. manipulation experience in Studies 2 and 3, which restricts the interpretation in terms of experience-specificity. Former research suggests, that the ventrolateral prefrontal cortex generates the N700 (Adorni & Proverbio, 2012). The ventrolateral prefrontal cortex is probably involved in general semantic retrieval mechanisms (Hoffman, Jefferies, & Lambon Ralph, 2010; Musz & Thompson-Schill, 2017). The N700 may thus be involved in the general imagery-based retrieval of semantic information and might not be specifically restricted to visual information. This interpretation would be in line with an ERP study in which concrete words elicited higher N700 amplitudes than abstract words, even though they were matched for visual imageability (Barber et al., 2013). In Study 1, however, we exclusively provided visual information, which makes it likely that visual imagery caused the N700 effect. Notably, the N700 was more pronounced for words associated with object than structure pictures, which could suggest that object pictures either elicited a higher degree of imageability or even induced other qualities of experience due to, e.g., object-inherent affordances.

Study 2 delivers evidence for experience-specific sensorimotor reactivations during conceptual processing. Especially the early beta but also the slightly delayed mu rhythm desynchronization seem to reflect a reactivation of motor and sensorimotor areas (Ritter, Moosmann, & Villringer, 2009) after manipulation vs. merely visual training. One point of critique concerning Study 2 and generally studies interpreting their findings in terms of conceptual reactivations might be that we did not measure brain activity during the experience (i.e., trainings). In contrast to studies on real words, however, our lexical stimuli were perfectly matched and void of any meaning before the trainings. Therefore, the experience gained during the trainings is the only possible cause for the found processing differences.

Study 2 unexpectedly revealed no significant differences between manipulated novel object names and pseudowords. We stated the possible post-hoc explanation that these non-significant differences arose from compensatory motor activations inherent to pseudoword processing. Such motor activations elicited by pseudowords have been found in previous fMRI research (Carreiras et al., 2007; Mechelli et al., 2005) as well as in our Study 3. Further, Bellebaum et al. (2013) provided evidence for a down-regulation of motor-related brain areas after visual training. The authors showed that processing visually trained object pictures led to a reduced connectivity in the left fronto-parietal tool-network. These findings suggest that visual experience might have led to a down-regulation of sensorimotor activation involved in pseudoword processing also in Study 2, while manipulation training might have qualitatively changed pseudoword-inherent motor activations.

However, such a down-regulation of motor activity by visual experience should go hand in hand with an up-regulation of activity in areas involved in visual information processing. We found no evidence for such an up-regulation in our chosen measures. Previous research suggests that modulations of the beta and alpha range are not as sensitive to visual information as in the theta range (Huang, Zhao, & Hwang, 2014; Krause et al., 2006; Mishra, Martinez, Schroeder, & Hillyard, 2012). It seems important for future research to explore the role of different experiential qualities in concept formation and their subsequent interaction in conceptual processing. The inclusion of several experiential channels in the trainings (i.e., vision, manipulation, haptics, and sound) would allow investigating more complex and thus naturalistic conceptual representations, enhancing the external validity of future training studies.

The analyses in Study 3 did not reveal the hypothesized experience-specific regional activation effects. In the conceptual processing of object pictures, the same amount of training with the same objects led to experience-specific activations of areas in the fronto-parietal tool-network (Bellebaum et al., 2013; Ruther et al., 2014b) and an early mu rhythm desynchronization over motor areas (Ruther et al., 2014a). In Study 2, also the processing of the novel object names led to activations of sensorimotor areas in form of a stronger mu and beta ERD. Therefore, different task-demands, together with the newly introduced lexical instead of pictorial stimuli in the post-training measurements, seem to account for the heterogeneous findings on conceptual reactivations in Studies 2 and 3. The post-hoc functional connectivity analysis in Study 3, however, revealed that the semantic network involved in the processing of the novel object names showed experience-specific functional connections to other brain areas. Especially active manipulation training selectively enhanced functional connectivity between the semantic hub areas involved in episodic retrieval and modal areas involved in aspects of tool use and tool processing (among others). Study 3 thus delivers further evidence for the retrieval of experience-specific information during the lexical-semantic processing of novel object names.

Finally, Study 4 provides evidence for experience-dependence (in this case the quantity of experience) in the abstract domain. The higher amount of real-life mathematical experience led to a selectively reduced N400 and enhanced LPC in mathematical word processing only for mathematical experts. Importantly, amplitudes for non-mathematical words did not differ between groups, as well as the LPC amplitudes for mathematical and non-mathematical words within the novice group. The experts' reduced N400 amplitude for processing mathematical words in Study 4 suggests a reduced reliance on (multi-)modal experience (Barber et al., 2013). A previously found reduced reliance on spatial information by mathematical experts (Cipora et al., 2016) supports this interpretation. However, based on the approach of comparing experts and novices in Study 4, we cannot pinpoint the exact experiential channels involved in concept formation and experience-specificity remains speculative (Locatelli et al., 2012, stated a similar critique on expert studies in the action domain). This is a serious limitation, because the experiential channels underlying abstract concepts are not as well understood as in the concrete domain. Research just recently began to explore the experiential channels involved in abstract (Ghio et al., 2013; Troche et al., 2014) and more specifically in mathematical concepts (Fischer & Shaki, 2018; Zhang, Chen, & Zhou, 2012).

The modulation of the parietal LPC by mathematical expertise in Study 4 suggests an experience-specific recruitment of the intraparietal sulcus, which is involved in magnitude processing (Amalric & Dehaene, 2016; Dehaene et al., 2004). This recruitment seems to play a role, however, only at this later stage of conceptual processing. Further, given the poor spatial resolution of the EEG, this interpretation has to be taken with caution. Future research could apply high-density EEG or MEG together with functional localizer tasks and source localization methods (as e.g., done for action verbs, see Klepp et al., 2014; Niccolai et al., 2014). In this way, one could investigate whether different stages of mathematical conceptual processing in experts recruit experience-specific brain regions.

Study 4 stresses the necessity to extend embodied and grounded theories to include experiential channels for abstract conceptual knowledge on the same level as perceptual modalities are included for concrete concepts. Strictly embodied theories try to ground abstract knowledge in (primary) sensorimotor areas through perceptual information associated with situations, in which abstract concepts occur (Glenberg, 2015; Glenberg et al., 2008). Recent approaches identified emotion (i.e., valence and arousal; Vigliocco et al., 2014) and introspection, a sense of magnitude and mental activity as important experiential channels especially in the abstract domain (Binder et al., 2016; Ghio et al., 2013; Troche et al., 2014). Future research should try to define and investigate experiential channels involved in abstract knowledge. The definition of the experiential channels as well as identification of their neural correlates is crucial for, e.g., the development of suitable training paradigms and thus the investigation of experience-specific effects in the abstract domain.

3.2 Flexibility of Conceptual Reactivations

As discussed above, we found experience-specific beta and alpha desynchronizations in Study 2, but no experience-specific regional activations in Study 3. This was unexpected, given the comparable training protocol and lexical access in both studies. Notably, the tasks used in studies 2 and 3 differed. Previous research on consolidated concepts delivered evidence for task- or context-dependency of conceptual reactivations during lexical-semantic processing. Perceptual tasks could, e.g., suppress the dominant motor-features of tools (Rey et al., 2015). Depending on the (linguistic) context, early stages of conceptual processing reactivated object concept-inherent action or visual features more strongly (Hoenig et al., 2008; van Dam, Brazil, Bekkering, & Rueschemeyer, 2014; van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012). One possible mechanism underlying context-dependent flexibility in conceptual reactivations is a top-down allocation of attentional resources (Kiefer & Martens, 2010; Trumpp, Traub, & Kiefer, 2013). The training-condition-matching task applied in Study 2 explicitly required the participants to retrieve training information, in opposite to the implicit LDT in Study 3. A more explicit task in Study 3 might thus have led to find the hypothesized experience-specific regional activations.

Additionally, the task-difficulty may have provided another form of contextual information leading to conceptual reactivations in Study 2, but not Study 3. Throughout the studies included in this dissertation, participants reached a descriptively higher accuracy in the implicit LDTs (Study 3: ~ 98 % and Study 4: ~ 99 %) than the concreteness judgment and training condition matching task (Study 1: ~ 90 % and Study 2: ~ 80%). The experience-specific effects in Studies 1 and 2 could thus also reflect the recruitment of an additional resource. This might have been necessary in the context of a higher task difficulty as was found for unfamiliar vs. familiar semantic tasks before (Chiou et al., 2018). The results of Study 4, which revealed experience-specific effects in an implicit LDT, seem to contradict this interpretation. However, the experience-dependent effects in Study 4 hint at differences between recently formed vs. consolidated conceptual representations. The former may rely on additional resources for the task solution, while for the latter, conceptual reactivations might occur because of a strong associative connection based on accumulated experience (Cantou, Platel, Desgranges, & Groussard, 2018).

Aside from differences in chosen tasks, the studies presented in this dissertation differ in the methods chosen to measure conceptual processing. Former research provides evidence for a higher sensitivity of EEG for semantic effects. One study detected semantic priming effects in a word-picture task in a left temporal source region with EEG, but not with simultaneously acquired fMRI (Geukes et al., 2013). Another study detected task-dependent semantic processing difference in ERPs starting within 150 ms after stimulus presentation measured with EEG/MEG, but not fMRI (Chen, Davis, Pulvermuller, & Hauk, 2013). Importantly, source localization identified a broad network including occipital, temporal, precentral and inferior frontal regions underlying the task-dependent effects. The latter study further hints at the possibility that the lower sensitivity of fMRI might be partly due to its poorer temporal resolution.

Future studies should thus bear in mind that conceptual reactivation of experiential brain areas occurs flexibly based on task-demands and the given context (Chen et al., 2013; Lebois, Wilson-Mendenhall, & Barsalou, 2015). Furthermore, further research should examine the sensitivity of EEG and fMRI for semantic processes, ideally in direct comparison provided by simultaneous measurements (Geukes et al., 2013). Such differences in the sensitivity to detect subtle semantic effects could have contributed to the heterogeneous findings on embodied semantic processing (Chen et al., 2013; Geukes et al., 2013; Visser, Jefferies, & Lambon Ralph, 2010).

3.3 Strategical Episodic Retrieval

The studies comprised in this dissertation deliver some evidence that relatively late and thus strategic episodic memory retrieval supports conceptual processing for novel (Study 1 and 3) as well as particularly consolidated knowledge (Study 4). We found a more pronounced posterior LPC for novel object words vs. pseudowords in Study 1 and activation of the dentate and parahippocampal gyri only for novel but not real object words vs. pseudowords in Study 3. Those effects might reflect the recruitment episodic information as an additional processing resource of recently acquired conceptual representations based on reduced qualities and/or quantity of experience (Long & Kahana, 2015; Takashima, Bakker, van Hell, Janzen, & McQueen, 2014). Alternatively, episodic information was involved because the recently formed representations have not yet been abstracted from their underlying experience (Baddeley, 1988; Greenberg & Verfaellie, 2010).

In Study 3, the activation of the parahippocampal and dentate gyri was restricted to novel vs. pseudowords. In Study 1, the more pronounced LPC was not restricted to the novel words, but also emerged for real concrete vs. abstract words. This might be due to either the intermixed presentation of real and novel words in Study 1, but not Study 3, or the more explicit task demands of the training-condition-matching task in Study 1 vs. the LDT in Study 3. The intermixed presentation might have led to an adoption of an episodic retrieval strategy from novel word processing to the processing of real concrete words. In previous studies, real word concreteness modulated LPC amplitudes in a comparably explicit old/new recognition task (Strozak et al., 2016), but not in an implicit LDT (Barber et al., 2013). Therefore, the chosen task possibly introduced strategic episodic memory retrieval also for these consolidated concepts. Taken together, Study 1 and 3 deliver first evidence for a relatively higher reliance on episodic memory retrieval in the lexical-semantic processing of recently formed vs. consolidated conceptual representations.

Study 4 revealed an experience-dependent modulation of LPC amplitudes elicited by consolidated concepts. One possible interpretation stated above is that this LPC reflects the retrieval of information from the intraparietal sulcus. It could, however, also (or additionally) reflect episodic memory retrieval. As discussed in Study 4, the mathematicians' expertise itself might have motivated the memory retrieval at this late processing stage for concepts in the domain of expertise even in the implicit LDT. This alternative explanation, however, seems rather implausible as in experts the mathematical experience should have been generalized and abstracted more strongly from distinct times and places than in novices. The design of Study 4 does not allow to reject either of these explanations. Therefore, future research should explore the modulation of the LPC by mathematical expertise more closely. In addition to the source localization suggested above, one could compare an implicit task like the chosen LDT with a task explicitly demanding episodic retrieval of mathematical experience. This would also allow to examine the flexibility of experiential reactivations in the abstract domain, a research question, which – to my knowledge – has not yet been addressed.

3.4 Modality-Independent Conceptual Processing

The ATL is a central hub in semantic processing (Patterson et al., 2007). Research revealed a largely modality-independent involvement of the ATL in lexical-semantic processing of real, consolidated concepts (Jefferies, Patterson, Jones, & Lambon Ralph, 2009; Lambon Ralph et al., 2017; Visser, Embleton, Jefferies, Parker, & Ralph, 2010) with a graded functional specialization (Hoffman et al., 2015; Lambon Ralph et al., 2017). The training Studies 1 and 3 comprised in this dissertation allow further direct and indirect insights into the involvement of the ATL in recently acquired conceptual object representations. In Study 1, the N400, which has been shown to be generated in the ATL by previous research (Klaver et al., 2005; Lau et al., 2008; Lau et al., 2016), was not modulated by mere unimodal visual experience. Previous research suggests that the N400 is especially involved in multimodal semantic integration (see also Barber et al., 2013; Takashima et al., 2014), which might not have been necessary for the training-induced novel object representations. An fMRI training study found that the ATL was involved in processing pseudowords associated with consolidated and thus richer, multimodal tool and animal concepts (Malone et al., 2016). This supports the interpretability of the absent N400 modulation in Study 1 to some extent. The connection of the N400 amplitude and ATL activity, however, is based on indirect evidence from source localization in previous studies.

Study 3 allows direct inferences about the ATL recruitment. The univariate analysis revealed a semantic network involved in processing the novel object names' meaning, which previous research identified to be largely content-independent (Binder et al., 2016; Binder et al., 2009). This network did not include the ventrolateral part of the ATL, which is considered the core of the semantic hub region (Lambon Ralph et al., 2017; Patterson et al., 2007). Moreover, processing real object names vs. pseudowords in Study 3 also relied on this semantic network. However, the post-hoc functional connectivity analysis in Study 3 revealed that the parahippocampal gyrus and precuneus comprised in this network showed a selectively enhanced functional coupling with two clusters in the ATL. Those clusters further extended to modal areas, which is in line with a functionally graded specialization of the ATL based on its proximity and connectivity with surrounding modal areas (Lambon Ralph et al., 2017). The results of Studies 1 and 3 suggest that the training-induced object representations based on reduced qualities and quantity of experience reflect a preliminary stage of semantic knowledge at which conceptual representations do not yet require highly transmodal integration processes in the ATL.

In contrast, the N400 as a correlate of semantic integration processes was sensitive to differences between real concrete and abstract words in Study 1, as well as real mathematical and non-mathematical words in Study 4. In fact, ATL activation seems to arise more commonly in comparisons of different categories of real words (Hoffman et al., 2015) than the words vs. pseudowords contrast (Binder et al., 2003; Carreiras et al., 2007; Mechelli et al., 2003). EEG studies, which either revealed an equally (Curran, 1999) or even more pronounced N400 for pseudowords vs. real words (Bermudez-Margaretto, Beltran, Dominguez, & Cuetos, 2015; Friedrich, Eulitz, & Lahiri, 2006; Trauer, Kotz, & Muller, 2015) provide a potential explanation for this. The N400 elicited by pseudowords has been interpreted to reflect a higher effort (Trauer et al., 2015) in post-lexical evaluation processing (Friedrich et al., 2006). Notably, this is also a potential cause for the comparable N400 amplitude elicited by novel object names and pseudowords in Study 1.

3.5 Semantic Control

One important limitation concerning not only the studies comprised in this dissertation but also the lion's share of research on semantic memory is the disregard of semantic control mechanisms (Lambon Ralph et al., 2017). Recent research suggests that semantic control forms a second, largely independent system (Lambon Ralph et al., 2017), which interacts with conceptual representations (Hoffman, 2016; Hoffman et al., 2015). Research identified the inferior prefrontal cortex to be critically involved in tasks with high demands on semantic control mechanisms (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Maril, Bjork, & Schacter, 2001; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Evidence from studies with healthy participants as well as aphasic patients with inferior frontal lesions suggest that processing abstract words, words without supporting contextual information (Hoffman et al., 2015; Hoffman et al., 2010) as well as words in uncommon semantic tasks (Chiou et al., 2018) pose higher demands on semantic control mechanisms. Semantic control mechanisms then recruit modal areas as an additional processing resource. Evidence for this comes from two studies, which showed that during non-dominant feature retrieval, modal areas were more strongly involved (Hoenig et al., 2008) and showed an enhanced functional connectivity with the inferior frontal cortex (Chiou et al., 2018). The neural substrates, which lead to lower demands on semantic control, however, are only poorly understood. Studies on expertise in the visual, cognitive, action, and musical domain suggest that they rely on an enhanced connectivity within the distributed network of conceptually bound modal information (Cantou et al., 2018; Harel, 2016; Lu, Zhao, Wang, & Zhou, 2018; Song, Peng, Liu, & Wang, 2019).

The newly formed object representations in Studies 1 to 3 and the consolidated mathematical representations in Study 4 should thus pose different demands on semantic control mechanisms. The reduced qualities of perceptual experience introduced especially in Study 1 but also Study 2 and 3 in a consistent context, might facilitate their retrieval in subsequent conceptual processing. However, the similarly reduced quantity of experience, which assumingly caused the recruitment of additional episodic memory retrieval as discussed above, might also have led to higher demands on semantic control mechanisms. Due to the chosen paradigms, we cannot provide any direct evidence for this hypothesis. Future research could manipulate the demands on semantic control by, e.g., including contextual vs. irrelevant cues (compare Hoffman et al., 2015) and/or introduce a varying degree of semantic diversity and/or complexity of provided information in a longitudinal training paradigm. While comparable studies have revealed important insights on the involvement of semantic control in the lexical-semantic processing of consolidated representations (Lambon Ralph et al., 2017), research on semantic control involved in recently acquired concepts is missing.

In Study 4, the accumulated experience in the mathematical domain possibly reduced demands on semantic control mechanisms in processing mathematical concepts. Experts' mathematical experience might have led to stronger associations between the experiential brain areas and therefore an easier retrieval of this information. Again, the chosen paradigm did not allow to measure the demands on semantic control. However, we are currently running a follow-up study, in which mathematical experts and novices process ambiguous abstract words following a contextual sentence highlighting the words' mathematical or non-mathematical meaning. This study could deliver first evidence of the interaction of the level of required semantic control and expertise in the abstract domain.

3.6 A Dynamic Model of Experience-Dependent Conceptual Processing

The findings presented in this dissertation allow generating tentative hypotheses concerning a theoretical framework of experience-dependent conceptual representations. The comprised studies deliver insights into the experience-dependent lexical-semantic processing of recently acquired (Studies 1 to 3) as well as consolidated conceptual representations in a specific field of expertise (Study 4). Based on these insights, it is possible to speculate that the mechanisms underlying conceptual processing interact dynamically and hierarchically in the process of concept consolidation.

First, the conceptual processing of recently acquired, novel representations may not yet involve the multimodal integration mechanisms in the ATL. Studies

1 and 3, which revealed no direct involvement of the ATL and the N400 in the processing of novel object representations, support this idea. Recent experience may however induce conceptual representations, whose processing relies on a broad semantic network, recruiting experience-specific information as shown in Study 3. Conceptual reactivations of experience-specific brain areas seem to depend largely on explicit demands introduced by the task, as revealed by the comparison of Studies 2 and 3, or stimulus format (compare Bellebaum et al., 2013; Ruther et al., 2014a; Ruther et al., 2014b). Post-conceptual, strategical processing phases could recruit additional resources such as episodic information or imagery in order to support conceptual processing. Semantic control mechanisms should be strongly involved in the retrieval of additional information in these post-conceptual processing stages, as the reduced quantity of experience would not yet have induced strong associations of the conceptually bound information.

Second, conceptual representations consolidated by every day experience should strongly rely on the ATL. Depending on the given context, reactivations of modality-specific areas flexibly occur during conceptual processing. Modality-specific areas could also be involved in later, strategical stages, possibly only, if the task demands it. Demands on semantic control possibly depend on the complexity of the underlying information as well as on the task. Most research on conceptual processing focused on these consolidated representations. Therefore, it is not surprising that the most recent theoretical approaches are the hybrid models of semantic memory (Barsalou, 2016; Lambon Ralph et al., 2017; Man et al., 2013; Patterson et al., 2007; Reilly & Peelle, 2008), suited to explain the flexible involvement of higher-order transmodal and modality-specific perceptual areas.

Last, conceptual processing in a specific domain of expertise should also rely on the ATL. However, experience-specific reactivations and their integration may be more central for conceptual processing and more easily or even automatically occur in early conceptual processing stages. The quantity of experience could further lead to an enhanced conceptual processing within experiential brain areas (Amalric & Dehaene, 2016; Beilock et al., 2008; Locatelli et al., 2012). Processes involved at late, strategical stages might support the retrieval of information from experiential brain areas. In case of less consolidated concepts, these processes are only involved when tasks explicitly demand them. In line with this, Study 4 showed that expertise alters the correlates of early and late semantic processing stages in an implicit task. Strong associations based on an enhanced connectivity of the conceptually bound information could reduce the demands on semantic control within the field of expertise.

When investigating the stages of conceptual consolidation described above, future research should not treat abstract knowledge representations as substantially different from concrete concepts. Study 4 supports the generalizability of experience-dependent conceptual processing from the concrete to the abstract domain. Therefore, it seems necessary to find a unifying model of semantic memory with common processes (Binder, 2016) in a hierarchical organization, taking into account suitable experiential channels for concrete as well as abstract concepts (Troche et al., 2014).

The suggested dynamic model of experience-dependent conceptual processing allows generating hypotheses about the flexible interplay of distributed experience-specific areas up to highly transmodal semantic hubs at different stages of concept consolidation. Additionally, the demands on semantic control mechanisms, partially introduced by qualitative differences in underlying experiences, should change throughout the spectrum of concept consolidation. Future research could test these hypotheses by

a) systematically varying the qualities of experience available during concept formation and investigating their subsequent conceptual reactivations. Importantly, neuroscientific methods with different sensitivity to semantic processes should be combined.
b) investigating the flexibility of conceptual reactivations dependent on context and task-demands.
c) investigating the effect of quality and quantity of experience on conceptual representations and semantic control mechanisms.

Longitudinal training paradigms including different classes of novel conceptual representations seem a promising approach to pinpoint the mechanisms involved in forming and processing conceptual representations. Including implicit and explicit tasks at different stages of the consolidation process could help elucidating the dynamics of flexible conceptual reactivations and semantic hub activity. Finally, a comprehensive investigation should include varying demands on semantic control.

3.7 Conclusion

To conclude, the results presented in this dissertation provide evidence for an experience-dependent formation and subsequent processing of conceptual representations in semantic memory. With the training paradigm applied in Studies 1 to 3 as well as the expertise approach of Study 4, we investigated the role of different qualities as well as the accumulation of experience on conceptual processing. Importantly, the presented results reflect conceptual processing untainted of any perceptual influences, as we accessed the conceptual representations via lexical stimuli. Study 4 further provides evidence for the generalizability of experience-dependent conceptual processing mechanisms to the abstract domain. This dissertation focused on the processing of recently acquired as well as extraordinarily consolidated conceptual representations, thereby revealing important insights into the dynamics of conceptual processing at different stages of consolidation. These first insights can be a starting point to investigate the experience-dependent dynamics of conceptual processing of abstract and concrete knowledge, contributing to a comprehensive understanding of semantic memory.

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5 APPENDIX A: AFFIDAVIT

Eidesstattliche Erklärung gemäß § 5 der Promotionsordnung vom 15.6.2018 der Mathematisch-Naturwissenschaftlichen Fakultät der Heinrich-Heine-Universität Düsseldorf:

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

Düsseldorf, den 8. Mai 2019 Laura Bechtold

Datum Laura Bechtold

6 Appendix B: Original Research Articles

Original Article of Study 1

Bechtold, L., Ghio, M., & Bellebaum, C. (2018). The Effect of Training-Induced Visual Imageability on Electrophysiological Correlates of Novel Word Processing. Biomedicines, 6(3). doi:10.3390/biomedicines6030075

I was the main author of this article. I contributed to the conceptualization and methodology and developed the paradigm. I planned and conducted the creation of the study material. I supervised the data acquisition, analyzed, and interpreted the data.

Original Article of Study 2

Bechtold, L., Ghio, M., Lange, J., & Bellebaum, C. (2018). Event-related desynchronization of mu and beta oscillations during the processing of novel tool names. *Brain and Language, 177-178*, 44-55. doi:10.1016/j.bandl.2018.01.004

I was the main author of this article. I contributed to the conceptualization and methodology and modified the original training paradigm. I conducted and supervised the data acquisition. I analyzed and interpreted the data.

ORIGINAL ARTICLE OF STUDY 3

Bechtold, L., Ghio, M., Antoch, G., Turowski, B., Wittsack, H.-J., Tettamanti, M., & Bellebaum, C. (in press). How words get meaning: The neural processing of novel object names after sensorimotor training. *Neuroimage*. doi:https://doi.org/10.1016/j.neuroimage.2019.04.069

Dr. Marta Ghio and I were the main authors of this article. I contributed to the conceptualization and methodology and modified the original training paradigm. I conducted and supervised the data acquisition. Dr. Marta Ghio and I analyzed the data. I interpreted the data.

ORIGINAL ARTICLE OF STUDY 4

Bechtold, L., Bellebaum, C., Egan, S., Tettamanti, M., & Ghio, M. (2019). The role of experience for abstract concepts: Expertise modulates the electrophysiological correlates of mathematical word processing. *Brain and Language, 188*, 1-10. doi:10.1016/j.bandl.2018.10.002

I was the main author of this article. I contributed to the conceptualization, methodology, and development of the paradigm. I supervised the data acquisition and subsequently analyzed and interpreted the data.

biomedicines

Article

The Effect of Training-Induced Visual Imageability on Electrophysiological Correlates of Novel Word Processing

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Abstract: The concreteness effect (CE) describes a processing advantage for concrete over abstract words. Electrophysiologically, the CE manifests in higher N400 and N700 amplitudes for concrete words. The contribution of the stimulus-inherent imageability to the electrophysiological correlates of the CE is not yet fully unraveled. This EEG study focused on the role of imageability irrespective of concreteness by examining the effects of training-induced visual imageability on the processing of novel words. In two training sessions, 21 healthy participants learned to associate novel words with pictures of novel objects as well as electron-microscopical structures and were additionally familiarized with novel words without any picture association. During a post-training EEG session, participants categorized trained novel words with or without picture association, together with real concrete and abstract words. Novel words associated with novel object pictures during the training elicited a higher N700 than familiarized novel words without picture-association. Crucially, this training-induced N700 effect resembled the CE found for real words. However, a CE on the N400 was found for real words, but no effect of imageability in novel words. The results suggest that the N400 CE for real words depends on the integration of multiple semantic features, while mere visual imageability might contribute to the CE in the N700 time window.

Keywords: N400; N700; concreteness; imageability; novel words; learning

1. Introduction

Language processing requires an association of a word's form with its referent's conceptual representation in semantic memory. Conceptual representations combine information taken from learning experience with the word and/or its referent and provide this information in the course of conceptual processing [1,2]. Depending on experiential differences concerning the words' referents, words are often classified as either concrete or abstract (for a review see [3]). Concrete words' referents (e.g., hammer) are perceivable with the external bodily senses. Abstract words refer to states or entities (e.g., harmony), which are not directly perceivable via external bodily senses, but rather arise from lexical information [4] or internal bodily senses (e.g., mental or emotional experience) [3,5–7].

The concreteness effect (CE) describes a processing advantage for concrete over abstract words in memory, comprehension and production tasks (for reviews see [3,8,9]). The dual-coding theory [4] explains the CE in terms of richer conceptual representations of concrete words, based on sensory as well as lexical information, while representations of abstract words rely on lexical information only. The context availability model [8] attributes the CE to an easier retrieval of a greater amount of conceptual information for concrete than abstract words. By now, novel approaches integrate dual-coding and context availability (e.g., the extended dual-coding theory) [10,11], as they seem to highlight the two distinct but compatible semantic processes of concept representation and retrieval, which rely on different interacting neural correlates [3,12].

One component considered crucially relevant for processing differences between concrete and abstract words is their imageability. Dual-coding as well as context availability accounts assign concrete words a higher imageability in terms of conceptually integrated visual sensory information [9] and accessibility of mental images [13], respectively. Language processing advantages driven by imageability have been shown in children, who initially acquire [14–16] and subsequently learn to read [17] highly imageable words earlier and better. Moreover, concrete and/or highly imaginable word processing is often less severely impaired by clinical disorders like semantic dementia [18,19], dyslexia [20–25] and Alzheimer's disease [26]. Kellogg, et al. [27] showed that a concurrent visual working memory task impaired the performance of healthy young adults in a definition production task for concrete but not abstract words, further supporting the role of imageability in the CE. Therefore, it is not surprising that concreteness and imageability ratings are highly correlated [28] and the two terms are often used interchangeably [3,29].

In electroencephalography (EEG) studies, the CE becomes manifest in higher amplitudes of the N400 and N700 event-related potential (ERP) components for concrete in comparison to abstract words [30]. The N400 has been interpreted to reflect the strength of the activation of the semantic network and integration of semantic information (for extensive reviews see [31,32]). The frontally pronounced N700 has been linked to mental imagery processes [10,30,33–35]. Findings of Barber, et al. [36] question the role of imageability for the electrophysiological CE. They matched concrete and abstract words for imageability and found a reversed behavioral CE but still higher N400 amplitudes for concrete than abstract words. Therefore, the effects of imageability and concreteness on word processing seem to be at least partially dissociable.

One recent line of research made important contributions for disentangling the effects of imageability and concreteness on N400 and N700 amplitudes. Concrete and abstract words (as stand-alone stimuli, see [35]; or in a sentential context, see [34,37]) were processed in an image generation as well as in a lexical and/or surface-level processing task in order to manipulate stimulus- and task-driven imagery processes, respectively. Altogether, these studies suggest that word concreteness and imageability are distinct semantic features, which are integrated in the processing stage reflected by the N400. At the later processing stage reflected by the N700, mental images of words might be generated, but only when the task as well as the stimuli afford it (for a detailed discussion and information on methodological differences see [35]). Gullick, Mitra and Coch [35] interpret their findings based on the extended dual-coding theory [10,11], and suggest that concreteness is not merely relying on sensorimotor information but includes lexically mediated information as well, while imageability is derived from (in their case visual) sensory information alone. In order to test this assumption, one could investigate the contribution of word imageability and concreteness to N400 and N700 modulations separately by employing stimuli with just one or the other semantic feature.

This study aimed at investigating the extent to which visual imageability untainted by concreteness modulates the N400 and N700 by using formerly meaningless, novel words that were either associated with visual stimuli during a training phase or not. In particular, in a two-day training, subjects learned to associate novel words with pictures of novel, unknown objects (OPic; see [38]) or of electron-microscopical structures (SPic). The two types of pictorial stimuli were chosen because of the different types of visual information they provide and were thus expected to lead to differences in imageability between the associated word stimuli. More specifically, the OPic were expected to lead to higher imageability than the SPic as we chose them to more distinctively depict one coherent entity. As a control condition, participants learned novel words that were not associated with any visual stimulus (NoPic). We thereby manipulated the novel words' imageability, without introducing any additional (lexical or sensory) information possibly contributing to the CE [3,39–41]. In a post-training EEG session, we examined the processing of the novel words while participants performed a concreteness-judgment task.

The results for the N400 could help to elucidate the role of imageability for the CE. If imageability itself contributes to the N400 CE, training-induced higher visual imageability should lead to higher N400 amplitudes. If, however, the N400 CE depends on an integrative interaction of sensorimotor and lexically coded features underlying word concreteness [32,35,42], no effect should be seen at this processing stage. For the N700, we expected to see larger amplitudes for higher imageability, as the task used in our study was designed to afford imagery processes [35]. Finally, as the effect of visual imageability on word processing presumably contributes to the electrophysiological CE, we presented concrete and abstract real words intermixed with the novel words in our study. The aim was to elicit a classical CE in the N400 and N700 time windows within the same experimental paradigm and qualitatively compare the CE in real words with the effects of imageability on novel words.

2. Materials and Method

2.1. Participants

Twenty-four healthy German native speakers (age from 19 to 34 years) took part in the study. Three participants were excluded from the analyses due to a poor learning performance and thus too few trials for the EEG analyses (<20 for at least one experimental condition). The remaining 21 participants (10 women; mean age = 24.8 years, SD = 4.1 years) had normal or corrected to normal vision and were right handed as indicated by the Edinburgh Handedness Inventory [43] (scores between 0.55 and 1, M = 0.88, SD = 0.14). All participants gave their written informed consent. After participation, they received course credit or monetary compensation. This study was in line with the declaration of Helsinki and was approved by the ethics committee of the Faculty of Mathematics and Natural Sciences.

2.2. Material

2.2.1. Visual Stimuli

The visual stimuli were 8-bit color JPG images of 15 unfamiliar objects (OPics) and 15 electron-microscopical pictures of structures (SPics). The objects were built of a construction toy (K'NEX^{TM}) and had already been used in previous training studies [38,44–47]. For each object, photographs from four isometric perspectives were available. The electron-microscopical pictures were acquired via google image search and consisted of different living and non-living structures (e.g., legionella, rocks, asbestos, skin). They were each cut into four partially overlapping segments and a slight vignette, extracted from the object picture backgrounds, was added. Electron-microscopical images were originally monochrome. The color information of the OPics was extracted, smoothed and transferred onto the SPics via the GNU Image Manipulation Program (GIMP, version 2). The mean brightness (measured with the pictures' histograms, from 0 = white to 255 = black with GIMP) of the 60 OPics (M = 176.77, SD = 8.49) and 60 SPics (M = 176.77, SD = 8.46) was carefully matched, $t(118) = 0.001$, $p = 0.999$.

2.2.2. Verbal Stimuli

The 60 word-like pseudo-words used as novel words in this study were created by changing two to three letters in real German words, following phonological rules (e.g., Himmar, Neribon). This pool of stimuli was divided into four subsets, each including 15 words. Each subset was assigned to one of the experimental conditions, namely OPic, SPic, NoPic (familiarized in the training but without associated pictures, served as a lexical baseline condition) and New (only used as filler stimuli for the EEG task, see below). The novel words in these four subsets were matched for the number of letters ($M_{OPic} = 7.67$, $SD_{OPic} = 0.90$; $M_{SPic} = 7.67$, $SD_{SPic} = 0.90$; $M_{NoPic} = 7.73$, $SD_{NoPic} = 0.88$; $M_{New} = 7.87$, $SD_{New} = 0.92$; Kruskal-Wallis-test for independent samples, $H(3) = 0.250$, $p = 0.969$) and syllables ($M_{OPic} = 2.53$, $SD_{OPic} = 0.52$; $M_{SPic} = 2.53$, $SD_{SPic} = 0.52$; $M_{NoPic} = 2.53$, $SD_{NoPic} = 0.52$; $M_{New} = 2.47$, $SD_{New} = 0.52$; Kruskal-Wallis-test for independent samples, $H(3) = 0.197$,

p = 0.978). The 60 real words additionally used in the EEG concreteness-judgment task consisted of 30 concrete and 30 abstract words. They were also matched for the number of letters ($M_{concrete}$ = 7.07, $SD_{concrete}$ = 1.02; $M_{abstract}$ = 7.10, $SD_{abstract}$ = 1.79; Kruskal-Wallis-test for independent samples, $H(1)$ = 0.052, p = 0.820) and syllables ($M_{concrete}$ = 2.40, $SD_{concrete}$ = 0.50; $M_{abstract}$ = 2.47, $SD_{abstract}$ = 0.51; Kruskal-Wallis-test for independent samples, $H(1)$ = 0.267, p = 0.605). Concrete and abstract real words were additionally matched for their lexical frequency as assessed via a word database of the university of Leipzig, (http://wortschatz.uni-leipzig.de, 20 March 2015; $M_{concrete}$ = 1726.68, $SD_{concrete}$ = 1698.92; $M_{abstract}$ = 1746.57, $SD_{abstract}$ = 2124.28; Kruskal-Wallis-test for independent samples, $H(1)$ = 0.514, p = 0.473). All real words were rated regarding eight different psycholinguistic variables (Concreteness, Imageability, Arousal, Valence and their association with Action, Emotion, Perception and Thinking) by a sample of 39 (28 female) participants aged between 18 years and 44 years (M = 25.31 years, SD = 6.73) in a preceding rating-study (see Table S1 in the Supplementary Materials for descriptive and inferential statistics).

2.3. Procedure

2.3.1. Training Sessions

The training sessions took place with one or two participants in one room of the Department of Biological Psychology at Heinrich Heine University Düsseldorf. The training period for each participant included two training sessions on separate days with two training-blocks in each session, run with PsychoPy (version 1.81.03, avaliable online: http://www.psychopy.org/changelog.html#psychopy-1-81-03) [48] on a Fujitsu Lifebook A512. A two-minute break separated the two blocks. In both blocks, all OPic, SPic and NoPic words were presented four times each for 5000 ms in a randomized order. The ISI was set to 500 ms. Within each block, each OPic word was combined once with each of the four pictures of the assigned object taken from different perspectives. Similarly, each SPic word was combined once with each of the four sections of one structure picture. In this way, each OPic and each SPic word appeared four times per block and thus eight times per training and each OPic word could be associated with one object and each SPic word could be associated with one structure. NoPic words were presented as often as the OPic and SPic words, but they appeared alone on the computer screen without any additional picture. Participants were asked to memorize the presented words and, for the OPic and SPic words, their associated pictures. Each block took about 15 min to complete. Participants were told that learning performance checks would be conducted after the training session. At first, free reproduction was assessed followed by a multiple-choice and picture assignment questionnaire (for details see Section 2.3.3).

2.3.2. EEG Session

EEG was acquired individually in an electrically shielded EEG chamber in the department of Biological Psychology at Heinrich Heine University Düsseldorf. During the EEG session, concrete and abstract real words as well as the novel words were presented intermixed in three blocks. The novel words included the 45 words that appeared during the training, as well as the 15 non-trained novel words (New condition). In each block, each novel and real word was presented once, and the order of presentation was randomized.

The participants' task was to judge whether the real and novel words were either concrete or abstract. This task was chosen because the definitions of concrete and abstract could be applied to both the real and novel words. This made it possible to use the same task for both types of words, which was especially important, as the words appeared intermixed. In the instructions for the participants, concrete was defined as referring to something perceivable via the senses (e.g., sight, touch) including real concrete words as well as the newly learned OPic and SPic words, which referred to the associated picture stimuli. Abstract was defined as referring to something not perceivable via the senses, including real abstract words as well as the NoPic and New words. The latter were introduced as filler stimuli to provide the same number of real and novel words.

Each trial started with a fixation cross with a jittered duration between 1200 ms and 1600 ms. Then the word was presented for 800 ms, followed by a jittered blank screen of 300 ms to 500 ms duration. Afterwards, the assignment of the left and right Ctrl-button of a computer keyboard to the concrete and abstract response option appeared on the screen. The button-response assignment varied randomly between trials to make sure that motor preparation would not confound the recorded ERPs. The inter-trial interval was again randomly jittered between 300 ms and 500 ms. Participants had the possibility to take a self-paced break every 20 trials. Participants were asked to keep their left and right index fingers on the Ctrl-buttons in order to reduce movement artifacts. The EEG task took about 30 min to complete. Subsequent to the EEG task, participants completed the multiple-choice and picture assignment learning performance checks.

2.3.3. Learning Performance Questionnaires

Different questionnaires assessed the participants' learning performance. A free reproduction task tested the ability to recall the learned words freely after both training sessions. Following each training and the EEG session, a multiple-choice questionnaire with a list of all words tested the participants' ability to assign the novel words to their category (based on the training condition associated with object, structure and no picture). In an attached picture assignment task, participants were additionally asked to assign each novel word to the printed photographs of the objects/structures. In the learning performance tests, participants could reach one point per correct free reproduction and assignment of the novel words to their category (OPic, SPic, NoPic) or picture (OPic, SPic), respectively. In all versions of the multiple-choice questionnaire, the order of the words was randomized. For each category and learning performance measure, the percentage of correct reproduction and assignments was calculated.

2.4. EEG Recording and Preprocessing

2.4.1. Recording

EEG was recorded via 28 silver/silver chloride ring-electrodes, on a textile cap with pre-mounted holders (actiCap; Brainproducts GmbH, Germany) following the extended 10–20 system [49] (electrode sites were F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, and PO10). Additionally, two electrodes at the outer canthi of the eyes and one above and below the right eye, respectively, recorded horizontal and vertical eye movements. The ground electrode was attached at electrode site AFz and the online reference was attached to the nose. Impedances were kept below 5 kΩ. EEG data were amplified via a BrainAmp DC amplifier (BrainProducts GmbH, Gilching, Germany). The Brain Vision Recorder software (Version 1.20.0506, Brain Products GmbH) was used for data acquisition with a sampling rate of 1000 Hz and an online lowpass filter of 100 Hz on a Windows 10 Dell Intel Premium PC. The software Presentation (Version 17.0, Neurobehavioral Systems Inc., Albany, CA, USA) on a Windows 10 Dell Intel Premium PC controlled the timing of stimulus presentation during the EEG session on a 22″ LED Dell monitor with 1680 × 1050-pixel resolution and a refresh rate of 60 Hz. The software also recorded the participants' responses given via a Microsoft USB keyboard.

2.4.2. Preprocessing

EOG electrodes were re-referenced bipolarly and scalp electrodes were referenced to an average reference including all electrodes (C3, C4, CP3, CP4, CPz, Cz, F3, F4, F7, F8, FC3, FC4, FCz, FT7, FT8, Fz, P3, P4, P7, P8, PO3, PO4, PO7, PO8, POz, Pz), except for T7 and T8, which showed extensive muscle artifacts in some participants. Next, data underwent a global direct current detrend [50]. We applied butterworth zero-phase filters with a highpass threshold of 0.5 Hz and a lowpass threshold of 20 Hz, both with 24 dB/Oct. Additionally, a 50 Hz notch-filter was applied. After a classic ICA in semiautomatic mode on 120 s of the data, components including sharp, frontally pronounced positive deflections caused by blinking were detected by visual inspection and removed from the signal via an ICA back transformation. For 18 participants, one single component could be identified depicting the eye blink artifact. For the remaining three participants two or three components were excluded before the back transformation. Continuous data were segmented starting 300 ms pre- and ending 1200 ms post-stimulus onset. After a baseline correction for the 300 ms pre-stimulus interval, an automatic artifact rejection was applied with the following parameters: a maximal allowed voltage step of 50 μV/ms, a maximal/minimal amplitude difference between the highest and the lowest data point of 100/0.1 μV in 100 ms, and a maximally/minimally allowed amplitude of ±100 μV. Subsequently, artifact-free segments were divided into the experimental conditions OPic, SPic, NoPic and New for novel words, and concrete and abstract for real words. In the OPic, SPic and NoPic conditions, only those novel words were included, which participants correctly assigned to their training condition in the multiple-choice questionnaire after the EEG session. This resulted in a mean number of 38.8 trials (*SD* = 7.4) in the OPic, 37.6 trials (*SD* = 7.2) in the SPic and 36.5 trials (*SD* = 8.4) in the NoPic condition entering into the averaged ERP waveforms. In real-word conditions, all artifact-free segments (concrete: *M* = 89.2, *SD* = 2.1; abstract: *M* = 89.0, *SD* = 2.2) entered into the average ERP waveforms.

2.4.3. ERP Analyses

Nine electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) equally distributed across the head were chosen for the ERP analyses. ERP time windows were set after visual inspection of the grand average ERP waveforms and in line with previous studies [30,31]. For the N400, the mean amplitude was extracted from the time window between 300 ms and 500 ms. The N700 is more a slow wave rather than a clearly defined ERP component, and the visual inspection of our data suggested different result patterns early and late in the N700 time window between 500 ms and 900 ms. We thus split the time window and analyzed an early N700 (from the 500 ms to 700 ms, compare, e.g., [34,35,51]) and a late N700 (from 700 ms to 900 ms) separately (compare, e.g., [36,52]). Novel words from the New condition were excluded from ERP analyses as they were only introduced as filler stimuli and we were not interested in studying old/new ERP effects, which are typically very pronounced [53,54].

2.5. Statistical Data Analyses

Data analysis was conducted with IBM SPSS Statistics (version 23, IBM corporation, Armonk, NY, USA). Behavioral learning and concreteness-judgment performance as well as electrophysiological data were analyzed with different repeated measures analyses of variance (ANOVA). If the Mauchly test indicated a violation of the assumption of sphericity, Greenhouse-Geisser correction was applied and corrected degrees of freedom and *p*-values will be reported. For significance, an α-level of 0.05 was assumed. Post-hoc pairwise comparisons were Bonferroni corrected.

3. Results

3.1. Behavioral Data

3.1.1. Learning Performance

Free Reproduction

In order to check how well participants learned the novel words, a Category (OPic, SPic, NoPic) × Session (first and second training session) repeated measures ANOVA was conducted on the performance in the free reproduction task (see Figure 1, left). This analysis revealed that the Category did not have a significant effect on the percentage of correct free reproductions, $p = 0.211$. Correct free reproductions significantly increased from the first to the second training session, $F(1, 20) = 44.607$, $p < 0.001$, $\eta_p^2 = 0.690$. The Category × Session interaction was significant, $F(1.450, 28.992) = 3.784$,

$p = 0.047$, $\eta_p^2 = 0.159$. Paired *t*-tests revealed that the performance increase was significant for all novel word categories, all $p < 0.001$, with the largest increase for OPic, followed by SPic and NoPic.

Multiple-Choice

Performance in the multiple-choice test (see Figure 1, middle) served as a second measure of learning of the novel words. This measure was not only applied after each of the two learning sessions, but also after the EEG session. A Category (OPic, SPic, NoPic) × Session (first and second training session, EEG session) repeated measures ANOVA showed that neither the main effect of Category nor the Category × Session interaction were significant for the multiple-choice learning performance, both $p \geq 0.078$. We found a significant main effect of Session, $F(1.424, 28.483) = 15.923$, $p < 0.001$, $\eta_p^2 = 0.443$. Pairwise comparisons showed a significant performance increase from the first to the second training session and from the first training to the EEG session, $p = 0.002$ and $p < 0.001$, respectively. The second training session and the EEG session did not differ significantly, $p = 1.000$.

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< 0.001, $\eta_p^2 = 0.443$. Pairwise comparisons showed a significant performance increase from the first to the second training session and from the first training to the EEG session, $p = 0.002$ and $p < 0.001$, respectively. The second training session and the EEG session did not differ significantly, $p = 1.000$.

Picture Assignment

A Category (OPic, SPic) × Session (first and second training session, EEG session) repeated measures ANOVA was performed on the performance in the picture assignment test (see Figure 1, right), with the aim of determining how well participants learned to associate the novel words with the respective pictures. The ANOVA showed that neither the main effect of Category nor the Category × Session interaction affected the percentage of correct picture-assignments significantly, both $p \geq 0.511$. Again, the Session had a significant effect, $F(1.234, 24.673) = 17.753$, $p < 0.001$, $\eta_p^2 = 0.022$. Pairwise comparisons revealed a significant increase in correct assignments from the first to the second training session, and from the first training to the EEG session, $p = 0.002$ and $p < 0.001$, respectively. The second training and EEG session did not differ significantly, $p = 1.000$.

Picture Assignment

A Category (OPic, SPic) × Session (first and second training session, EEG session) repeated measures ANOVA was performed on the performance in the picture assignment test (see Figure 1, right), with the aim of determining how well participants learned to associate the novel words with the respective pictures. The ANOVA showed that neither the main effect of Category nor the Category × Session interaction affected the percentage of correct picture-assignments significantly, both $p \geq 0.511$. Again, the Session had a significant effect, $F(1.234, 24.673) = 17.753$, $p < 0.001$, $\eta_p^2 = 0.022$. Pairwise comparisons revealed a significant increase in correct assignments from the first to the second training session, and from the first training to the EEG session, $p = 0.002$ and $p < 0.001$, respectively. The second training and EEG session did not differ significantly, $p = 1.000$.

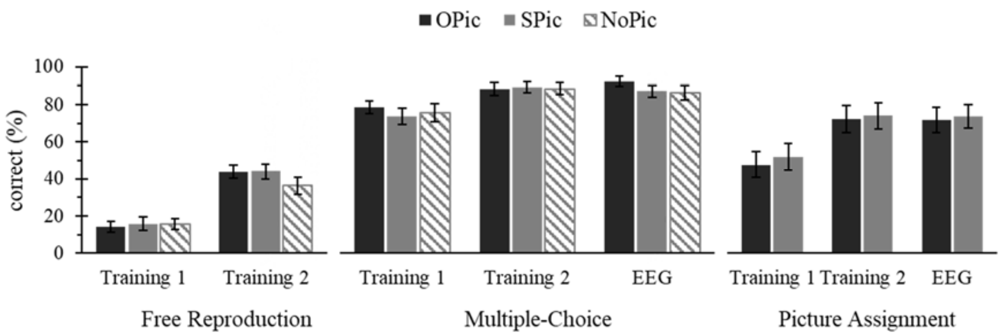

Figure 1. Novel word learning performance. The mean (± one standard error for $n = 21$) learning performance (% correct) for the free reproduction task (**left**), multiple choice questionnaire (**middle**) and picture assignment (**right**), separately for novel words associated with object (OPic), structure (SPic) or no picture (NoPic). Please note that the latter two learning measures were additionally acquired after the EEG session.

Figure 1. Novel word learning performance. The mean (± one standard error for $n = 21$) learning performance (% correct) for the free reproduction task (**left**), multiple choice questionnaire (**middle**) and picture assignment (**right**), separately for novel words associated with object (OPic), structure (SPic) or no picture (NoPic). Please note that the latter two learning measures were additionally acquired after the EEG session.

3.1.2. Concreteness-Judgment Task in the EEG Session

Error rates were calculated as the percentage of wrong responses of all given responses and were averaged separately for each experimental condition (real word Concreteness: concrete and abstract; novel word Category: OPic, SPic, NoPic).

3.1.2. Concreteness-Judgment Task in the EEG Session

Error rates were calculated as the percentage of wrong responses of all given responses and were averaged separately for each experimental condition (real word Concreteness: concrete and abstract; novel word Category: OPic, SPic, NoPic).

Error Rates for Real Words

Mean error rates were 2.3% ($SE = 0.7\%$) for concrete words and 3.2% ($SE = 0.7\%$) for abstract words. A paired *t*-test did not reveal a significant difference between concrete and abstract words, $t(20) = -1.057$, $p = 0.303$.

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Error Rates for Novel Words

Mean error rates were descriptively smallest in response to OPic ($M = 8.3\%$, $SE = 2.2\%$), followed by SPic ($M = 12.3\%$, $SE = 2.6\%$) and NoPic ($M = 17.3\%$, $SE = 4.0\%$). In a repeated measures ANOVA the effect of the Category on error rates did not reach significance, $p = 0.068$.

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3.2. Electrophysiological Data

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3.2.1. ERP Effects for Real Words

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Firstly, we aimed at replicating the well-known CE for real words with our experimental paradigm and setup. Therefore, amplitudes of the N400 and the early and late N700 were analyzed via repeated measures ANOVAs with the factor Concreteness (concrete, abstract) and the topographical factors Frontality (frontal, central, parietal) and Laterality (left, middle, right). Figure 2 shows the grand averages for concrete and abstract words for all analyzed electrodes. Inferential statistics are listed in Table 1. Descriptive statistics (M, SE) for the amplitudes of the ERP components elicited by concrete and abstract words at each electrode site can be found in Table S2 in the Supplementary Materials. Only main and interaction effects involving the factor Concreteness will be reported in the text.

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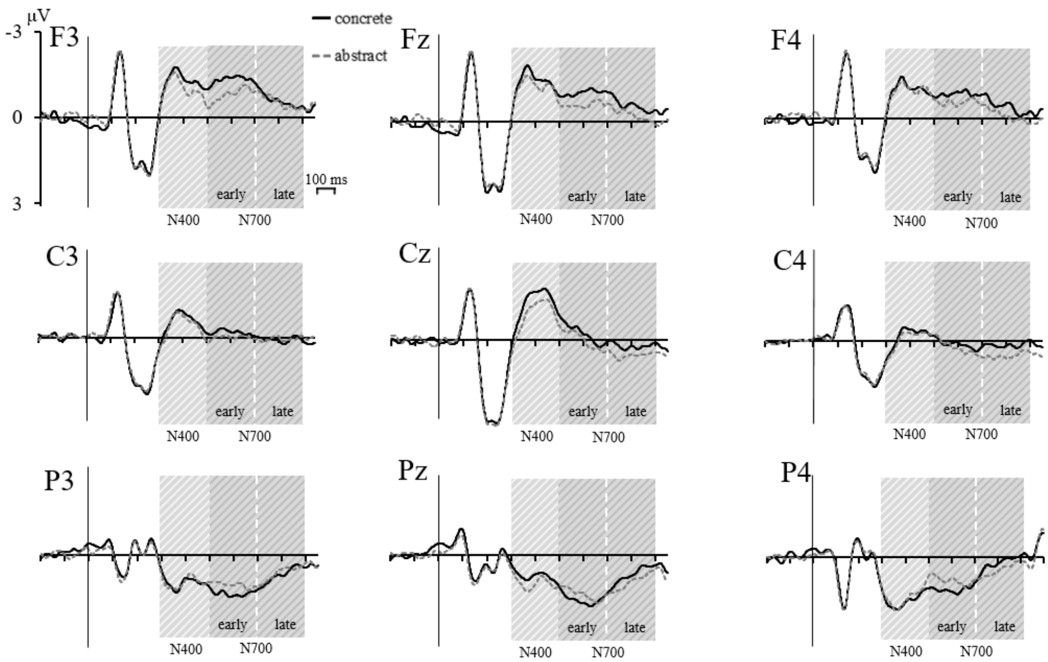

Figure 2. Real word ERPs. Grand averages (n = 21) of the ERP waveforms elicited by concrete and abstract words for all analyzed electrodes. The shaded areas mark the time windows of the N400 (300–500 ms), the early N700 (500–700 ms) and late N700 (700–900 ms).

Figure 2. Real word ERPs. Grand averages (n = 21) of the ERP waveforms elicited by concrete and abstract words for all analyzed electrodes. The shaded areas mark the time windows of the N400 (300–500 ms), the early N700 (500–700 ms) and late N700 (700–900 ms).

Real Word N400

Real Word N400

Concreteness had a significant effect on N400 amplitudes, p = 0.006, with higher (i.e., more negative) amplitudes for concrete (M = −0.259 μV, SE = 0.135 μV) than abstract words (M = −0.124 μV, SE = 0.128 μV). The Concreteness × Laterality interaction was significant, p = 0.023. Subsequent paired t-tests comparing abstract and concrete words for each of the three levels of Laterality revealed a significantly higher (i.e., more negative) N400 amplitude for concrete words only at electrodes of the midline (mean difference: −0.274 μV, SE = 0.062 μV), $t(20)$ = −4.442, p < 0.001. The differences were significant at neither the left side, nor at right side electrodes, both $p \geq 0.078$. Neither the two-way interaction Concreteness × Frontality nor the three-way interaction Concreteness × Frontality × Laterality reached significance, both $p \geq 0.060$.

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Real Word N700

Concreteness had a significant effect on early N700 amplitudes, p = 0.016, with a higher (i.e., less positive) amplitude for concrete (M = 0.068 μV, SE = 0.093 μV) than abstract words (M = 0.171 μV, SE = 0.092 μV). The Concreteness × Frontality interaction was significant, p = 0.005. Subsequent paired t-tests

Real Word N700

Concreteness had a significant effect on early N700 amplitudes, p = 0.016, with a higher (i.e., less positive) amplitude for concrete (M = 0.068 μV, SE = 0.093 μV) than abstract words (M = 0.171 μV, SE = 0.092 μV). The Concreteness × Frontality interaction was significant, p = 0.005. Subsequent paired t-tests comparing abstract and concrete words for each of the three levels of Frontality revealed a significantly more negative early N700 amplitude for concrete words at frontal (mean difference: −0.408 μV, SE = 0.117 μV), $t(20) = -3.500$, p = 0.002, and central electrodes (mean difference: −0.168 μV, SE = 0.066 μV), $t(20) = -2.549$, p = 0.019. The pattern was inversed at parietal electrodes, where concrete words elicited a significantly more positive amplitude than abstract words (mean difference: 0.270 μV, SE = 0.119 μV), $t(20)$ = 2.275, p = 0.034. Neither the two-way interaction Concreteness × Laterality nor the three-way interaction Concreteness × Frontality × Laterality reached significance, both $p \geq 0.363$.

Concreteness also had a significant effect on late N700 amplitudes, p = 0.002, again with higher (i.e., less positive) amplitudes for concrete (M = 0.055 μV, SE = 0.064 μV) than abstract words (M = 0.252 μV, SE = 0.076 μV). The Concreteness × Laterality interaction was significant, p = 0.025. Subsequent paired t-tests comparing abstract and concrete words for each of the three levels of Laterality revealed a significantly higher late N700 amplitude for concrete words at midline (mean difference: −0.298 μV, SE = 0.088 μV), $t(20) = -3.387$, p = 0.003, and right side (mean difference: −0.300 μV, SE = 0.084 μV), $t(20) = -3.574$, p = 0.002 electrodes. Amplitudes elicited by concrete and abstract words did not differ significantly at left side electrodes, p = 0.916. Neither the two-way interaction Concreteness × Frontality nor the three-way interaction Concreteness × Frontality × Laterality reached significance, both $p \geq 0.656$.

Table 1. Real Word Analyses. Full inferential statistics of the 2 × 3 × 3 repeated measures ANOVAs on N400, early N700 and late N700 amplitudes.

Effect	*df*	*F*	*p*	η_p^2
N400 (300–500 ms)				
Concreteness	1, 20	9.566	0.006	0.324
Concreteness × Frontality	1.251, 25.023	0.472	0.540	0.023
Concreteness × Laterality	1.302, 26.036	5.203	0.023	0.206
Concreteness × Frontality × Laterality	4, 80	2.363	0.060	0.106
Frontality	1.135, 22.691	21.042	<0.001	0.513
Laterality	2, 40	5.614	0.007	0.219
Frontality × Laterality	2.544, 50.884	2.136	0.116	0.096
early N700 (500–700 ms)				
Concreteness	1, 20	6.961	0.016	0.258
Concreteness × Frontality	1.173, 23.451	8.588	0.005	0.300
Concreteness × Laterality	2, 40	1.039	0.363	0.049
Concreteness × Frontality × Laterality	4, 80	1.019	0.403	0.048
Frontality	1.364, 27.271	37.281	<0.001	0.651
Laterality	2, 40	0.849	0.435	0.041
Frontality × Laterality	1.643, 32.859	3.326	0.057	0.143
late N700 (700–900 ms)				
Concreteness	1, 20	12.796	0.002	0.390
Concreteness × Frontality	1.142, 22.845	0.247	0.656	0.012
Concreteness × Laterality	1.346, 26.920	4.974	0.025	0.199
Concreteness × Frontality × Laterality	4, 80	0.187	0.944	0.009
Frontality	1.314, 26.286	21.153	<0.001	0.514
Laterality	2, 40	1.456	0.245	0.068
Frontality × Laterality	2.178, 43.553	7.345	0.001	0.269

3.2.2. ERP Effects for Novel Words

The main analysis examined the effects of the training-induced visual imageability of the novel words on linguistic processing. Repeated measures ANOVAs with the training-induced factor Category

(OPic, SPic, NoPic) and the topographical factors Frontality (frontal, central, parietal) and Laterality (left, middle, right) were conducted on the amplitudes of the N400 and the early and late N700. Figure 3 shows the grand averages for OPic, SPic and NoPic words for all analyzed electrodes. Inferential statistics are listed in Table 2. Descriptive statistics (*M*, *SE*) for the ERP components elicited by OPic, SPic and NoPic words at each electrode site can be found in Table S3 in the Supplementary Materials. Only main and interaction effects involving the factor Category will be reported in the text.

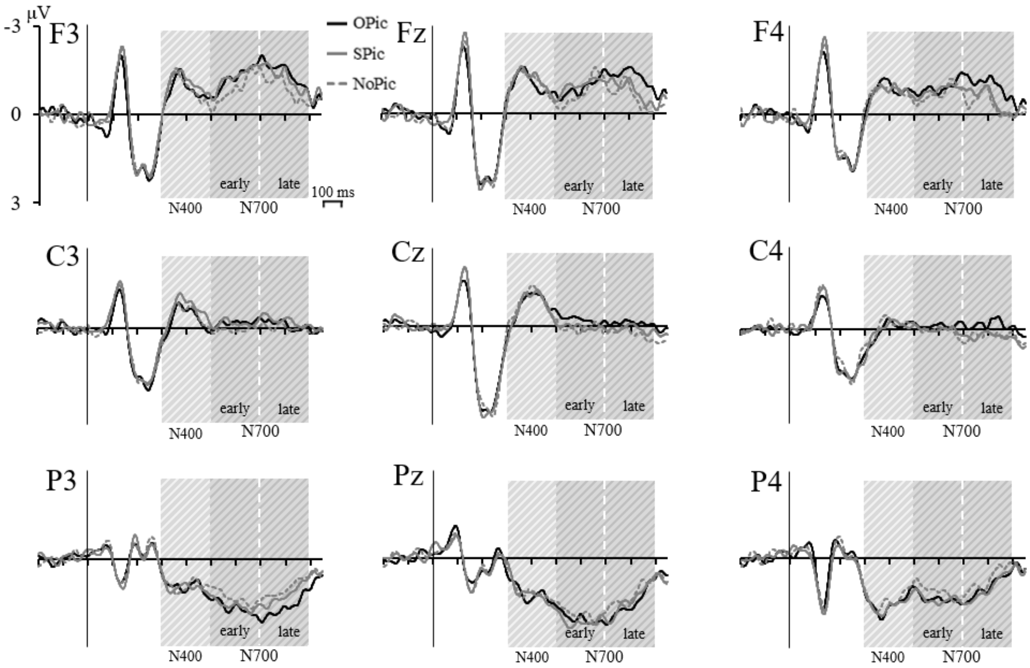

Figure 3. Novel word ERPs. Grand averages (*n* = 21) of the ERP waveforms elicited by novel words associated with object (OPic), structure (SPic) or no pictures (NoPic) for all analyzed electrodes. The shaded areas mark the time windows of the N400 (300–500 ms) and the early N700 (500–700 ms) and late N700 (700–900 ms).

Novel Word N400

For N400 amplitudes, neither the main effect of Category nor any of its interactions with the topographical factors reached significance, all $p > 0.399$.

Novel Word N700

For the early N700, neither the main effect of Category nor any of its interactions with the topographical factors reached significance, all $p > 0.141$.

For the late N700, the two-way interaction Category × Frontality was significant, $p = 0.014$. In order to resolve this interaction, repeated measures ANOVAs investigated the effect of Category separately for each level of Frontality. The Category had a significant effect on the late N700 amplitudes at frontal ($p = 0.008$) and parietal ($p = 0.043$) but not at central ($p = 0.066$) electrode sites. Pairwise comparisons for the frontal electrodes showed that OPic words ($M = -1.244$ µV, $SE = 0.256$ µV) elicited a significantly more negative amplitude than NoPic words ($M = -0.624$ µV, $SE = 0.227$ µV), $p = 0.021$. The comparisons of SPic ($M = -0.858$ µV, $SE = 0.277$ µV) to OPic and NoPic did not reach significance, $p = 0.087$ and $p = 0.741$, respectively. The pattern was inverted at parietal electrodes, where OPic words ($M = 1.374$ µV, $SE = 0.197$ µV) elicited a more positive amplitude than NoPic words ($M = 0.978$ µV, $SE = 0.172$ µV) which was at trend level after Bonferroni correction, $p = 0.099$. Again, the comparisons of SPic ($M = 1.206$ µV, $SE = 0.214$ µV) to OPic and NoPic were not significant, $p = 0.396$ and $p = 0.571$, respectively. The two-way interaction Category × Laterality was also significant, $p = 0.047$. In order to

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Inferential statistics are listed in Table 2. Descriptive statistics (M, SE) for the ERP components elicited by OPic, SPic and NoPic words at each electrode site can be found in Table S3 in the Supplementary Materials. Only main and interaction effects involving the factor Category will be reported in the text.
Figure 3. Novel word ERPs. Grand averages (n = 21) of the ERP waveforms elicited by novel words associated with object (OPic), structure (SPic) or no pictures (NoPic) for all analyzed electrodes. The shaded areas mark the time windows of the N400 (300–500 ms) and the early N700 (500–700 ms) and late N700 (700–900 ms).
Novel Word N400
For N400 amplitudes, neither the main effect of Category nor any of its interactions with the topographical factors reached significance, all p > 0.399.
Novel Word N700
For the early N700, neither the main effect of Category nor any of its interactions with the topographical factors reached significance, all p > 0.141.
For the late N700, the two-way interaction Category × Frontality was significant, p = 0.014. In order to resolve this interaction, repeated measures ANOVAs investigated the effect of Category separately for each level of Frontality. The Category had a significant effect on the late N700 amplitudes at frontal (p = 0.008) and parietal (p = 0.043) but not at central (p = 0.066) electrode sites. Pairwise comparisons for the frontal electrodes showed that OPic words (M = −1.244 µV, SE = 0.256 µV) elicited a significantly more negative amplitude than NoPic words (M = −0.624 µV, SE = 0.227 µV), p = 0.021. The comparisons of SPic (M = −0.858 µV, SE = 0.277 µV) to OPic and NoPic did not reach significance, p = 0.087 and p = 0.741, respectively. The pattern was inverted at parietal electrodes, where OPic words (M = 1.374 µV, SE = 0.197 µV) elicited a more positive amplitude than NoPic words (M = 0.978 µV, SE = 0.172 µV) which was at trend level after Bonferroni correction, p = 0.099. Again, the comparisons of SPic (M = 1.206 µV, SE = 0.214 µV) to OPic and NoPic were not significant, p = 0.396 and p = 0.571, respectively. The two-way interaction Category × Laterality was also significant, p = 0.047. In order to resolve this interaction, repeated measures ANOVAs investigated the effect of Category separately for each level of Laterality. The Category had a significant effect on late N700 amplitudes only at right side electrodes, p = 0.027 (left side and midline both p ≥ 0.153). Pairwise comparisons for the right side electrodes showed

resolve this interaction, repeated measures ANOVAs investigated the effect of Category separately for each level of Laterality. The Category had a significant effect on late N700 amplitudes only at right side electrodes, $p = 0.027$ (left side and midline both $p \geq 0.133$). Pairwise comparisons for the right-side electrodes showed that OPic words ($M = -0.075$ µV, $SE = 0.130$ µV) elicited a more negative amplitude than SPic words ($M = -0.235$ µV, $SE = 0.147$ µV) and NoPic ($M = -0.178$ µV, $SE = 0.136$ µV) which was at trend level after Bonferroni correction, $p = 0.076$ and $p = 0.080$, respectively, while the latter two did not differ significantly, $p = 1.000$. Neither the Category main effect nor the three-way interaction Category × Frontality × Laterality were significant, both $p \geq 0.080$.

Table 2. Novel word analyses. Full inferential statistics of the 3 × 3 × 3 repeated measures ANOVA on N400, early N700 and late N700 amplitudes as well as repeated measures ANOVAs with the factor Category (OPic, SPic, NoPic) resolving the significant interactions.

Effect	*df*	*F*	*p*	η_p^2
N400 (300–500 ms)				
Category	2, 40	0.559	0.576	0.027
Category × Frontality	2.242, 44.834	0.135	0.895	0.007
Category × Laterality	4, 80	1.026	0.399	0.049
Category × Frontality × Laterality	8, 160	0.858	0.554	0.041
Frontality	1.138, 22.768	21.611	<0.001	0.519
Laterality	2, 40	2.387	0.105	0.107
Frontality × Laterality	2.351, 47.021	1.924	0.151	0.088
early N700 (500–700 ms)				
Category	2, 40	0.556	0.578	0.027
Category × Frontality	2.115, 42.309	2.033	0.141	0.092
Category × Laterality	4, 80	0.415	0.797	0.020
Category × Frontality × Laterality	5.126, 102.523	1.214	0.308	0.057
Frontality	1.198, 23.956	28.031	<0.001	0.584
Laterality	1.328, 26.560	1.150	0.311	0.054
Frontality × Laterality	1.747, 34.947	4.832	0.017	0.195
late N700 (700–900 ms)				
Category	2, 40	2.698	0.080	0.119
Category × Frontality	1.912, 38.243	4.917	0.014	0.197
Category [a]: Repeated measures ANOVA				
frontal	2, 40	5.450	0.008	0.214
central	1.567, 31.341	3.185	0.066	0.137
parietal	2, 40	3.408	0.043	0.146
Category × Laterality	4, 80	2.533	0.047	0.112
Category [a]: Repeated measures ANOVA				
left side	2, 40	1.189	0.315	0.056
midline	1.509, 30.187	2.255	0.133	0.101
right side	2, 40	3.941	0.027	0.165
Category × Frontality × Laterality	4.367, 87.338	0.395	0.828	0.019
Frontality	1.161, 23.225	27.382	<0.001	0.578
Laterality	1.500, 30.009	0.807	0.423	0.039
Frontality × Laterality	2.164, 43.278	12.682	<0.001	0.388

[a] Resolutions of the significant interactions by repeated measures ANOVA with the factor Category.

4. Discussion

This study investigated the effect of visual imageability on linguistic processing untainted of lexical concreteness. In a two-day training paradigm, we induced visual imageability by letting participants associate novel words with two qualitatively different kinds of pictures. In a post-training EEG session, which also entailed real concrete and abstract words, we replicated the classical CE for real word processing, with higher (i.e., more negative) N400 and N700 amplitudes for concrete than abstract words. In the early N700 time window (500–700 ms), concrete words elicited significantly more negative amplitudes at frontal and central, but more positive amplitudes at parietal electrode sites. In the late N700 time window (700–900 ms), the CE was modulated by the laterality, with a significant CE at right side and midline, but no significant CE at left side electrodes. Concerning the processing of the novel words, we did not find effects of imageability on N400 amplitudes when comparing novel words associated with pictures and familiarized novel words without any picture association. For the late N700 time window, we found an imageability effect: Novel words associated with pictures of novel objects elicited significantly more negative amplitudes at frontal and more positive amplitudes at parietal electrode sites than non-imageable novel words. The direction of this effect at frontal electrode sites is in line with the hypothesis that a higher imageability contributes to the real word CE at this later conceptual processing stage reflected by the higher N700, while the N400 CE might reflect the interaction of sensorimotor and lexically coded conceptual features.

The higher N400 and N700 amplitudes for concrete in comparison to abstract real words are in line with the well-known CE and underline the suitability of our paradigm to uncover such semantic processing differences. The classical view explains N400 and N700 CEs on the basis of the extended dual-coding theory, namely to reflect a reliance on more easily accessible and qualitatively different information when processing concrete as compared to abstract concepts [10,33]. The concrete words used in the present study were rated higher in concreteness, imageability and their association with action and perception than abstract words (see Table S1 in the Supplementary Materials). The rating scores thus suggest that concrete conceptual representations are based on multi-modal information experienced with the external bodily senses, in line with previous psycholinguistic studies [3]. Hence, stronger semantic integration processes might explain the N400 CE, and stronger mental imagery processes driven by integrated sensory information the N700 CE [35] in our study. We did not find a behavioral CE on error rates, but a dissociation of behavioral and electrophysiological CEs is known from previous literature [36].

In order to interpret the electrophysiological results for the novel word processing against the background of their visual imageability, the validity of the training paradigm has to be examined. The participants' performance in the assessed learning questionnaires suggests that the training paradigm successfully established an association between the novel words and the assigned pictures. Free reproduction as well as multiple-choice and picture assignment performance showed an increase over the sessions for all three novel word categories. The novel words associated with pictures in our study seem to have additionally profited from their induced imageability, as indicated by the Category × Session interaction effect on the percentage of correct free reproductions. This is in line with another word-learning study, which traced back a learning advantage for concrete over abstract words to a stronger activation in the ventral anterior fusiform gyrus, which is involved in higher order visual processing [55].

The training-induced visual imageability did not affect the N400 amplitudes elicited during the processing of the novel words in the EEG session. As the novel words' imageability arose from mere visual information, they lacked concreteness in terms of lexically and multi-modally coded information, which seems to be crucial for the N400 CE [35,42]. An alternative explanation might be that the imageability induced for novel words was not sufficiently consolidated to elicit N400 effects. Other word-learning studies did neither find word-like N400 effects after a short training [56] nor before a consolidation period [57], while later ERP effects were found. However, our study consisted of two training sessions on separate days before the EEG acquisition and should thus have provided a sufficiently long period for consolidation. In addition, our analyses were restricted to those words for which the training condition was correctly recognized after the EEG assessment. Furthermore, Palmer, Macgregor and Havelka [29] found an N400 CE for words with merely lexically acquired concreteness (associated to written definitions) at the very same day. Hence, our data can reasonably be interpreted as being consistent with the hypothesis that the N400 CE relies on the interaction of several semantic features, to which isolated visual imageability does not contribute autonomously.

In line with our hypothesis, we found an effect of the training-induced imageability on late N700 amplitudes. This effect interacted with the topographical factors. OPic words elicited a significantly higher late N700 amplitude than NoPic words at frontal electrode sites. Amplitudes elicited by SPic processing were descriptively between those for OPic and NoPic but did not differ significantly from either of them. Only at electrode sites over the right hemisphere, OPic words elicited higher late N700 amplitudes than both SPic and NoPic at trend level. In a recent study on single-word processing, N700 imageability effects only arose when both, the task and the stimuli, afforded them [35]. The N700 result for the real words employed in the present study appears to indicate that the chosen task was appropriate for eliciting imagery processes. Concerning the lateralization of the N700 CE, previous studies yielded inconsistent findings, with more pronounced CEs either over the left [35] or right hemisphere ([34], but at occipital electrode sites), or no laterality difference at all [36,51,52]. However, in our study, the lateralization is in line with the stronger right hemispheric late N700 CE found for real abstract and concrete words.

Our pattern of results for novel words might suggest that the qualitative differences between the two kinds of employed pictures caused the late N700 modulation. The novel object pictures showed unique manmade objects, which formed a distinct entity: this characteristic might underlie advantages in early learning of imageable words [16]. The electron-microscopical pictures, in turn, although also containing coherent elements, were more heterogeneous and clearly less tangible. A possible alternative explanation for the graded late N700 effects might be a systematically weaker association of SPic words with their pictures. This explanation, however, seems implausible regarding the comparable performance in learning of SPic and OPic words. Notably, the deflection in the late N700 time window was positive at parietal electrodes, possibly reflecting a late positive component (LPC), usually interpreted to stand for the recollection of individual experience in linguistic processing [58,59]. In a word-learning study employing an old/new task, LPC amplitudes elicited by novel words were even higher after a consolidation period, while amplitudes decreased for familiar words [60]. The authors suggest that conscious recognition favors novel word learning. In our study, the LPC pattern was also found with more positive early N700 amplitudes elicited by concrete compared to abstract word processing.

As both the frontal N700 and the parietal LPC were delayed for novel (late N700) compared to real word CE (early N700), this might suggest a functional dissociation within the N700 time window. The relatively later N700 modulations by the imageability of novel words in our study might be due to their novelty, which could have led to a delayed processing in comparison to familiar concrete and abstract words. Previous findings concerning the temporal dynamics of the N700 for familiar words, however, are inconsistent, with findings of early onsets around 500 ms (compare e.g., [35,51]) as well as relatively late onsets only after 700 ms (compare e.g., [36]). Thus, exploring the functional role of different stages of the N700 might be a promising approach for further research.

Findings of Barber, et al. [36] challenge the classical interpretation of the N400 and N700 CE. In their ERP study, they controlled for concrete and abstract words' imageability and other psycholinguistic variables that are known to lead to concrete word processing advantages (i.e., familiarity, age of acquisition and context availability) and still found higher N400 and N700 amplitudes for concrete words. They suggest that the CE in these two ERP components is rather modulated by the degree of multimodality inherent to the underlying conceptual information. Following this suggestion, the lacking effect of the novel word category on N400 amplitudes might be explained by the unimodal visual information the words received during the training. At a later stage of semantic processing, additional information arising from mental imagery might have been processed, leading to effects of the novel word category in the late N700 time window. The tangible appearance of the novel object pictures might have led to an impression of an affordance inherent to graspable objects [61,62] despite the lack of former experience with them. Linguistic processing might rely on this information [62,63], but rather at a later, more explicit processing stage, reflected by the N700.

In former studies, the electrophysiological CE could not easily be attributed to either the words' concreteness or imageability, as the two variables are highly correlated [3], and in most studies the terms were either used interchangeably or alone without controlling the other (for a counterexample see [36]). By modulating the visual imageability of former meaningless, novel words in a word learning paradigm, and thereby ruling out any possible confounds of word concreteness and other psycholinguistic variables, this study delivers insights into the isolated effect of words' imageability on linguistic processing. It seems that mere visual imageability plays a role at later explicit imagery processing stages (N700) but not in automatic semantic feature integration (N400). The effects in the N700 time window might also be explained by additional multi-modal information introduced by the novel object pictures and processed during mental imagery, which are not available at automatic stages of semantic processing.

Supplementary Materials: Supplementary materials can be found at http://www.mdpi.com/2227-9059/6/3/75/s1.

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Event-related desynchronization of mu and beta oscillations during the processing of novel tool names

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ABSTRACT

According to the embodied cognition framework, the formation of conceptual representations integrates the type of experience during learning. In this electroencephalographic study, we applied a linguistic variant of a training paradigm, in which participants learned to associate novel names to novel tools while either manipulating or visually exploring them. The analysis focused on event-related desynchronization (ERD) of oscillations in the mu and beta frequency range, which reflects activation of sensorimotor brain areas. After three training sessions, processing names of manipulated tools elicited a stronger ERD of the beta (18–25 Hz, 140–260 ms) and the lower mu rhythm (8–10 Hz, 320–440 ms) than processing names of visually explored tools, reflecting a possible reactivation of experiential sensorimotor information. Given the unexpected result that familiarized pseudo-words elicited an ERD comparable to names of manipulated tools, our findings could reflect a suppression of sensorimotor activity during the processing of objects with exclusively visual features.

1. Introduction

The semantic memory system contains our knowledge about the world. It provides the basis for many complex behaviors, from the categorization of stimuli to the communication with others. The neural underpinnings of semantic knowledge are still a matter of debate. Theoretical approaches range from amodal/symbolic (e.g. Fodor, 1975) to strongly embodied theories (Gallese & Lakoff, 2005; Glenberg, 1997; Glenberg & Kaschak, 2003). They form the extremes of a continuum of theoretical accounts, with the former postulating a complete independence, the latter a complete dependence of semantic processing on modality-specific systems (e.g. sensory but also motor and emotional; for reviews see Binder & Desai, 2011; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). According to more moderate accounts, semantic processing is associated with (Mahon & Caramazza, 2008; Patterson, Nestor, & Rogers, 2007) or partially relies on (Barsalou, 2008; Pulvermuller, 2001) modality-specific systems, in coordination with higher order convergence zones (Binder & Desai, 2011; Meteyard et al., 2012). The exact role of modality-specific systems, however, is still debated. The focus of the debate concerns the hypothesis put forward by embodied accounts that the representation and retrieval of semantic knowledge partially reactivates the respective modality-specific networks that were active during the original experience with the concepts' referents (Barsalou, 2008; Meteyard et al., 2012; Pulvermuller, 2001). Focusing on knowledge about manipulable objects such as tools, their function, manipulation, and motion can be considered as particularly relevant types of experiential information (Beauchamp & Martin, 2007), which are thus supposed to become an integral part of the tool concepts' neuronal representation (Kiefer & Pulvermuller, 2012).

The role of experience postulated by embodied cognition accounts has been supported by neuroimaging studies on conceptual processing of familiar tools. They revealed an activation of a left-hemispheric fronto-parietal network, which comprised, among others, action-related areas underlying object manipulation as well as areas subserving functional knowledge (Canessa et al., 2008; Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Dekker, Mareschal, Johnson, & Sereno, 2014; Devlin, Rushworth, & Matthews, 2005; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Perani et al., 1995; Simanova, Hagoort, Oostenveld, & van Gerven, 2014). Results were similar when conceptual representations were accessed either via tool pictures or tool names (for reviews see Cappa, 2008; Noppeney, 2008). Patients with lesions in this network were shown to be impaired in their ability to generate or imitate tool-directed movements (Buxbaum, Shapiro, & Coslett, 2014) and showed deficits in conceptual processing of action-features in an object identification task (Lee, Mirman, & Buxbaum, 2014).

The role of experience in acquiring and processing conceptual representations, however, can more directly be tested by applying

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training protocols on unfamiliar objects. In this case, concept acquisition takes place in a laboratory environment, and the modalities of experience can be experimentally controlled. Manipulation training studies showed an activation increase in a distinctive, action-related fronto-parietal network for processing pictures of knots (Cross et al., 2012) or novel tool-like objects (Bellebaum et al., 2013; Ruther, Tettamanti, Cappa, & Bellebaum, 2014; Weisberg, van Turennout, & Martin, 2007).

The timing of the recruitment of modality-specific brain regions is of particular importance in order to unravel the nature of their contribution to conceptual processing (Kiefer & Pulvermuller, 2012). Using electroencephalography (EEG) and familiar object concepts, object-category selective effects were seen between 110 and 250 ms after the presentation of words or pictures referring to tools vs. other objects in event-related potentials (ERPs; Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Proverbio, Adorni, & D'Aniello, 2011). In an extensive training study with novel objects and their names, the early P1 ERP component reflected a functional experience-dependent priming effect of object category names on the processing of pictures of novel objects already 117 ms after stimulus onset (Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007). In this study, a source analysis linked ERP components between 270 ms and 400 ms to the premotor cortex for categories defined by object function. ERP studies thus provided evidence of an early experience-dependent recruitment of motor areas during conceptual processing, suggesting that conceptual information is grounded in modality-specific regions (Kiefer & Pulvermuller, 2012).

An EEG-based measure often linked to the activation of (primary) sensorimotor areas is the suppression of the so-called mu rhythm in the alpha frequency range of 8–12 Hz and frequencies in the beta range of 13–35 Hz (Neuper, Wortz, & Pfurtscheller, 2006). The mu rhythm itself reflects an idling state of reduced activity of the sensorimotor cortex (Kuhlman, 1978) whereas the beta rhythm has been linked more closely to the primary motor cortex (Jasper & Penfield, 1949). Consequently, electro- and magnetoencephalographic studies showed that mu and beta rhythm suppression occurs before and/or during active movement (Chatrian, Petersen, & Lazarte, 1959; Pfurtscheller & Neuper, 1992; Pfurtscheller, Stancak, & Neuper, 1996; Salenius, Schnitzler, Salmelin, Jousmaki, & Hari, 1997). There is evidence that it also occurs during movement observation (Babiloni et al., 2002; Caetano, Jousmaki, & Hari, 2007), and movement imagination (Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006; Pfurtscheller & Neuper, 1997). Studies combining electrophysiological measures and functional magnetic resonance imaging could further show that the mu and beta frequency are inversely related to activation within sensorimotor and motor areas in movement execution and imagery (Bonstrup, Schulz, Feldheim, Hummel, & Gerloff, 2016; Formaggio, Storti, Cerini, Fiaschi, & Manganotti, 2010; Jancke, Lutz, & Koeneke, 2006; Pfurtscheller, 2001; Ritter, Moosmann, & Villringer, 2009; Yin, Liu, & Ding, 2016).

In the context of conceptual processing, the perception of familiar tool pictures (140 ms after stimulus onset) or reachable and graspable objects in a virtual reality environment (300 ms after stimulus onset) elicited a mu rhythm suppression (10–12 Hz in Proverbio (2012); 8–12 Hz in Wamain, Gabrielli, and Coello (2016), respectively). The perception of manipulable objects in different contexts elicited beta (12–16 Hz and 20–25 Hz) suppression in sensorimotor areas after 400–600 ms (Natraj et al., 2013). Further, the beta band (16–24 Hz) desynchronization differentiated between meaningful and meaningless object-directed movements (van Elk, van Schie, van den Heuvel, & Bekkering, 2010). Notably, action-related language processing also appears to recruit sensorimotor areas, as mu and beta frequencies were modulated within 500 ms after the stimulus presentation (Alemanno et al., 2012; Moreno, de Vega, & Leon, 2013; Moreno et al., 2015; Niccolai et al., 2014; van Elk, van Schie, Zwaan, & Bekkering, 2010; for a review on beta oscillations see Weiss & Mueller, 2012).

For experience-induced novel tool representations, effects on mu rhythm suppression have been found as well. Ruther, Brown, Klepp, and Bellebaum (2014) reported a stronger suppression during the processing of object pictures in the lower mu frequency band (8–10 Hz), which occurred over central electrodes after observational manipulation training as compared to visual exploration training. A potential criticism when using tool pictures as stimuli is that the visual input might prime actions afforded by the objects (e.g., Tucker & Ellis, 2004), especially as embodied conceptual action-information cannot be disentangled from affordances (Glenberg, 1997). To address this issue, the present study applied a linguistic variant of the training paradigm with novel tool-like objects (from now on referred to as tools; Bellebaum et al., 2013; Ruther, Brown, et al., 2014; Ruther, Tettamanti, et al., 2014). As described above, linguistic stimuli can indeed access conceptual representations of tools as well as action verbs in semantic memory, while their visual appearance does not carry any motor- or action-related information.

In this linguistic variant of the training paradigm, we let our participants form conceptual representations of novel tools through either active manipulation or visual experience. Meanwhile, they learned a pseudo-word assigned to each tool, which served as the tool's name. In a post-training EEG session, we applied a linguistic task to investigate whether the processing of the newly learned names recruits sensorimotor areas differentially, depending on whether the names referred to tools associated with either active manipulation or visual experience in the learning phase. In order to examine the time-course of the recruitment of sensorimotor areas in the processing of the novel tool names, we applied the event-related de-/synchronization method (ERD/ERS; Pfurtscheller & Lopes da Silva, 1999) on mu and beta frequency bands measured via EEG.

We hypothesized to find a stronger sensorimotor activation, reflected in mu and beta desynchronization, during the processing of names of actively manipulated tools compared to the names of tools that were only visually explored as well as to familiar pseudo-words without any object-association. For the mu frequency, we expected experience-dependent effects to occur especially in the lower range (8–10 Hz), which is thought to be less movement-type-specific than the upper range (10–12 Hz) (Pfurtscheller, Neuper, & Krausz, 2000), as the objects we used required different manipulations (see also Ruther, Brown, et al., 2014). For beta, we analyzed the 18–25 Hz beta frequency band since comparable ranges showed the strongest response in conceptual action-language processing (Moreno et al., 2013; Schaller, Weiss, & Muller, 2017; van Elk, van Schie, Zwaan, et al., 2010). Finally, the high temporal resolution of the ERD/ERS method is critical for assessing whether the recruitment occurs during early conceptual word processing or in a later, post-conceptual phase (according to embodied and disembodied theories, respectively; for a discussion, see Mahon & Caramazza, 2008). In addition, we considered also the temporal alignment of mu and beta effects. Sebastiani et al. (2014) showed a dissociation of these two frequency bands during action execution and observation and interpreted it in terms of different underlying motor-activation processes. The literature on action-language processing is contradictory with respect to the relative timing of mu and beta desynchronization (compare e.g. Niccolai et al., 2014; van Elk, van Schie, Zwaan, et al., 2010), so that this aspect was of particular interest for the present study.

2. Method

2.1. Participants

Twenty-three healthy German native speakers took part in this study. One participant had to be excluded from data analysis due to performance at chance level in the EEG task (mean accuracy = 48.2%). This resulted in a sample of 22 (six men) healthy young adults aged between 19 and 31 years (M = 23.3 years, SD = 3.7 years) without a history of psychiatric or neurological diseases. All participants reported to be right-handed, as indicated by the Edinburgh Handedness

Inventory (scores between 0.5 and 1, $M = 0.8$, $SD = 0.2$; Oldfield, 1971) and had normal or corrected-to-normal vision. All participants were students at the Heinrich Heine University, Düsseldorf, Germany.

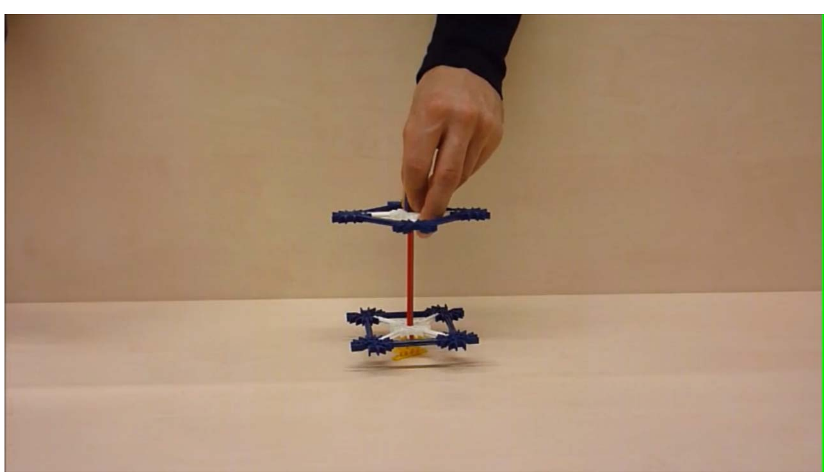
The study was approved by the ethics committee of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University and is in line with the declaration of Helsinki. All participants gave their written informed consent prior to participation, for which they received monetary compensation or course credit. The three participants with the best learning performance additionally received a 30 €-voucher for an internet-based retailer. This was announced to all participants prior to participation for motivational purposes.

2.2. Stimulus material

2.2.1. Novel tools

In the present study, we used 36 novel tools built of small pieces of different color and form taken from a construction toy (K'NEX™). The tools were the same as in previous training studies of our group (Bellebaum et al., 2013; Ghio, Schulze, Suchan, & Bellebaum, 2016; Ruther, Brown, et al., 2014; Ruther, Tettamanti, et al., 2014). Six tools each were associated with six different functions (transport, push, pull, move, separate, destroy), which could be performed on tool-specific small items (e.g., paper sheets, ping pong balls, plastic cups). The overall number of 36 tools was divided into three sets of 12 (two per function; for further details see Bellebaum et al., 2013).

For each tool, a video without verbal instructions showed one full manipulation of the tool, displaying the function performed on the respective small items (e.g., destroy a paper cup). In the videos, a male person demonstrated the tool manipulation on a wooden table desk in front of a wooden background. Only the manipulator's hands and forearms were visible and he wore a black long-arm shirt. The manipulator was standing opposite to the camera so that the observer of the video had the impression to be facing the manipulator (see Fig. 1A and Video V1 in the supplementary material). The video length varied with the complexity of the manipulation from 17 to 47 s, and mean length did not differ significantly between the three sets ($M_{Set1} = 27.8$ s, $SD_{Set1} = 6.9$ s; $M_{Set2} = 25.9$ s, $SD_{Set2} = 5.9$ s; $M_{Set3} = 27.8$ s, $SD_{Set3} = 8.4$ s), as revealed by a Kruskal-Wallis-test for independent samples, $H(2) = 0.166$, $p = .920$.



Video V1.

2.2.2. Novel tool names

Each tool received a specific novel name. The 36 tool names were pseudo-words constructed from two- or three-syllabic real German nouns by exchanging two to three letters, in accordance with phonetical rules (e.g., Neribon, Wechir, Erfonk). The tool names for the three different sets were balanced for the mean number of letters ($M_{Set1} = 7.6$, $SD_{Set1} = 1.1$; $M_{Set2} = 7.7$, $SD_{Set2} = 0.8$; $M_{Set3} = 7.8$, $SD_{Set3} = 0.7$; Kruskal-Wallis-test for independent samples, $H(2) = 0.429$, $p = .807$), and syllables ($M_{Set1} = 2.5$, $SD_{Set1} = 0.5$; $M_{Set2} = 2.5$, $SD_{Set2} = 0.5$; $M_{Set3} = 2.6$, $SD_{Set3} = 0.5$; Kruskal-Wallis-test for independent samples, $H(2) = 0.217$, $p = .897$).

2.3. Training protocol and experimental task

2.3.1. General procedure

We trained participants not only by having them manipulate one set of tools and visually explore a second set (see previous studies by Bellebaum et al. (2013), Ruther, Brown, et al. (2014), Ruther, Tettamanti, et al. (2014)) but also learning the name of each tool. This allowed us to examine the effects of visual vs. active manipulation training on the processing of the newly learned tool names, which were presented in written form on a computer screen in a post-training experimental EEG task (see Section 2.3.3).

Overall, the procedure for every participant consisted of three training sessions with the novel tools and their novel names, and a subsequent EEG recording session (see Fig. 1B). All sessions took place on separate days, with a mean of 2.0 nights ($SD = 1.2$) between the single sessions. The trainings and the EEG recording took place in the Department of Biological Psychology at Heinrich Heine University Düsseldorf. Each of the training sessions, which were all conducted with one participant at a time, consisted of two tool-related training conditions: active manipulation (ACT), and visual exploration (VIS) training. For ACT and VIS, participants learned the specific tool-name associations and details about tools for one set each, that is, two times 12 tools (see Section 2.3.2). As an additional condition, a pseudo-word familiarization training (PSEUDO) was included, in which participants learned the 12 remaining pseudo-words associated with the tools of the third set without seeing or interacting with the tools and without learning any tool-name associations. The subjects were not informed that the words in this training condition belonged to a third set of tools. Each training session ended with a check of the learning performance concerning the names (see Section 2.3.4 for a detailed description). All subjects went through all three training conditions in a within-subject design. The assignment of the three tool/pseudo-word sets to the three training conditions (ACT, VIS, PSEUDO) was counterbalanced between participants and held constant across the training sessions for each participant. In addition, the order of the training conditions, which were conducted in blocks, was counterbalanced between participants and held constant in all three training sessions for each participant as well. Finally, the order of presented tools/words within each training condition was determined randomly for each participant and training session.

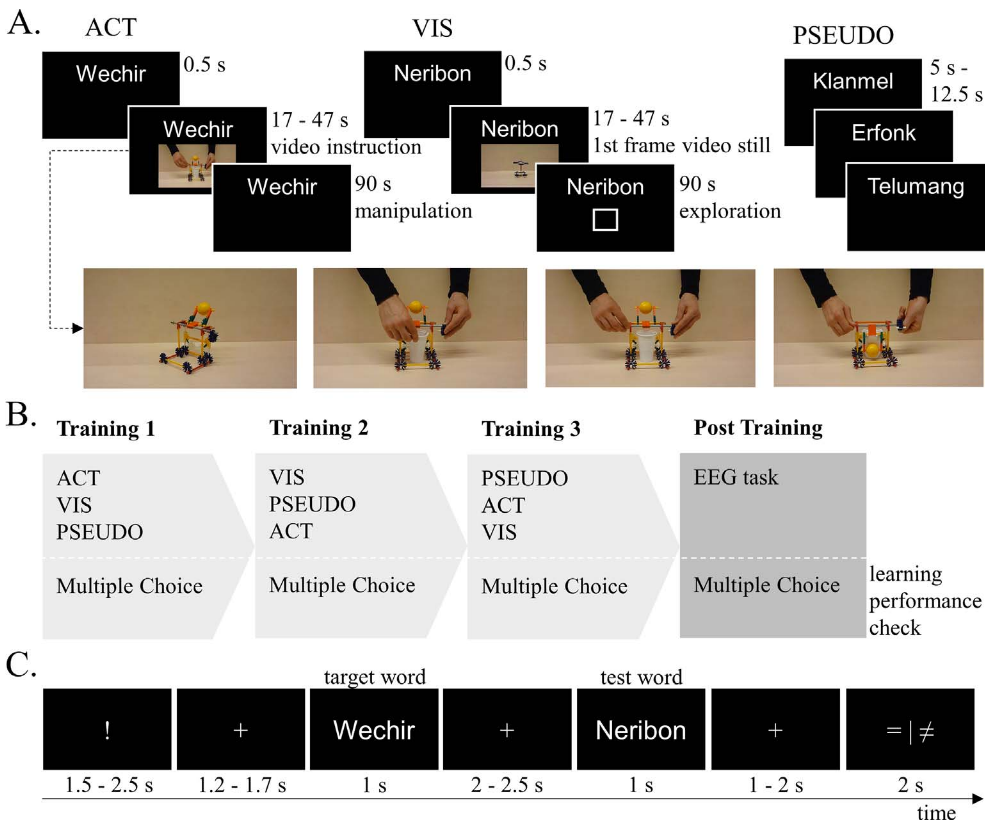


Fig. 1. A. Time course of the three training conditions (ACTive manipulation, VISual exploration and PSEUDO words), and four frames of an exemplary video instruction. B. Overview of the general training procedure with three training sessions, a post-training EEG measurement and checks of the learning performance. C. Exact timing of one trial of the EEG task. Variable intervals were randomly jittered within the depicted temporal ranges.

2.3.2. Training protocol

PsychoPy (version 1.81.03; Peirce, 2007) controlled the presentation of the training protocol on a Windows 10 Intel Premium PC with an internal graphics card and a 27’ Ben Q LED monitor with 1920 × 1080 pixel resolution and a refresh rate of 60 Hz.

In the ACT training condition (see Fig. 1A, left), the tool name appeared first in white letters on a black background at the top of the screen. Participants read out the name aloud as soon as it appeared. This was done to focus their attention on the name they were asked to associate with the upcoming tool. After 500 ms, the video of the respective tool started automatically, serving as a standardized nonverbal instruction on tool manipulation (see also Section 2.2.1). As soon as the video ended, the experimenter placed the respective tool in front of the participant. From then on, participants were asked to manipulate the tool for 90 s as shown in the video. The experimenter corrected the manipulation if necessary. For manipulations where the associated small items were moved, transported, tagged or pushed, a start and end point of the movement was marked on the table. Participants moved (pushed, etc.) the small items from start to end and back, until the time was over. An automatic beep tone and the written request to stop the manipulation marked the end of the 90 s manipulation time. The ACT training took about 25 min to complete.

The VIS training had the same timing as the ACT training (see Fig. 1A, middle). As in the ACT training, the name appeared at the top of the screen 500 ms before a tool was presented, and participants read the name aloud. Crucially, instead of a video displaying the tool specific manipulation, a still picture of the first frame of the video displaying solely the tool placed on a table was shown. It stayed on screen for the length of the manipulation video of the respective tool. The experimenter then placed the tool on the table in front of the participant for the visual exploration phase, but the participant was not allowed to touch or manipulate the tool. The first 15 s of the 90 s exploration duration were free exploration time. Then five pictorial instructions appeared on the screen, one at a time and each for 15 s, to guide the participant’s exploration. Each pictorial instruction (e.g., blue icon) indicated to the participants to look for the frequency of occurrence of a particular piece that the tools were built of (e.g., how many blue pieces are within the tool). Overall, there were 15 different pictorial instructions used during the training: eight different colors (blue, green, grey, orange, red, violet, white, yellow), four different forms (circle, line, rectangle, polyangle) and three different angles (bigger, smaller and equal to 90°). Each pictorial instruction appeared once per tool over the three training sessions. After the 90 s exploration time, an automatic beep tone and the written request to stop the exploration ended the exploration time. The VIS training also took about 25 min to complete.

In the PSEUDO training, participants were only presented with the names (i.e., pseudo-words, see Fig. 1A, right) of the non-used third set of tools (see Section 2.2.1). Each pseudo-word was presented four times on the screen, with different presentation durations (5, 7.5, 10, and 12.5 s, respectively) in a randomized order. As the participants did not have any additional task in the PSEUDO condition and could solely focus on the written tool name, we decided not to keep the timing of the PSEUDO condition parallel to the other two but chose shorter presentation times with more repetitions. Participants again read the word aloud and pressed the space bar as soon as a new word appeared to make sure they paid attention. Between the words, a 500 ms blank screen appeared. The PSEUDO training took about eight minutes to complete. The PSEUDO condition served mainly as a behavioral control condition in the post-training EEG task, indicating the participants’ ability to distinguish between tool-related and other familiar pseudo-words (see Section 2.3.3 for details of the task).

2.3.3. EEG task

After the training period, participants engaged in an experimental task, which required the processing of the words from the three training sessions while their brain activity was recorded with EEG. Each trial started with a fixation cross for a variable duration between 1.2 s and 1.7 s. Subsequently, a target word from one of the three training conditions was presented for one second. Then for another variable interval of 2–2.5 s a fixation cross came on, before a test word was presented for one second and a final variable interval (1–2 s) with a fixation cross followed. At the end of the trial, subjects had to decide whether the two words were taken from the same or two different training conditions by pressing the left or right Ctrl-button (see Fig. 1C for the sequence of events in one trial). The inter-trial interval showed an exclamation mark and varied between 1.5 and 2.5 s. The durations of all variable intervals were jittered randomly within the indicated ranges. Only EEG data following the target word of each trial were included in the analysis. The 12 ACT, 12 VIS, and 12 PSEUDO words were presented six times each, three times as target and three times as test word, respectively. This resulted in 108 trials, with 36 target word presentations per training condition. The same word never appeared twice within one trial. Additionally, the ratio of same:different training condition pairs was 1:2. Apart from those restrictions, the order of presentation of the experimental trials was randomly generated for each participant. The button assignment to the same (=) or different (≠) training conditions was varied and occurred at the end of every trial by presenting an answer screen with the same/different button assignment (Fig. 1C). Participants kept their left and right index fingers on the buttons in order to reduce movement artifacts. There was a break of self-determined length every 20 trials.

2.3.4. Assessment of learning performance

After each training and the EEG session, a multiple-choice recognition questionnaire assessed the learning of the association between each word and its training condition. This test consisted of all pseudo-words/names in a random order. Participants were asked to assign each word to one of the training conditions (ACT, VIS, and PSEUDO, respectively) in a forced-choice task. The multiple-choice questionnaire existed in four different versions, varying the order of the appearance of the different words between the four assessments per subject.

2.3.5. EEG recording

The EEG data acquisition was conducted with an actiCap (Brainproducts GmbH, Germany) textile softcap with pre-mounted electrode holders based on the extended 10–20 system (Chatrian, Lettich, & Nelson, 1985). Scalp potentials were recorded via 28 Ag/AgCl electrodes and a BrainAmp DC amplifier. The ground electrode was attached to the AFz position, the online reference to FCz. Four electrodes monitored eye movements: two at the outer canthi of the eyes and one above and below the left eye respectively. The other electrode positions were: F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, and PO10. A Windows 10 Dell Intel Premium PC recorded the EEG data using the Brain Vision Recorder software (version 1.20.0506, Brain Products GmbH, Germany) with a sampling rate of 1000 Hz and an online lowpass filter of 100 Hz. Impedances were kept below 15 kΩ. The software Presentation (version 17.0, Neurobehavioral Systems Inc., Albany, CA, USA) controlled the timing of stimulation and the recording of responses during the EEG task on a Windows 10 Dell Intel Premium PC with a 22″ LED Dell monitor with 1680 ∗ 1050 pixel resolution and a refresh rate of 60 Hz. Responses were given via a Microsoft USB keyboard.

2.4. Data analysis

2.4.1. Behavioral data

Behavioral data were obtained in the learning phase and during the EEG task. They were analyzed by means of different repeated measures ANOVAs (for details see below). In case sphericity was violated, the Greenhouse-Geisser correction method was applied. For all post hoc tests, Bonferroni correction was applied.

2.4.1.1. Learning performance. In the multiple-choice questionnaire, participants could reach a maximum score of 36 points, one point for each correct answer. Absolute values were transformed into percentage-correct values for the performance after each of the three training sessions and after the EEG session. A repeated measures ANOVA with the four-level factor Session (three training sessions and one EEG session) and the three-level factor Training (ACT, VIS, PSEUDO) compared the accuracy in the multiple-choice learning performance over the course of the study and between training conditions.

2.4.1.2. EEG task. For the description of the behavioral data of the EEG task, we excluded trials without response (1% of the data). For the remaining trials, percentage accuracy as well as mean reaction times were calculated as overall descriptive performance measures. Effects of training condition on task performance could only be analyzed for those trials, in which both stimuli were from the same condition. For these trials, repeated measures ANOVAs with the factor Training (ACT, VIS, PSEUDO) were performed on accuracy and reaction times.

2.4.2. EEG data

2.4.2.1. Data preprocessing. Data from all scalp recording sites including the online reference FCz were re-referenced to the average of the scalp electrodes. Data for channel FCz were reconstructed. Then data underwent a global direct current detrend to correct for direct current drift artifacts (Hennighausen, Heil, & Rosler, 1993). A low cutoff filter of 0.53 Hz (time constant 0.3) with 12 dB/Oct, a high cutoff filter of 30 Hz with 24 dB/Oct, and a 50 Hz notch-filter were applied. After a fast ICA on an excerpt of 120 s of the continuous EEG data, we detected one component reflecting eye blinks and eliminated it from the data via ICA back transformation. Data were segmented into epochs of 6 s length, from 3 s before to 3 s after the onset of the target word. We chose this length in order to be able to cut out filtering artifacts at the edges after the sharp and narrow bandpass filtering for the ERD/ERS analysis (see Section 2.4.2.2). Segments were baseline corrected relative to the signal between −300 ms and 0 ms relative to the target word. A time window of 1300 ms pre- to 1600 ms post-stimulus was then inspected for non-physiological and muscle artifacts with the following parameters: 70 μV/ms maximal allowed voltage step, 200 μV maximal allowed difference of values within 200 ms intervals, maximal/minimal allowed amplitude of ± 150 μV, minimum activity of 0.1 μV within 100 ms intervals. These analysis steps were carried out on 27 electrodes, as T7 and T8 were excluded from further analyses due to frequent muscle artifacts. Moreover, for each participant individually, we only considered those trials in which the presented target word was assigned to the correct training condition in the multiple-choice questionnaire after the EEG session. After artifact rejection and the exclusion of non-learned stimuli, the mean number of trials entering analyses was 30.5 (SD = 5.5), 29.3 (SD = 6.7) and 33.3 (SD = 3.6) for ACT, VIS, and PSEUDO condition, respectively. The number of trials differed significantly between conditions, $F(2, 42) = 5.404$, $p = .008$, $\eta_p^2 = 0.205$, with more trials in the PSEUDO than in both the ACT ($p = .040$) and VIS ($p = .028$) condition.

2.4.2.2. ERD/ERS data analysis. For the ERD/ERS analysis, data were bandpass filtered with a Butterworth Zero Phase Filter, separately for the frequency ranges between 8 and 10 Hz (lower mu), 10–12 Hz (upper mu) and 18–25 Hz (beta) with 48 dB/Oct. Separately for each training condition, ERD/ERS was calculated as a percentage signal change after stimulus onset compared to a −1200 ms to −200 ms pre stimulus reference interval with the inter-trial variance method and subsequent averaging over all trials within one condition (Kalcher & Pfurtscheller, 1995). Positive values indicate a synchronization, negative values a desynchronization of the analyzed frequency band, following the formula $ERD\% = [(A - R)/R] * 100$ (with A = the active interval and R = reference interval; Pfurtscheller, 2001). Data were smoothed with a moving average using a time window of 126 ms (Ruther, Brown, et al., 2014).

The averaged and smoothed ERD/ERS data for learned target words from the ACT, VIS and PSEUDO training condition were exported from Brain Vision Analyzer and all further analysis steps were conducted using Matlab (version R2015a) and the Matlab-based toolbox FieldTrip (version 20170601, www.fieldtriptoolbox.org; Oostenveld, Fries, Maris, & Schoffelen, 2011). The statistical test described in the following was applied separately for the lower and upper mu and the beta rhythm. To test for statistical differences between conditions, we applied a nonparametric cluster-based randomization test for all the time-electrode samples of interest, comparing always two conditions at a time (Lange, Christian, & Schnitzler, 2013; Maris & Oostenveld, 2007; Pavlidou, Schnitzler, & Lange, 2014b). Based on this procedure, we first compared the ACT and VIS conditions in order to assess modality-specific, training-induced effects. This comparison allowed us to address the main experimental question, i.e. whether the processing of the newly learned names referring to tools associated with active manipulation versus visual exploration experience differentially modulates the activity in sensorimotor areas. Furthermore, for comparing the processing of the newly acquired tool names with processing pseudo-words that were similarly familiar, we carried out two additional pair-wise comparisons, namely ACT versus PSEUDO, and VIS versus PSEUDO. Prior to statistical testing, data were downsampled to 50 Hz in order to reduce the number of samples that went into the cluster based permutation analysis. Precision in the frequency domain is inversely related to precision in the time domain. Filtering can lead to a temporal smearing in the range of tens of milliseconds (Rousselet, 2012; Vanrullen, 2011; Widmann & Schroger, 2012). Applying the cluster statistics on the data with the original sampling rate might thus lead to an overestimation of temporal precision. The temporal resolution of 50 Hz after downsampling is still far better than the resolution of functional neuroimaging methods and can provide a valid measure of the onset of effects in certain frequency ranges (see Richter, Babo-Rebelo, Schwartz, & Tallon-Baudry, 2017 for a recent example of downsampling EEG data for the purpose of frequency analyses).

The analysis comparing ERD/ERS values consisted of two steps: In the first step, we compared neuronal activity in two conditions by means of a dependent-samples *t*-test. This test was performed independently for each time sample (0–1000 ms) and electrode, resulting in a *t*- and *p*-value for each time and electrode sample. In the second step, we performed a nonparametric randomization test to identify time-electrode clusters showing similar effects. Uncorrected *p*-values of the independent-samples *t*-test (see above) were thresholded at $p < .05$ and spatially and temporally neighboring samples fulfilling the threshold criterion were combined to a cluster, but only if at least two neighboring electrodes fulfilled this threshold criterion. While neighboring time points were defined on temporal adjacency, neighboring

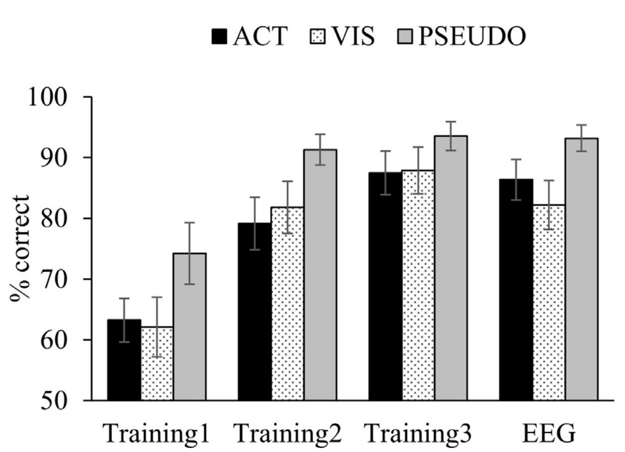


Fig. 2. Mean accuracy (%) in the multiple-choice learning performance checks after the three training sessions and the EEG session for each training condition (ACTive manipulation, VISual exploration and PSEUDO words) separately. Error bars represent ± one *SE*.

electrodes were defined on spatial adjacency (neighboring distance of 0.225 a.u. in FieldTrip, resulting in two to nine neighboring electrodes per electrode, $M = 5.2$, $SD = 2.1$). To determine neighboring electrodes, we applied the acticap-64ch-standard2.mat 2D template layout (Fieldtrip, version 20170601). Next, *t*-values of all samples in a cluster were summed up and used as the test distribution for the second-level cluster statistic.

To create a reference distribution, we randomly permuted the data of the two conditions and repeated the steps above. This process was repeated 1000 times. Finally, test and reference distributions were used to estimate a *p*-value for each cluster (two-sided test). This permutation analysis avoids the multiple comparisons problem of spatiotemporal samples while having a higher sensitivity than conservative Bonferroni corrected alpha-levels (Maris & Oostenveld, 2007). Importantly, this approach does not rely on a priori selection of electrodes.

3. Results

3.1. Behavioral data

3.1.1. Learning performance

Fig. 2 shows the multiple-choice learning performance for all four sessions and training conditions. The repeated measures ANOVA revealed a main effect of Session, $F(1.925,40.434) = 28.431$, $p < .001$, $\eta_p^2 = 0.575$. Post-hoc tests revealed a significant increase in the percentage of correct responses from the first to the second training session, $p < .001$. From the second to the third training session as well as from the third training session to the EEG session there were no significant changes of performance (both $p > .160$). The Training condition had a significant effect on the learning performance as well, $F(2,42) = 8.712$, $p = .001$, $\eta_p^2 = 0.293$. Pairwise comparisons showed that learning performance for ACT and VIS did not differ significantly, $p = 1$. The Training effect was instead driven by a significantly higher performance in the PSEUDO condition compared to ACT and VIS, $p = .003$ and $p = .008$, respectively. This pattern was consistent over all the sessions, as indicated by a non-significant Session by Training interaction, $F(3.219,67.599) = 0.795$, $p = .509$, $\eta_p^2 = 0.036$.

3.1.2. EEG task

On average, participants reached an accuracy level of 84.6% ($SD = 10.8\%$) in the EEG task. Mean reaction times across trials were 666 ms ($SD = 104$ ms). Considering only those trials with two words from the same condition (see Section 2.4.1.2 EEG Task), accuracy levels did not differ significantly between ACT ($M = 80.1\%$, $SD = 20.9\%$), VIS ($M = 80.2\%$, $SD = 19.0\%$) and PSEUDO ($M = 84.2\%$, $SD = 19.3\%$), $F(2, 42) = 0.448$, $p = .642$, $\eta_p^2 = 0.021$. However, the Training condition did have a significant effect on reaction times, $F(2, 42) = 4.257$, $p = .021$, $\eta_p^2 = 0.169$. Pairwise comparisons revealed significantly faster reaction times for PSEUDO ($M = 621$ ms, $SD = 23$ ms) compared to ACT ($M = 678$ ms, $SD = 26$ ms), $p = .030$, whereas the comparisons between PSEUDO and VIS ($M = 661$ ms, $SD = 26$ ms), $p = .140$, and between VIS and ACT were not significant, $p = 1$.

3.2. ERD/ERS data

Fig. 3 shows the time course of ERD/ERS for words from all three conditions pooled over the representative electrode sites F3, Fz, F4, FC1, FCz, FC2, C3, Cz and C4 for the lower (A) and upper mu (B) and the beta rhythm (C). Grand averages for all conditions and frequency bands separately for each of the mentioned electrode sites are provided in the supplementary material.

3.2.1. ACT vs. VIS

The processing of ACT tool names elicited a significantly stronger 8–10 Hz mu ERD compared to VIS in a cluster ranging from 320 ms to

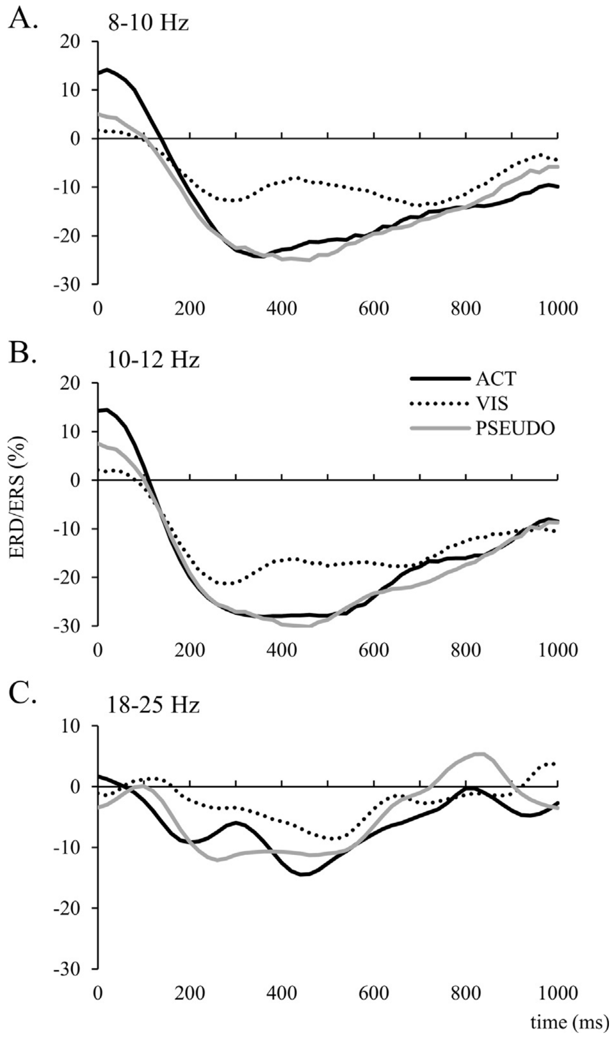


Fig. 3. Time course of ERD/ERS elicited by the processing of tool names from ACTive manipulation, VISual exploration training and PSEUDO words, pooled over the electrode sites F3, Fz, F4, FC1, FCz, FC2, C3, Cz and C4. A. ERD/ERS of the lower mu (8–10 Hz), B. of the upper mu (10–12 Hz) and C. of the beta (18–25 Hz) frequency band.

440 ms, $p = .038$. The cluster comprised bilateral fronto-central electrodes (F3, Fz, FC1, FCz, C3, Cz, C4, CP2). Fig. 4A shows the topographical development of the cluster over time. The mean ERD elicited by ACT name processing in this spatiotemporal cluster was −23.7% (SD = 20.7%). Mean ERD elicited by VIS name processing was −9.8% (SD = 26.4%). Fig. 4B shows the temporal development of the ERD/ERS, pooled across all electrodes of the cluster.

The comparison of ACT and VIS tool name processing in the 10–12 Hz mu frequency band did not yield any significant differences.

The processing of ACT tool names elicited a stronger 18–25 Hz beta ERD compared to VIS between 140 ms and 260 ms, $p = .023$, in a fronto-central cluster (Fz, FC1, FCz, FC2). Fig. 4C shows the topographical development of the cluster over time. Mean ERD elicited by ACT name processing in this spatiotemporal cluster was −10.7% (SD = 16.7%). Mean ERD elicited by VIS name processing was 1.4% (SD = 15.4%). Fig. 4D shows the temporal development of the ERD/ERS, pooled across all electrodes of the cluster.

3.2.2. ACT vs. PSEUDO

The comparison between ACT and PSEUDO ERD/ERS did not reveal any clusters with significant differences in any of the examined frequency bands (see Fig. 3).

3.2.3. VIS vs. PSEUDO

PSEUDO words elicited a significantly higher ERD than VIS tool names in the lower (8–10 Hz) and upper (10–12 Hz) mu rhythm band, $p = .028$ and $p = .037$, respectively. In both frequency bands, the time window of the cluster ranged from 360 ms to 520 ms. Fig. 5A shows the topographical development over time of the cluster in the lower, 8–10 Hz mu rhythm, which consisted of nine fronto-centro-parietal electrodes (F3, Fz, FC1, FCz, FC2, Cz, C4, CP2, Pz). Mean ERD elicited by PSEUDO word processing in this spatiotemporal cluster amounted to −27.0% (SD = 18.7%), mean ERD elicited by VIS name processing was −12.0% (SD = 27.2%). Fig. 5C shows the topographical development over time of the cluster in the upper, 10–12 Hz mu rhythm, which consisted of six fronto-central electrodes (F3, Fz, F4, FC1, FCz, Cz). In this spatiotemporal cluster, mean ERD for PSEUDO was −32.0% (SD = 20.4%), and mean ERD for VIS was −15.7% (SD = 33.0%). Fig. 5B and 5D show the temporal development of the ERD/ERS in, respectively, the lower and upper mu rhythm, pooled across all electrodes of the respective clusters.

The comparison between VIS and PSEUDO 18–25 Hz beta ERD/ERS did not reveal any clusters with significant differences.

4. Discussion

To examine the role of active manipulation experience in shaping conceptual tool representations we set up a linguistic variant of a previously applied training paradigm with novel tool-like objects (e.g. Bellebaum et al., 2013). In this variant, participants learned the names of the novel tools while actively manipulating (ACT) or visually exploring (VIS) them. In a post-training EEG session, the novel tool names were used as stimuli in a linguistic task. Results revealed that, although the learning performance was comparable for ACT and VIS tool names, the processing of ACT tool names elicited a significantly stronger ERD in the beta band at frontal and fronto-central electrode sites between 140 and 260 ms after word presentation. This effect was followed by a significantly stronger ERD of the lower mu band (8–10 Hz) at frontal to centro-parietal electrodes between 320 and 440 ms. Unexpectedly, the processing of the ACT tool names and of familiarized pseudo-words (PSEUDO) elicited comparably strong ERDs in all frequency bands. PSEUDO also elicited a stronger ERD compared to VIS in the lower and upper mu rhythm bands at fronto-centro-parietal electrodes between 360 and 520 ms.

The linguistic variant of the training paradigm provides the possibility to interpret the modulation of the cortical motor activity during the linguistic processing of ACT versus VIS names as a result of the learning experience (see also Fargier et al., 2012). Indeed, ACT and VIS names were identical in all respects but the type of associated learning experience, namely manipulation vs. visual. Both the beta and mu desynchronization have previously been linked to activity in sensorimotor cortex areas, with which the frontal and fronto-central topographies of our effects are compatible. Following the rationale of embodied semantics, the activation of sensorimotor areas for semantic processing of the ACT names might be interpreted as reflecting the reactivation of active manipulation experience gained during concept acquisition. In this sense, our results are consistent with previous findings of sensorimotor activations for post-training processing of pictorial stimuli associated with action/manipulation experience (Bellebaum et al., 2013; Cross et al., 2012; Kiefer et al., 2007; Ruther, Brown, et al., 2014; Ruther, Tettamanti, et al., 2014; Weisberg et al., 2007). Given the arbitrary relationship between the visual form of the linguistic stimuli and the tools they refer to, we extend previous training studies by showing that such activations are not entirely determined by object affordances elicited by an object's picture.

Our findings concerning the lower mu rhythm for processing tool names (i.e. nouns) complement another training study with novel verbal stimuli associated with movements vs. images. Fargier et al. (2012) showed experience-dependent sensorimotor reactivation in form

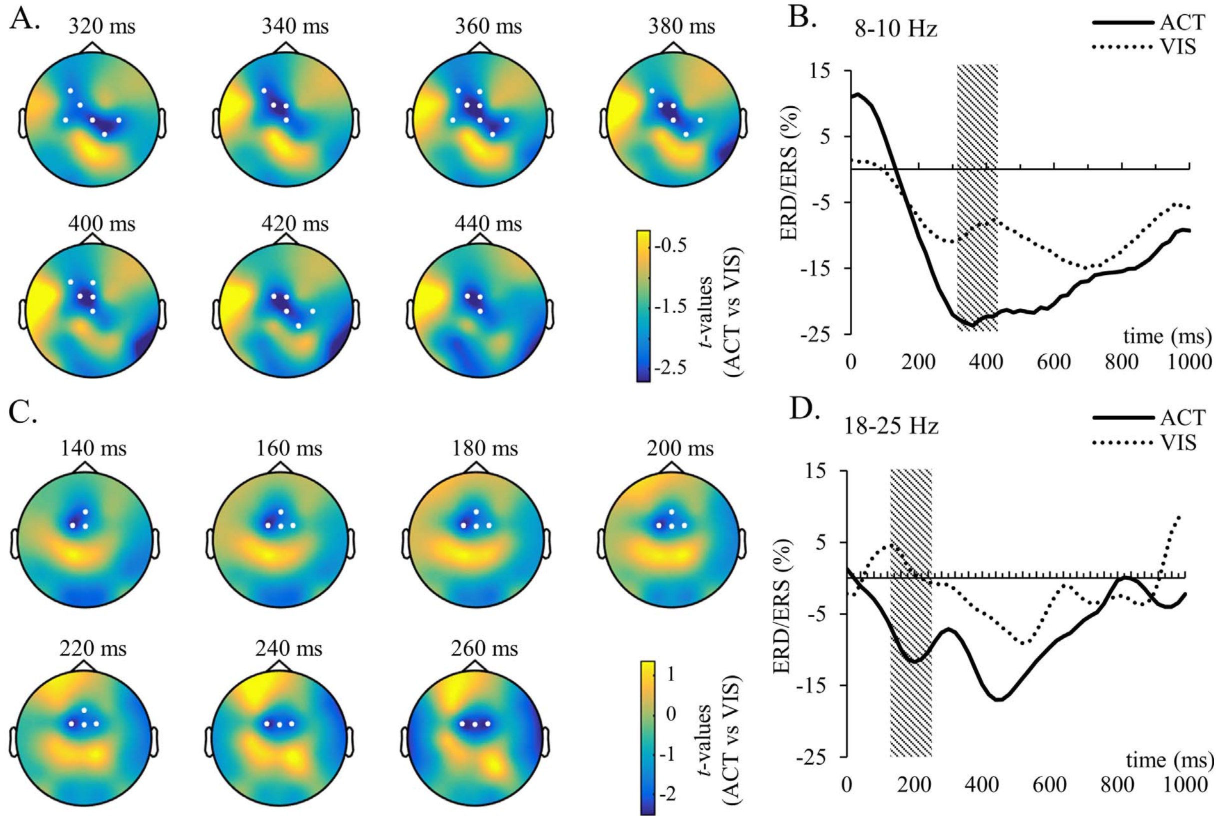


Fig. 4. Results for the comparison of ERD/ERS elicited by the processing of tool names from ACTive manipulation and VISual exploration training. A. and C. show the time series of topographical representations of *t*-values for the lower mu (8–10 Hz), the beta frequency band (18–25 Hz), respectively. Electrodes of the cluster are marked by white dots. B. and D. show the mean ERD/ERS averaged across electrodes of the cluster in the 8–10 Hz, and the 18–25 Hz frequency band, respectively. Shaded areas mark time points of the cluster with significant differences.

of a desynchronization of frequencies between 8 and 12 Hz. In a follow-up study, Fargier et al. (2014) showed that the processing differences were caused by the newly established word-referent association already after a few hours of training.

In addition to the analysis of the mu rhythm we also analyzed the beta frequency band. While the rolandic mu rhythm in the alpha range arises from sensorimotor as well as somatosensory areas, the source of beta oscillations is thought to be restricted to primary and supplementary motor areas (Ritter et al., 2009). Furthermore, during movement perception, beta modulations in sensorimotor areas seem to play a role in accessing internal movement representations (Pavlidou, Schnitzler, & Lange, 2014a). They are sensitive to plausibility during action processing (Pavlidou et al., 2014b) and seem to mediate between visual and sensorimotor areas, where internal representations are stored (Lange, Pavlidou, & Schnitzler, 2015; Pavlidou, Schnitzler, & Lange, 2014c; Tucciarelli, Turella, Oosterhof, Weisz, & Lingnau, 2015). Thus, the beta desynchronization elicited by the processing of ACT names with active manipulation experience in our study could reflect a matching process with internal movement representations.

As outlined in the Introduction, the timing of sensorimotor activation in the processing of stimuli referring to entities in semantic memory provides an important hint on its functional significance. Theoretical frameworks postulate a time window of up to 500 ms for language comprehension (Bastiaansen & Hagoort, 2006), with some suggesting a very fast and thus automatic sensorimotor information access within 100–250 ms after the linguistic stimulus is presented (Pulvermuller, Shtyrov, & Hauk, 2009). Such early time ranges are thought to represent a sensorimotor contribution to conceptual processing (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006; Hauk, Shtyrov, & Pulvermuller, 2008). Previous studies on mu and beta desynchronization during the processing of linguistic stimuli are rather inconsistent with regard to the temporal dynamics. Mu desynchronization for action language processing has been found as early as ~160 ms after word onset (van Elk, van Schie, Zwaan, et al., 2010), peaking at later processing stages between about 540 and 640 ms (Alemanno et al., 2012). Interestingly, the latency of the effect we found in the lower mu band (320–440 ms) is consistent with the study by Fargier et al. (2012), in which processing novel words with acquired movement associations elicited an 8–12 Hz mu ERD between 300 and 450 ms after word onset. This latency, however, is delayed as compared to the ERD evoked by familiar and novel tool pictures (within 200 ms; Proverbio, 2012; Ruther, Brown, et al., 2014). One potential explanation is related to the use of linguistic rather than pictorial stimuli. Also in ERP studies with familiar stimulus material, picture presentation resulted in earlier processing differences between conditions than word processing (200–300 ms; Hauk et al., 2008). Alternatively, the temporally delayed mu ERD could partly reflect attentional and memory mechanisms of language processing (Bastiaansen & Hagoort, 2006; Schaller et al., 2017). Effects in temporal ranges as they occurred in the current study for the beta oscillations have been found for processing hand-related verbs in a study by Niccolai et al. (2014; around ~200 ms after stimulus onset). These early effects have usually been linked to automatic recruitment of motor regions for conceptual processing (Hauk et al., 2006, 2008).

The temporally differential involvement of the mu and beta oscillations is an especially interesting point of our findings. As described in the Introduction, mu and beta rhythms go hand in hand in action execution, observation and imagery. Also in action language processing, the modulations of mu and beta have been interpreted as reflecting the same processes (Moreno et al., 2013). However, Sebastiani et al. (2014) could show that in action observation (as compared to action execution), the temporospatial dynamics of the two frequency ranges are

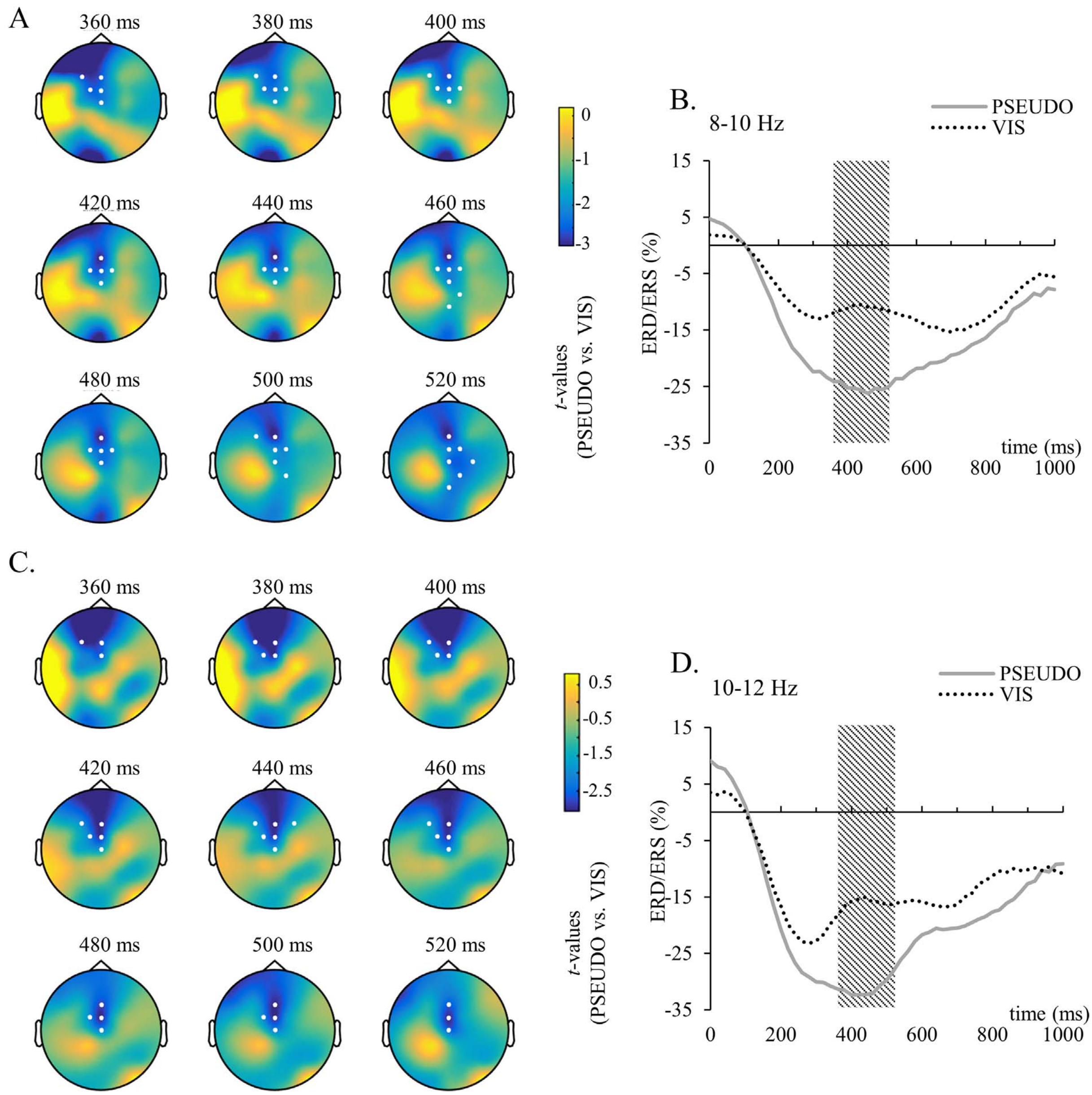


Fig. 5. Results for the comparison of ERD/ERS elicited by the processing of PSEUDO words and tool names from VISual exploration training. A. and C. show the time series of topographical representations of *t*-values for the lower (8–10 Hz) and upper (10–12 Hz) mu frequency band, respectively. Electrodes of the cluster are marked by white dots. B. and D. show the mean ERD/ERS averaged across electrodes of the cluster in the 8–10 Hz and 10–12 Hz frequency band, respectively. Shaded areas mark time points of the cluster with significant differences.

dissociable. The authors conclude that mu and beta frequencies play a different functional role in signal conduction during the perception and concomitant generation of motoric actions, with beta being more strongly involved in the matching of perception and prediction during movement observation. It remains unclear, in how far these results can be transferred to language processing. Supporting evidence for different processes underlying mu and beta modulations arose from two studies, which revealed different temporal dynamics in the two frequency ranges during conceptual language processing. For verbs embedded in sentences van Elk, van Schie, Zwaan, et al. (2010) found a mu ERD (~160 ms) followed by a beta ERD (~500–600 ms). For single grasping verbs, in turn, Niccolai et al. (2014) found a beta ERD (~200 ms) followed by a mu ERD (~400 ms, in the upper band), broadly consistent with the ERD sequence in the present study. Niccolai et al. (2014) speculated that this temporal sequence could reflect the actual dynamics of movement execution, with motor commands generated in the primary motor cortex, reflected by beta ERD, followed by somatosensory motor feedback, as reflected by mu desynchronization. Considering the methodological similarities (single words instead of words in a sentence context like in van Elk, van Schie, Zwaan, et al. (2010)) this interpretation could be applied also to the mu and beta ERD in the present study. However, more research is needed to investigate the temporal dynamics of language processing at different levels of complexity to resolve these conflicting patterns of results.

The result pattern for the PSEUDO condition was unexpected. As the words of the PSEUDO condition did not refer to any object, they were expected to yield no or a very small ERD/ERS. The observed high ERD in the PSEUDO condition, which did not differ significantly from the ACT condition, thus seemingly contradicts the interpretation of the ACT vs. VIS processing differences as experience-dependent reactivation of sensorimotor information during conceptual processing. At the same time, methodological and theoretical reasons question the comparability of the PSEUDO and ACT conditions. First, the PSEUDO condition was initially included as a behavioral control condition in the post-training EEG task in order to assess the participants' ability to distinguish between tool-related and other familiar pseudo-words rather than to investigate training-induced effects. Indeed, the PSEUDO training clearly differed from the ACT and VIS training procedures, not only with respect to the task but also, for example, in the number of repetitions of the words. These fundamental differences in the training procedures may have resulted in differences in task difficulty which then led to higher learning performance during the training as well as shorter reaction times for PSEUDO words in the EEG task. Due to the more similar training procedures for ACT and VIS words, it is conceivable that the PSEUDO words "popped out", which can further explain the faster reaction times in the EEG task.

Second, while these methodological aspects cannot explain the high ERD for PSEUDO words, some functional interpretations for this finding can be attempted. One potential interpretation is that, since alpha and beta oscillations are involved in many different cognitive processes (Bastiaansen & Hagoort, 2006; Pavlidou et al., 2014a), the ERD evoked by ACT and PSEUDO conditions might reflect different processes with different underlying generators. There is functional neuroimaging evidence that pseudo-words elicit stronger activations compared to words in motor areas such as the left precentral and bilateral postcentral gyrus, and the left pre-supplementary and supplementary motor area in different tasks (Carreiras, Mechelli, Estevez, & Price, 2007; Hagoort et al., 1999; Mechelli et al., 2005; Protopapas et al., 2016). This has been interpreted in terms of phonological and articulatory processing (Mechelli et al., 2005) or compensatory mechanisms, as semantic processing cannot take place (Carreiras et al., 2007).

The results of the present study do not allow to draw conclusions on qualitative differences in activations. However, it is at least conceivable that the ERD elicited by ACT and PSEUDO, despite being comparable in magnitude in all three frequency bands, represents phonological-articulatory processes for PSEUDO, but motor-experience specific processes for ACT word processing. The different patterns for PSEUDO vs. VIS and ACT vs. VIS ERD further support this interpretation. The ERD for PSEUDO is enhanced only in the less specified mu rhythm, which also reflects attentional processes as mentioned above. A beta band modulation, which is thought to be more motor-specific, was seen only in the comparison of ACT and VIS word processing.

Another interpretation for the comparable ERD elicited by PSEUDO and ACT, as well as the stronger PSEUDO vs. VIS ERD, is in terms of a baseline or default ERD pattern elicited by pseudo-word processing. For VIS, visual features could have become predominant, thus suppressing the motor associations inherent to pseudo-words. As the processing of a tool's motor features can be suppressed by task demands (Rey, Roche, Versace, & Chainay, 2015), it seems possible that the visual experience in our training paradigm led to a comparable suppression, even though visual processing was not necessary during our task. Usually, a suppression of motoric activation goes hand in hand with mu and beta ERS (Neuper et al., 2006). In our case, however, motor activation due to task demands and motor suppression due to conceptual processing of VIS names could have resulted in a diminished ERD in the VIS condition. Following this logic, motor associations could have stayed the same from pre- to post-training for PSEUDO, while being altered in their content, but not their form for ACT.

4.1. Conclusion

In conclusion, this study shows that after a short training period of learning the manipulation of novel tools, processing their associated novel names leads to an experience-dependent activation of sensorimotor areas. This was revealed by a stronger ERD of the mu and beta rhythm for processing names referring to tools with a history of manipulation experience compared to names referring to tools that were only visually explored, but not compared to PSEUDO words not referring to any object. Interestingly, effects in the beta frequency range, which is more directly linked to motor areas, appeared earlier during processing than effects in the mu rhythm, reflecting activation of sensorimotor areas. We interpret our findings as a (re)activation of experiential sensorimotor information during conceptual processing.

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Statement-of-significance

This study investigates the acquisition of object concepts and learning of word meanings. Results show that a short training history is enough for names of novel tools with manipulation experience to reactivate sensorimotor brain regions that were also active during concept acquisition. These activations seemingly represent conceptual processing.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2018.01.004.

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How words get meaning: the neural processing of novel object names after sensorimotor training

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Abstract

The hypothesis that individual experience affects the formation and processing of conceptual representations is controversially debated. Previous training studies with novel tool-like objects have found experience effects on conceptual representations as measured in tasks requiring the processing of object pictures. This study instead explored the neural processing of training-induced word meaning of novel object names. We asked whether the type of experience gained during object concept formation specifically modulates object name processing. In three training sessions with novel tool-like objects, two groups of healthy participants gained either active or observational manipulation experience as well as purely visual experience, while learning pseudowords serving as object names. In an fMRI session after training, participants were presented with the learned novel object names in a lexical decision task. Results revealed that processing novel object names in comparison to meaningless pseudowords elicits a word-like activation pattern in frontal, parietal and temporal regions known to underlie lexical-semantic processing, thus suggesting word meaning formation. Experience-specific modulations did not emerge as regional activation effects. However, a post-hoc analysis revealed that the type of experience (manipulation versus visual) as well as the way, in which the manipulation was learned (active versus observational) led to specific functional connectivity increases between semantic regions and neuronal assemblies in brain areas coding for object manipulation and related visuospatial information. These results suggest that the emergence of conceptual processing for novel object names might be grounded in functional brain networks specifically coding for the experience with their referents.

Keywords: experience, semantic memory, grounded cognition, fMRI, tool, novel words

1. Introduction

Our capability to convey meaning through language relies on the association of words with their referent's representations in semantic memory. There, knowledge we initially gained through experience is combined and stored in the form of concepts (Kiefer and Pulvermuller, 2012). Theoretical approaches differ concerning the role they ascribe to modality-specific areas involved in experience with the concepts' referents in conceptual-semantic neural representations (for a review see Meteyard et al., 2012). While amodal (Fodor, 1975, 1994) and domain-specific theories (Caramazza and Shelton, 1998; Mahon and Caramazza, 2009, 2011) postulate an independence of conceptual knowledge from modality-specific areas, embodied theories (Gallese and Lakoff, 2005; Glenberg and Kaschak, 2003) assume that conceptual processing recruits the same brain areas as the initial experience. Intermediate accounts (e.g., grounded cognition theory, Barsalou, 2008) assume a weaker form of embodiment and suggest that conceptual representations result from the interplay between modality-specific sensorimotor areas and one or multiple hubs, which mediate cross-modal integration (for recent reviews see Binder, 2016; Lambon Ralph et al., 2017).

The assumption of at least a certain degree of embodiment found broad support in neuroimaging research on manipulable objects, whose conceptual representations comprise information about their associated perceptual features, actions and functions (for reviews see Cappa, 2008; Noppeney, 2008). For example, functional magnetic resonance imaging (fMRI) studies showed that the processing of tool pictures or names draws on an extensive left-hemispheric network including portions of the premotor, parietal, and posterior temporal cortices, which are involved in actual object-directed movements and object use (Beauchamp and Martin, 2007; Ishibashi et al., 2016; Martin, 2007). The comparable activation patterns elicited by the processing of pictures and written as well as spoken tool names suggest that conceptual representations can be accessed in different ways (Chao et al., 1999; Devlin et al., 2005). Furthermore, lesions in the left-hemispheric fronto-parietal tool-network lead to deficits in imitating tool-use (Buxbaum et al., 2014) and in the conceptual processing of action-related features in object identification (Lee et al., 2014), as well as a selectively impaired recognition of tool words (Dreyer et al., 2015). This evidence refutes a merely epiphenomenal nature of sensorimotor activations during conceptual tool (name) processing (but see Mahon, 2015). However, these studies only provided indirect evidence for the role of sensorimotor experience in the formation of novel concepts.

In order to directly control the quantity and quality of experiential information that forms the objects' conceptual representations, one line of research has employed training paradigms with novel tool-like objects (Bellebaum et al., 2013; Kiefer et al., 2007; Ruther et al., 2014b; Weisberg et al., 2007). Weisberg et al. (2007) found that after three training sessions, actively manipulated novel tool-like objects elicited activations in left-hemispheric brain areas involved in motion and manipulation processing for common tools. In a subsequent study, the left premotor and inferior parietal cortices were found to be recruited more strongly by the processing of manipulated than visually explored tools (Bellebaum et al., 2013). Comparable findings were obtained in a study with observational instead of active manipulation training, suggesting a common mechanisms for both types of experience in forming conceptual object representations (Ruther et al., 2014b).

In a previous electroencephalography (EEG) study, our working group tested if also lexical-semantic processing leads to a (re-)activation of recently acquired experiential information in modality-specific brain areas. We applied a variant of the novel objects training paradigm, in which participants additionally learned names for the objects, thereby acquiring novel word meanings (Bechtold et al., 2018). In an EEG measurement after training, processing the names of novel objects that were actively manipulated elicited a stronger beta and mu rhythm suppression than processing the names of visually explored objects, indicating an experience-dependent involvement of the sensorimotor cortex in the processing of novel tool names (Bechtold et al., 2018). The distinguishing characteristic of this study, namely presenting object names instead of pictures during the post-training task, made sure that the measured effects were unaffected by the object's perceptual qualities (Binder et al., 2009) such as affordances (Borghi and Riggio, 2015).

The present study aimed to further investigate the role of sensorimotor information in the formation of novel word meanings by exploring the specific spatial characteristics of training-induced neural representations with fMRI. Like in our previous EEG study (Bechtold et al., 2018), a group of participants gained manipulation and visual experience with novel objects in a training paradigm during which they also learned the novel objects' names. Another group of participants instead gained observational manipulation and visual experience. This between-groups distinction was introduced, since a direct comparison of active and observed manipulation has not been provided so far. In the fMRI session after training, participants processed the names of the novel objects in a lexical decision task (LDT).

Firstly, we aimed to examine neural correlates of training-induced word meaning. When compared to meaningless pseudowords (PWs), the processing of words leads to so-called lexicality effects as a result of accessing conceptual knowledge in semantic memory. Functional neuroimaging studies on lexicality effects, but also on the comparison of semantic and phonological processing of real words, revealed a left-lateralized brain network extending from heteromodal prefrontal to inferior posterior parietal areas and reflecting semantic processing (for a meta-analysis see Binder et al., 2009). We hypothesized that the training protocol would induce meaning in all novel object names by forming conceptual object representations associated with the novel word. Processing novel object names should thus show a word-like activation pattern in comparison to unfamiliar PWs (Binder et al., 2003; Mechelli et al., 2003). We expected this effect to arise to a comparable degree after (active and observational) manipulation as well as visual exploration training (Binder et al., 2009). The second aim was to investigate training-induced experience-specific effects by directly comparing the processing of novel object words from the different training conditions. We hypothesized that active as well as observational manipulation training leads to stronger activations in regions within the tool-related fronto-parietal network than the visual exploration training (Ishibashi et al., 2016; Noppeney, 2008). Additionally, active manipulation might lead to stronger effects than observed manipulation (Cannon et al., 2014; Macuga and Frey, 2012).

2. Method

2.1 Participants

Forty-six volunteers took part in this study. We excluded three participants due to artifacts in the imaging data, and two other participants due to a learning performance at chance level (see below for details in how learning was assessed). Of the remaining 41 participants, 20 (11 females) were part of the active (ACT) and 21 (15 females) of the observational (OBS) group. All were healthy adults aged from 18 to 35 years (ACT: M = 23.30 years, SD = 4.93 years; OBS: M = 23.19 years, SD = 3.53 years), with no significant difference in age between the two groups, $t(34.305) = .081$, $p = .936$. None of the participants had any history of psychiatric or neurological diseases. All had normal or corrected-to-normal visual acuity and were right-handed according to their scores in the Edinburgh Handedness Inventory (Oldfield, 1971; ACT: M = 0.92, SD = 0.11; OBS: M = 0.82, SD = 0.22). Mean handedness scores did not differ significantly between the two groups, $t(29.871) = 1.842$, $p = .075$. All participants gave their written informed consent prior to participation and subsequently received monetary compensation or course credit. Additionally, the five participants with the highest learning performance received a 30 € voucher of an internet-based retailer, which was announced for motivational purposes. The study received approval by the ethics committee of the Medical Faculty at Heinrich Heine University Düsseldorf, Germany, and the study procedures were in line with the declaration of Helsinki.

2.2 Stimulus Material

2.2.1 Novel objects

Thirty-six novel tool-like objects were composed from a children's construction toy (K'NEX^{TM}, for an example see Figure 1) and have already been used in previous studies by our group (Bechtold et al., 2018; Bellebaum et al., 2013; Ghio et al., 2016; Ruther et al., 2014a; Ruther et al., 2014b). Each object had a specific tool-like function (i.e., transport, push, pull, move, destroy or separate) performed on small object-specific items (e.g., table tennis balls, paper cups, paper sheets). We divided the objects into two sets of 18 objects, including three objects for each function. The objects in the two sets were matched for visual complexity, singularity (i.e., how much an object "popped out" from the others) and similarity with real objects (see Ruther et al., 2014a for details on the rating procedure). For each object, a 640 x 360 pixel mp4 video served as non-verbal manipulation instruction. This video showed one full manipulation of the respective object, with a varying duration (17 s - 47 s, M = 27.00 s, SD = 6.98 s; see Figure 1A and video V1 in supplementary online material), depending on the manipulation's complexity. For the observational manipulation training, an additional video existed for each object, which showed continuous manipulations for 60 s.

2.2.2 Verbal stimuli

2.2.2.1 Novel Object Names and Pseudowords

We used the PW generator software *Wuggy* (Keuleers and Brysbaert, 2010) with the German language module to generate 36 PWs from real object names (see section 2.2.2.2). The output PWs were restricted to match the real object names with respect to the length of subsyllabic segments, word length (5-10 letters, M = 6.61, SD = 1.46), the transition frequencies between letters, and two out of three subsyllabic segments. Each novel object was uniquely assigned to one PW, which served as the novel object's name (e.g., *Zenkan*, *Tessen*).

Novel object names were presented in association with the objects during the training and participants were asked to learn them. After the training, the novel object names served as stimuli for our experimental LDT (see section 2.3.3.1), referred to as LDT_{NOV} in the following. By applying the specified parameters in Wuggy, we created two additional sets of PWs, which served as non-trained material in the LDT_{NOV} and in the localizer task on real object names (see Table S1A in Supplementary Material 1).

2.2.2.2 Real Object Names

We used 36 German nouns describing real objects for a functional localizer task (see Table S1A in Supplementary Material 1). Eighteen nouns referred to manipulable objects (e.g., *hammer*), the remaining 18 to non-manipulable objects with mainly visual features (e.g., *pillow*). Manipulable and non-manipulable object names were matched for length and frequency of occurrence. Further, 13 independent raters rated all real object names on 1-7 Likert scales regarding the strength of their association with actions and manipulations and how easy it was to imagine a function or use-related gesture. Manipulable object names were rated significantly higher than non-manipulable object names on all scales, all $p < .001$ (see Table S1B in Supplementary Material 1 for descriptive and inferential statistics on the psycholinguistic variables). An LDT served as localizer task (referred to as LDT_{LOC} in the following).

2.3 Procedure

2.3.1 General Procedure

Each subject underwent three training sessions and a subsequent fMRI session. The trainings were conducted in a laboratory room at Heinrich-Heine-University and the fMRI session took place at the University's medical center. For all participants, the intervals between sessions varied between one and five days, except for one participant of the ACT group, who completed the last training in the morning of the day the fMRI session took place. Of particular interest is the interval between the last training session and the fMRI session. This interval was significantly shorter in the ACT (M = 0.95 days, SD = 0.22 days) than in the OBS group (M = 1.62 days, SD = 0.92 days), $t(36) = -3.232$, $p = .004$. At the end of each training session and after the fMRI session, we applied a multiple-choice (MC) questionnaire, in which the participants were asked to assign each novel object name to its training condition (i.e., manipulation or visual, guessing would result in an average accuracy level of 50%). Notably, despite the longer interval before the fMRI session for the OBS than ACT group there was no group difference in MC test performance (see Section 3.1.1).

2.3.2 Training Procedure

The training sessions with the novel objects consisted of the manipulation condition (MAN), which was either active or observational for the participants of the two study groups, and the visual condition (VIS), which was identical for the participants of both groups. The assignment of the two object sets to the two training conditions was counterbalanced between and then held constant within participants. The order of conditions in each training session was counterbalanced within and between participants. The 18 objects within the MAN and VIS training conditions appeared in a randomized order. Note that, for any given participant, each object was only presented once, either in the VIS or in the MAN condition, according to the between-subjects counter-balanced object assignment to the two distinct sets. The software PsychoPy (version 1.81.03; Peirce, 2007) controlled the stimulus presentation in the training sessions on a Windows 10 PC with a 27’ Ben Q LED monitor with 1920 x 1080 pixel resolution. All stimuli were presented on a black background. Novel object names were presented in white (front: Arial, size: 72 pt). Each training session took about 90 min.

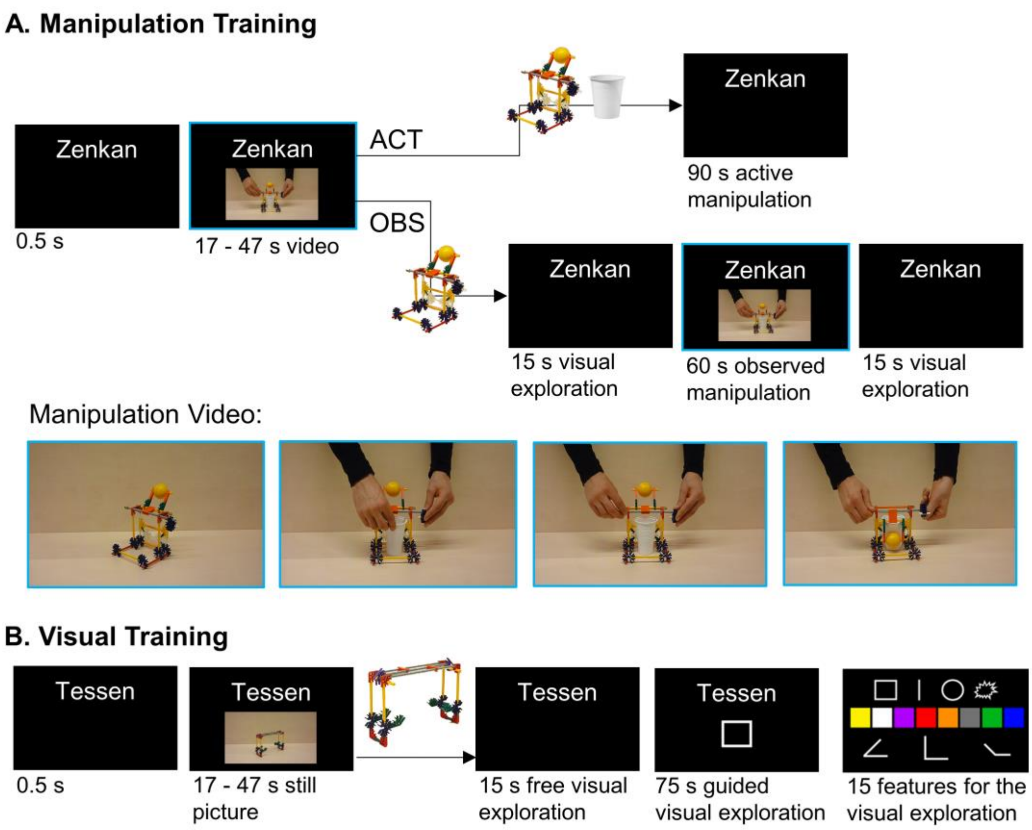

Figure 1. *Procedure of the manipulation and visual training*. A. Displays the timing of the trials in the manipulation training in the active (ACT) and observational (OBS) learning group and four exemplary frames taken from a manipulation video. B. Displays trial timing in the visual non-manipulation training, which was the same for both groups.

2.3.2.1 Manipulation Training

In the MAN training (see Figure 1A), the written name of one of the novel objects at a time appeared on the computer screen and the participants read the name aloud. After 0.5 seconds a video instruction started, showing one full manipulation of the object, while the name stayed on the screen. After the video, the experimenter placed the novel object in front of the participant. In the ACT group, the to-be-manipulated object-specific small items were additionally placed on the table and the participant was asked to manipulate the object for 90 s following the video instruction. The experimenter corrected the participant's manipulation if necessary. A beep tone and the written request to stop ended the manipulation time.

In the OBS group, the MAN training consisted of 15 s visual exploration of the novel object, which was prompted by a written request on the screen ("Please examine the object now”). Visual exploration took place twice, before and after the observational manipulation video, which lasted 60 s and showed continuous object manipulations (Figure 1A). For each object, the duration of the MAN training in the OBS group was thus also 90 s. By this procedure, the participants gained a real-life three-dimensional experience with the novel object, while at the same time observationally learning about its function without any actual object-directed movement or haptic experience. A beep tone and the written request to stop ended the manipulation time.

2.3.2.2 Visual Training

In the VIS training (see Figure 1B), the name of one novel object at a time appeared and was read out aloud by the participant. After 0.5 s a still picture (extracted from the video instruction for the MAN training) was presented for the duration of the manipulation of the respective object. Then, the experimenter placed the novel object in front of the participant and the 90 s visual exploration time started, of which the first 15 s were dedicated to free visual exploration. Afterwards, the exploration was guided by the visual presentation of five features, which the participants were asked to look for in the novel object for 15 s each. Overall, there were 15 different features (eight different colors, four forms, three angles; see Figure 1B), and five of these appeared for each novel object within each training session. Over the three training sessions, each feature appeared once for each novel object. The order was counterbalanced over the sessions. A beep tone and the written request to stop ended the exploration time.

2.3.3 fMRI Session

The fMRI session included two runs of the LDT_{NOV}, which took 5 min each and were separated by a standardized alertness task for 4.5 min (Zimmermann and Fimm, 1993). The alertness task was introduced in order to reduce repetition effects in the second LDT_{NOV} run.

Then, participants underwent the localizer task, consisting of one 5 min run, in which the participants performed the LDT_{LOC}. Before each run, the experimenter carefully instructed the participant about the task. The software Presentation (version 17.0, Neurobehavioral Systems Inc., Albany, CA, USA) controlled the stimulus presentation on a Dell Inspiron 15 7000 Series notebook. An LCD TFT Beamer (NEC, model MT1050, 1024 x 768 px resolution) projected the stimuli onto a translucent screen inside the scanner room. Participants could see the screen over a mirror construction attached to the birdcage coil. Responses were given on a Lumina Response Pad LS-PAIR for fMRI measurements (Cedrus Corporation, San Pedro, California, USA). The fMRI session ended with a T1-weighted anatomical image acquisition, which took about 11 minutes. The entire fMRI session lasted about 60 min.

2.3.3.1 Lexical Decision Task

In each LDT_{NOV} run, all 36 novel object names were presented intermixed with 36 meaningless PWs in white letters on a black background. The order was randomized once for each run, but then held constant across participants. Each object name and PW was shown for 1 s, preceded by a fixation cross for 0.45 s. The inter-trial-interval varied, with fixed durations of 1.7 s (42 times), 2.1 s (20 times) or 6 s (10 times). The participants responded by pressing one of two buttons with their left hand's index or middle finger. The participants were instructed to respond as fast as possible with the index finger to novel object names and with the middle finger to meaningless PWs. The same experimental paradigm was applied in the localizer task (LDT_{LOC}), in which 36 real object names were presented intermixed with a different set of 36 PWs.

2.3.3.2 fMRI Data Acquisition Parameters

Images were acquired with a 12-channel head coil on a 3T Siemens scanner (MAGNETOM Trio, A TIM system). During the two LDT_{NOV} runs as well as the LDT_{LOC} run, whole-brain functional images were acquired with a T2*-weighted gradient echo, echo-planar imaging sequence using a blood-oxygenation-level dependent contrast (repetition time = 2000 ms, echo time = 30 ms, flip angle = 90°). The functional images consisted of 31 axial slices parallel to the anterior-posterior commissure (4.0 mm thick, in plane resolution = 2 x 2 mm, no gap, field of view = 192 x 192 mm, acquisition order = ascending interleaved, odd first). For each participant, one functional image sequence including 150 volumes was gathered during both LDT_{NOV} runs and the LDT_{LOC} run, resulting in a total of 450 functional scans. Additionally, for each participant a T1-weighted anatomical image was acquired via three-dimensional spoiled-gradient-recalled sequences with a repetition time of 1850 ms and an echo time of 35 ms (240 slices, slice thickness = 0.7 mm, in plane resolution = 0.7 x 0.7 mm).

2.4 Data Analysis

2.4.1 Behavioral Data

We analyzed behavioral data with IBM SPSS Statistics (version 23, ©IBM). If the Mauchly test indicated a violation of the sphericity assumption, we applied the Greenhouse-Geisser correction and report corrected degrees of freedom and *p*-values. We considered an α-level of .05 as indicating statistical significance and applied the Bonferroni correction to post-hoc pairwise comparisons.

2.4.1.1 Learning performance

To assess learning performance, the percentage of object names that were correctly assigned to their training condition in the MC questionnaires after each session was determined for each participant, separately for the two training conditions. The percentage values of the MC performance were then analyzed with a 4 x 2 x 2 mixed ANOVA with the within-subjects factors Session (training session one, two, three; fMRI session) and Type of Word (MAN, VIS) and the between-subjects factor Learning Group (ACT, OBS).

2.4.1.2 LDT_{NOV}

For LDT_{NOV}, reaction times and accuracy (defined as the percentage of correct responses of all given responses) were analyzed via separate ANOVAs. We included the within-subjects factor Type of Word (MAN, VIS and PW) and the between-subjects factor Learning Group (ACT, OBS). For the sake of completeness, we analyzed the LDT_{LOC} accordingly (results are displayed in Supplementary Material 2A)

2.4.2 fMRI Data

We preprocessed the data with SPM8 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk/spm). The New Segment procedure was applied to the structural images of each participant, with registration to the Montreal Neurological Institute (MNI) standard space. Functional images were corrected for slice timing and spatially realigned. Subsequently, we normalized the images to the MNI space, using the New Segment procedure with the subject-specific segmented structural images as customized segmentation priors. Finally, the images were spatially smoothed with an 8-mm FWHM Gaussian kernel.

The data were further analyzed with SPM12 (version r7219). We adopted a two-stage random-effects statistical approach, and, at the second stage, we applied a partitioned error approach. The statistical analysis was restricted to an explicit mask including only the voxels with gray matter probability > 0.1 based on the segmented structural images of each participant. We corrected for multiple comparisons by applying the Gaussian random field theory as implemented in SPM12 to obtain clusters satisfying a cluster-level $p < .05$ family-wise error (FWE)-corrected threshold, with a $p < .001$ cluster-defining threshold.

At the first stage, we specified a general linear model (GLM) for each participant. We high-pass filtered each participant's time series at 128 s and modelled serial correlations by means of an autoregressive model AR(1). No global normalization was performed. We modelled the two LDT_{NOV} runs as two separate sessions, each including the conditions MAN, VIS, and PW as regressors of interest. These regressors contained the onsets of those novel object names and PWs, which were correctly identified in the LDT_{NOV}. Additionally, the MAN and VIS regressors contained only the onsets of those novel object names, which participants correctly assigned in the MC questionnaire after the last training session. This assured that only learned object names and correctly identified object names and PWs were considered as events of interest. If present, separate confounding regressors were modelled for unlearned object names (i.e., novel object names that participants did not correctly assign in the MC questionnaire after the last training session) and for trials in which participants gave erroneous LDT responses. Onset times for all these conditions were convolved with a canonical hemodynamic response function. We entered head movement realignment parameters into the model as covariates by implementing six regressors of no interest (three rigid-body translation, and three rigid-body rotation parameters).

2.4.2.1 Training-induced lexicality effects

In a first analysis, we aimed to examine the effects of training-induced lexicality by comparing the processing of novel object names (without distinguishing between MAN and VIS) and unfamiliar PWs. Although we did not expect differences between the ACT and OBS group, the factor Learning Group was entered into this analysis in order to control for group differences. We therefore applied a 2 x 2 factorial design with Lexicality as a within-subjects factor (Object Name [MAN + VIS], PW) and the between-subjects factor Learning Group (ACT, OBS). Within the estimated first-level GLM, we defined two first-level Student's *t*-test contrasts: (1) a contrast with a weight of +1 for MAN, +1 for VIS, -2 for PW and a weight of zero for all the other regressors; (2) a contrast with a weight of +1 for all the conditions of interest (MAN, VIS, PW) and a weight of zero for all the other regressors. In order to assess the main effect of the training-induced Lexicality, we used the contrast (1) to specify a second-level one-sample *t*-test design. To assess the main effect of Learning Group, we used the contrast (2) to create a second level two-sample *t*-test design (independence and unequal variances assumed between groups). Finally, we tested the Lexicality x Learning Group interaction by entering the contrast (1) into a two-sample *t*-contrast design (independence and unequal variances assumed between groups).

2.4.2.2 Training-induced experience-specific effects

The aim of the second analysis was to detect whether the specific type of training experience (manipulation vs. visual) with novel objects induced modulations of the activation patterns associated with novel object name processing, and whether these varied depending on whether the manipulation was learned actively or by observation. In this analysis, we thus omitted PWs and directly compared novel object names from the MAN and VIS training. We applied a 2 x 2 factorial design with Type of Word (MAN, VIS) as a within-subjects factor and the Learning Group (ACT, OBS) as the between-subjects factor. At the first stage, we defined two first-level Student's *t*-test contrasts: (1) a contrast with a weight of +1 for MAN and -1 for VIS and a weight of zero for all the other regressors; (2) a contrast with a weight of +1 for both MAN and VIS and a weight of zero for all the other regressors. In order to assess the main effect of Type of Word, we used the contrast (1) to specify a second-level one-sample *t*-test design. To assess the main effect of Learning Group, we used the contrast (2) to create a second level independent two-sample *t*-test design (independence and unequal variances assumed between groups). Finally, we tested the Type of Word x Learning Group interaction by entering the contrast (1) into an independent two-sample *t*-contrast design (independence and unequal variances assumed between groups). Additionally to the whole brain analysis, we applied a small volume correction ([SVC]; $p < .05$, FWE corrected; Poldrack, Mumford, & Nichols, 2011) to the analyses of the main effect of Type of Word and the Type of Word x

Learning Group interaction by using ROIs defined on the basis of the localizer task (see 2.4.2.3). This aimed at testing the experience-dependent activation of specific brain regions involved in the representation of real manipulable object words.

2.4.2.3 Localizer fMRI data

The localizer task comprising real object names was analyzed at the first stage by modelling the session including three regressors of interest, one for the manipulable object names, one for the non-manipulable object names and one for PWs. These regressors included the onsets of the words and PWs for which participants gave correct LDT_{LOC} responses. Separate regressors were modelled for erroneous LDT_{LOC} responses (if present) and the six head movement realignment parameters.

The aim of the analysis of the localizer task was to identify the activation network for processing words referring to real manipulable vs. non-manipulable objects in order to specify regions of interest for the SVC analysis of the novel object names (see section 2.4.2.2). For this purpose, at the first stage, we defined a first-level Student's *t*-test contrast with a weight of +1 for manipulable and -1 for non-manipulable object names and a weight of zero for all the other regressors. We then used this contrast to specify a second-level one-sample *t*-test design. The main effect of Learning Group was not entered into the analysis. For the sake of completeness, we however also verified that when we additionally included the Learning Group factor as a covariate, we obtained the same pattern of results. Processing manipulable object names led to significantly stronger left-hemispheric activations in two clusters. One was located in the inferior frontal gyrus (pars triangularis) and the precentral gyrus (peak coordinates: x = -42, y = 28, z = 20, cluster size: 226 voxels, $p = .001$, $z = 4.08$). The second was located in the superior and inferior parietal lobule extending to the middle occipital gyrus (peak coordinates: x = -30, y = -70, z = 40, cluster size: 140 voxels, $p = .012$, $z = 3.92$). We applied an SVC of the training-induced experience-specific effects (see section 2.4.2.2) using 6 mm sphere ROIs around these cluster's peak coordinates.

3. Results

3.1 Behavioral Data

3.1.1 Learning Performance

Table 1 displays the descriptive statistics of the MC performance assessing the learning of the novel words. Session had a significant effect on the MC performance, $F(3, 117) = 28.526$, $p < .001$, $\eta_p^2 = .422$. The learning performance increased significantly from the first to the following sessions, all $p < .001$. From the second session to the third, there was a further marginally significant increase, $p > .062$, but not from the second to the fMRI session, $p = .797$. Indeed, the learning performance dropped significantly from the third training to the fMRI session, $p = .002$. Neither the main effects of Type of Word or Learning Group nor any of their interactions were significant, all $p > .132$.

INSERT TABLE 1 HERE

3.1.2 LDT_{NOV}

Type of Word had a significant effect on reaction times, $F(1.492, 58.170) = 28.955$, $p < .001$, $\eta_p^2 = .426$. Participants reacted more slowly to PWs ($M = 724$ ms, $SE = 14$ ms) than to MAN ($M = 671$ ms, $SE = 12$ ms) and VIS ($M = 671$ ms, $SE = 11$ ms), both $p < .001$. MAN and VIS did not differ significantly, $p > .999$. Neither the main effect of Learning Group nor its interaction with Type of Word were significant, both $p > .711$. The mean accuracy was very high in all experimental conditions (ACT-MAN: $M = 97.6\%$, $SE = 0.7\%$; ACT-VIS: $M = 97.6\%$, $SE = 0.9\%$; ACT-PW: $M = 97.7\%$, $SE = 0.7\%$; OBS-MAN: $M = 98.1\%$, $SE = 0.7\%$; OBS-VIS: $M = 97.5\%$, $SE = 0.9\%$, OBS-PW: $M = 96.7\%$, $SE = 0.7\%$). Neither the main effect of Type of Word nor Learning Group nor their interaction significantly affected LDT_{NOV} accuracy, all $p > .467$.

3.2 fMRI Data

3.2.1 Training-induced lexicality effects

In order to investigate the effects of training-induced lexicality of the novel object names we compared the activation elicited by the processing of object names (averaged across MAN and VIS) and PWs. The brain regions showing significantly higher activations for object names than PWs are displayed in Figure 2A and listed in Table 2A. Processing object names elicited stronger activations in left-hemispheric frontal regions including the superior frontal gyrus, the middle frontal gyrus, the inferior frontal gyrus (pars triangularis), and the different portions of the orbital frontal gyrus. Significant activations were also found in the parietal cortex, with one cluster extending from the left cuneus to the bilateral precuneus and middle cingulate cortex, and, bilaterally, two clusters from the inferior parietal lobule to the angular gyrus. Finally, significant activations were observed in the left middle and inferior temporal gyrus as well as in the parahippocampal gyrus.

The brain regions showing significantly stronger activations for PW than object name processing are listed in Table 2B and displayed in Figure 2B. PWs led to significantly stronger activations in a large cluster extending from the right superior frontal gyrus, to the bilateral posterior-medial frontal gyrus, the left precentral and bilateral postcentral gyrus, and left inferior parietal lobule. Neither the analysis of the Learning Group main effect nor of the Lexicality by Learning Group interaction yielded any significant activation clusters.

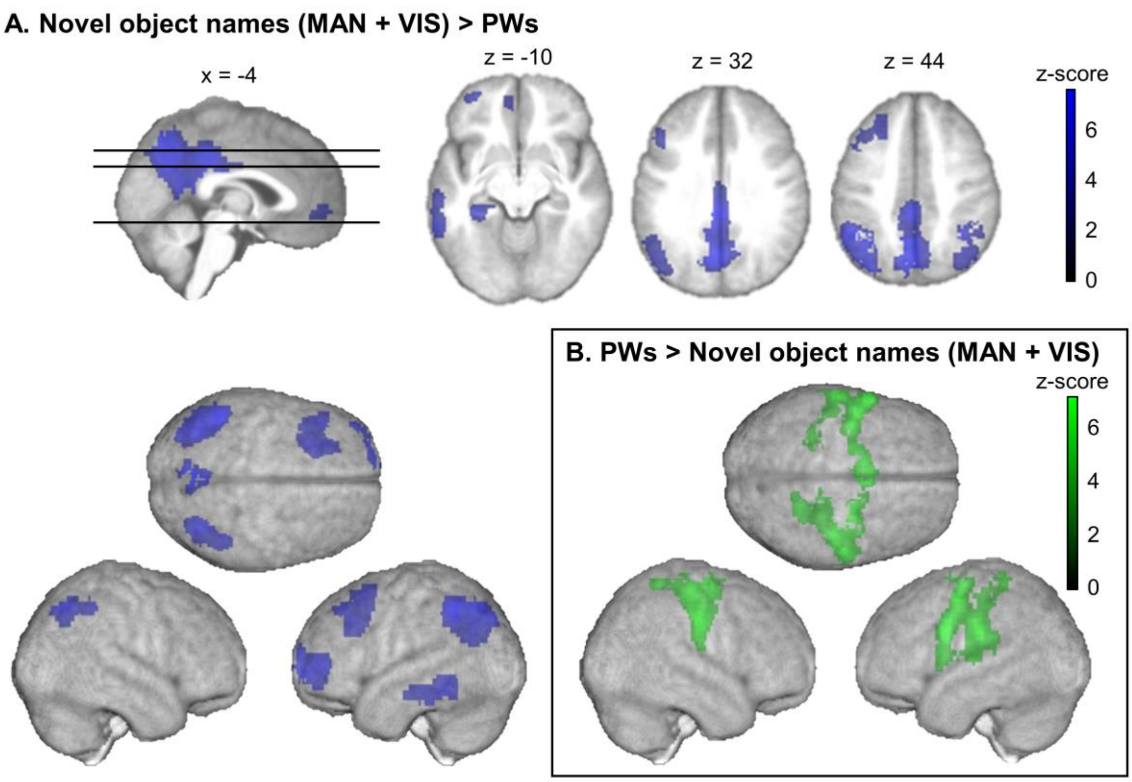

Figure 2. *Training-induced lexicality effects*. A. Activations specific to novel object names (manipulation [MAN] and visual [VIS] training) compared to pseudowords (PWs) and B. vice versa. Clusters reaching the cluster-level $p < .05$ (FWE corrected) significance threshold, with a $p < .001$ cluster-defining threshold are displayed on the normalized T1-weighted anatomical image averaged across all participants ($n = 41$).

INSERT TABLE 2 HERE

3.2.2 Training-induced experience-specific effects

To investigate the experience-specific effects induced by the different kinds of training, we directly compared activations elicited by MAN and VIS object names. We found neither significantly stronger activations for processing MAN than VIS, nor for VIS than MAN. Neither the Learning Group main effect nor of the Type of Word x Learning Group interaction yielded any significant activation clusters. Neither of these effects were significant, even when we applied an SVC approach using the two ROIs obtained by the functional localizer LDT_{LOC}.

3.2.3 Post-hoc analysis of training-induced functional connectivity

The examination of brain regions associated with the processing of novel object names vs. PW (i.e., lexicality pattern) revealed a network that was highly consistent with the conceptual hub network identified by a quantitative meta-analysis on semantic processing (Binder et al., 2016; Binder et al., 2009). All nodes within this network have been identified as high-level multimodal areas, which are characterized by a dense pattern of connectivity with multiple modality-specific areas (Binder et al., 2016; Lambon Ralph et al., 2017). Hubs have been ascribed a key role in forming multimodal semantic representations by integrating experiential information from different modalities (Binder et al., 2016; Binder and Desai, 2011; Lambon Ralph et al., 2017). The lack of experience-specific effects in our data despite this significant lexicality effect brought us to formulate an additional post-hoc hypothesis. We assumed that experience-specific effects might be reflected by a differential functional connectivity between the high-level multimodal hub areas involved in processing the novel object names and neuronal assemblies in modality-specific areas (for a comparable line of thought, see Chow et al., 2014; Malone et al., 2016).

To investigate training-induced experience-specific functional connectivity effects, we conducted a two-stage random-effects seed-to-voxel functional connectivity analysis, using the CONN toolbox (version 18b, Whitfield-Gabrieli and Nieto-Castanon, 2012, www.nitrc.org/projects/conn). As seed ROIs, we used the eight clusters of activation associated with the processing of novel object names vs. PWs (see Table 2A). For each subject, we imported the preprocessed structural and functional images and the specified first-level GLM (see section 2.4.2). We applied the default CONN denoising procedure and additionally specified first-order temporal derivatives as within-subject covariates. At the first level of the connectivity analysis, a correlation map for each condition (MAN, VIS) was generated. For this purpose, we applied a weighted GLM for computing bivariate Pearson's correlation coefficients of the condition-specific association between BOLD time series of the eight seed ROIs and each voxel in the brain. We applied Fisher's transformation to the resulting correlation coefficients to obtain normally distributed z-scores. We then entered the normalized connectivity maps of each subject into a second-level GLM. On the second level, we applied a 2 x 2 factorial design including the within-subjects factor Type of Word (MAN, VIS) and the between-subjects factor Learning Group (ACT, OBS). For each seed ROI, we tested the effect of Type of Word by applying a paired *t*-test (with a weight of +1 for MAN, -1 for VIS) and the effect of Learning Group by applying a two-sample *t*-test (with a weight of +1 for ACT, -1 for OBS), by always testing both the positive and the negative effect. We tested the Type of Word x Learning Group interaction by applying a mixed ANOVA interaction (with a weight of +1 for ACT, -1 for OBS, +1 for MAN and -1 for VIS). We report clusters satisfying a cluster-level false discovery rate (FDR)-corrected threshold of $p < .05$, with an uncorrected voxel-threshold of $p < .001$.

Table 3 provides a summary of the pattern of experience-specific functional connectivity. First, results revealed that the functional connectivity of two seeds was specifically influenced by the factor Type of Word (MAN, VIS). Processing MAN words selectively increased the functional connectivity of the seed ROI in the left parahippocampal gyrus with two clusters in the left temporal pole (extending, respectively, into the left middle/inferior temporal gyrus and the left frontal orbital cortex) and with a cluster in the left frontal pole (extending into the left superior frontal gyrus). The MAN condition also selectively increased the connectivity between the seed in the left superior frontal gyrus and a cluster in the cerebellum (lobule VIIb). We found no specific increases in functional connectivity for processing VIS object names.

Second, we observed specific modulations of the functional connectivity with two other regions of the semantic network by the factor Learning Group. Novel object name processing in the ACT group was specifically associated with increases in the functional connectivity of the right inferior parietal lobule seed with a cluster in the occipital pole and of the left inferior middle temporal gyrus seed with a cluster in the bilateral cerebellum (lobules VI-VIII). For the OBS group, in turn, we observed selective increases in the functional connectivity between the left medial orbital frontal gyrus seed and a cluster in the left cerebellum (lobules VIII-IX).

Finally, the results revealed a significant Type of Word x Learning Group interaction for two seed regions. In the ACT (more than OBS) group, the precuneus showed specific increases in functional connectivity with a cluster in the left superior parietal lobule extending into the superior lateral occipital cortex for MAN (more than VIS). Additionally, in the ACT (more than OBS) group the functional connectivity of the left parahippocampal seed with the right putamen and insular cortex was increased by processing MAN words (more than VIS).

4. Discussion

In this study, we investigated the neural correlates of training-induced word meaning of novel object names and whether the type of sensorimotor experience gained during the object concept formation modulates object name processing. We applied a paradigm with novel objects and their names including active or observational learning in a manipulation training condition as well as a visual training condition. Participants successfully acquired the novel object names in all training conditions, which was also reflected in faster reaction times in response to novel object names than meaningless PWs and a generally very high accuracy in the LDT after the training. The fMRI data showed a general effect of training-induced lexicality for the novel object names (vs. PWs), which elicited a distinct activation pattern in a broad network of multimodal hub areas known to underlie semantic processing of real words. As hypothesized, this lexicality effect did not differ between the active and the observational learning group. Contradicting our hypotheses, the univariate analysis did not reveal any training-induced effects specifically associated with the type of sensorimotor experience gained with the objects (i.e., active or observed manipulation vs. visual) as well as the type of manipulation learning (i.e., active vs. observational). Experience-specific effects, however, appeared as selective functional connectivity increases between the semantic hub areas and cortical, cerebellar and striatal areas, as revealed by a post-hoc connectivity analysis. In the following, we first discuss the semantic network associated with the processing of novel object words, and then the identified connectivity patterns.

4.1 Training-induced lexicality effects

As for the training-induced lexicality effects, the activation in left-hemispheric fronto-temporo-parietal areas elicited by the processing of the novel object names, in comparison to phonologically and orthographically matched PWs, largely overlaps with the network activated by real words in comparison to PWs in previous studies on lexical processing. This network has been associated with semantic processing (see e.g., Binder et al., 2009; Binder et al., 2003; Carreiras et al., 2007; Mechelli et al., 2003). Although the LDT is considered a rather implicit task, it has been shown to elicit semantic processing (Balota et al., 2004; Binder et al., 2003), with even stronger semantic effects when word-like PWs are used (Evans et al., 2012), as was the case in our study. Areas more strongly activated by PWs than novel object names included the precentral gyrus and supplementary motor area. This finding complements and further validates the lexicality effect described above, as it is consistent with findings on PW compared to real word processing in the literature (Binder et al., 2003; Carreiras et al., 2007) as well as in the present study (LDT_{LOC}, see Table S2 in Supplementary Material 2). Sensorimotor activations elicited by PWs have been interpreted as either reflecting phonological processing (Mechelli et al., 2005) or compensatory mechanisms if semantic processing cannot take place (Carreiras et al., 2007). Taken together, this word-like activation pattern suggests that the training successfully induced novel word meanings.

An alternative interpretation might be that differences in novel object name vs. PW processing reflect mere familiarity effects induced by repeated exposure throughout the trainings. This seems unlikely, however, as the brain network associated with processing novel object names (vs. PWs) largely overlaps with a semantic network identified in a meta-analysis on semantic processing (Binder et al., 2009; Binder, 2016). The inferior parietal cortex (including the angular gyrus), the precuneus, the middle and inferior temporal gyrus, the ventromedial temporal cortex (including the parahippocampal gyrus), the superior and middle frontal gyrus, the left inferior frontal and orbital frontal gyrus, which were involved in our lexicality effect, have been identified as semantic hubs (Xu et al., 2016). These regions have been shown to be connected with multiple modality-specific brain areas, and are considered to play a key role in integrating information from different modalities into multimodal high-level conceptual representations (Binder, 2016). The left inferior frontal and parietal regions as well as the left middle temporal gyrus involved in our lexicality effect have been shown to also be involved in processing tool-related information (for a review see Ishibashi et al., 2016) and showed training-induced activation specific for tool-related experience (Bellebaum et al., 2013; Malone et al., 2016; Weisberg et al., 2007).

Within the semantic hub network, nevertheless, differential functional roles of the nodes have been recognized. For example, the medial temporal lobe, including the dentate and parahippocampal gyri, has been interpreted as representing an interface between semantic and episodic memory (Binder et al., 2009). The parahippocampal gyrus might underlie strategical episodic retrieval, such as the recall of information about the training scene (Bird et al., 2010; Moscovitch et al., 2006; Yonelinas, 2013). Similarly, the precuneus has been linked to episodic retrieval and visuo-spatial imagery (Cavanna and Trimble, 2006). In previous studies, the left precuneus was more strongly activated when perceiving familiar than unfamiliar tools, reflecting automatically elicited processes of manipulation imagination (Vingerhoets, 2008). It has also been involved in willfully imagining the use of unfamiliar tools (Grezes and Decety, 2002). Notably, it has been shown that especially newly acquired semantic information strongly relies on strategic episodic memory retrieval (Smith and

Squire, 2009). This result is particularly relevant for our findings on novel object representations, where we observed activations of the dentate and parahippocampal gyri and the precuneus. Activations of these brain regions have not been consistently observed in previous studies on real words with consolidated meaning (Mechelli et al., 2003). Compatibly, in our study they were absent in the LDT_{LOC} (see Table S2 in Supplementary Material 2). Medial temporal structures and the precuneus thus appear to serve the more effortful processing of novel object names by supporting the retrieval of episodic and/or spatial information (Hebscher et al., 2018).

4.3. Training-induced experience-specific effects

The second aim of this study was to examine experience-specific effects by directly comparing novel object names from the MAN and VIS training conditions and a potential influence of the type of manipulation learning (active vs. observational). However, we did not find the hypothesized stronger activation of MAN compared to VIS object names within the tool-related fronto-parietal network, neither in analyses on the whole brain level nor in regions specifically involved in the representation of manipulable objects identified in the functional localizer task. We also did not find any effect of the type of learning (active vs. observational). Previous studies largely agree that active and observational tool-use draw on the same brain areas (for a meta-analysis see Lewis, 2006), a finding that is also consistent with our previous studies employing the novel object training paradigm (compare Bellebaum et al., 2013; Ruther et al., 2014b). However, the few studies directly comparing active and observed tool-use experience suggest a stronger involvement of the action-related brain areas during (Macuga and Frey, 2012) and after (Cannon et al., 2014) active experience, which contradicts our findings.

Previous research revealed that the involvement of experience-specific areas in conceptual processing is task- and context-dependent (Kiefer and Pulvermuller, 2012; Lebois et al., 2015). A more explicit task and/or context might thus have revealed experience-specific effects in our univariate analysis (see, e.g., Andres et al., 2013; Canessa et al., 2008). It seems very unlikely, however, that the chosen task was not appropriate to uncover experience-specific effects given the experience-specific effects for manipulation information in the LDT_{LOC}. Using object names instead of pictures might explain the discrepancy to previous fMRI studies, which revealed experience-specific effects after a comparable amount of training (Bellebaum et al., 2013; Ruther et al., 2014b). Indeed, a study with proficient children and adult readers suggests that it may take years of experience until reading written object names elicits modality-specific sensorimotor activations to a comparable degree as seeing object pictures (Dekker et al., 2014). Furthermore, the inclusion criterion for novel object names into the analyses based on the MC performance might not have guaranteed that only successfully established associations between the novel names and the respective objects entered the analyses. The performance in the multiple-choice test might be a more liberal criterion than, e.g. naming accuracy, which we did not assess.

It is, however, also conceivable that the differences in processing depending on the type of experience were more subtle in nature. As discussed above, processing the newly acquired object names in our study elicited a pattern, which was remarkably consistent with the semantic network identified for real word processing (Binder et al., 2009). As the nodes of this network are known to show a strong connectivity to modality-specific regions (Binder, 2016; Lambon-Ralph et al., 2017), we formulated the additional post-hoc hypothesis that experience-specific effects might be reflected by a differential functional connectivity between these high-level multimodal hub areas and neuronal assemblies inexperience-specific areas. In a study on the processing of short stories, Chow et al. (2014) could show a functional connectivity of a content-independent language network with content-specific brain areas involved in action, perception and emotion processing. In the absence of areas showing modality-specific effects in our study, we relied on a seed-to-voxel analysis, exploring functional connectivity between areas involved in our lexicality pattern and potentially modality-specific brain areas post-hoc.

4.4 Post-hoc analysis of training-induced functional connectivity

The functional connectivity analysis revealed a complex pattern of experience-specific functional connectivity of nearly all regions involved in the lexicality pattern with neocortical, cerebellar, and striatal areas. Different effects emerged for the two experimental factors (Type of Word, Learning Group) as main effects, as well as for their interaction. As for the main effect of Type of Word, processing object names from the manipulation training selectively increased the functional connectivity of the left mediotemporal parahippocampal/dentate gyri seed ROI with two clusters in the left temporal pole, which is considered a transmodal semantic hub (Patterson et al., 2007). The first cluster extended into the left middle/inferior temporal gyrus, an area known to be involved in processing visual information (Visser et al., 2012) and concrete concepts (Hoffman et al., 2015). The second cluster extended into the frontal orbital cortex. In an fMRI study on motor imagery, Mizuguchi et al. (2018) showed that orbitofrontal activity was associated with the vividness of mental imagery. This pattern of functional connectivity between the parahippocampal gyrus, as an interface between episodic and semantic memory (see above), and the anterior temporal lobe extending into further modality-specific areas might reflect enriched, multimodal episodic information integrated into the conceptual representations of novel object names after manipulation compared to visual training. The functional connectivity of the parahippocampal seed ROI with the left frontal pole extending to the superior frontal gyrus was also selectively enhanced for MAN vs. VIS. The functional coupling of these regions has been previously described in the literature and interpreted as reflecting cognitively controlled episodic retrieval along the ventral path (Barredo et al., 2015). MAN object names further specifically increased the functional connectivity of the dorsal superior frontal gyrus seed ROI, which is involved in semantic retrieval (Binder et al., 2009), and the cerebellar lobule VIIb. O'Reilly et al. (2008) could show that lobule VII is involved in temporo-spatial judgments on observed movements (i.e., velocity vs. mere direction judgments, O'Reilly et al., 2008). The functional connectivity of the superior frontal seed ROI and the cerebellum might thus reflect the retrieval of sequences from the active and observed manipulation during the trainings.

As for the main effect of Learning Group (active vs. observational) the active learning group showed a stronger functional connectivity than the observational learning group between the left middle temporal seed ROI and the cerebellar lobules VI-VIII. This finding is in line with previous research showing a stronger activation of the cerebellar lobules V-VIII in actively performing than observing grasp movements (Casiraghi et al., 2019). Further, in a meta-analysis, Stoodley and Schmahmann (2018) showed that cerebellar lobules V-VII are strongly involved in motor tasks (see also Ghio et al., 2018). In the active learning group, we also found increased functional connectivity between the right inferior parietal lobule/angular gyrus seed ROI and the occipital pole. These areas are part of the dorsal visual stream involved in guiding goal-directed actions (Frey, 2007; Goodale and Milner, 1992). Brandi et al. (2014) could show that its ventro-dorsal part (i.e., the middle occipital gyrus and inferior parietal lobule) plays a role in processing familiar object manipulations. Further, the two seed ROIs involved in this active learning-specific functional connection are both part of the left-hemispheric network involved in processing tool-related information (for a review see Ishibashi et al., 2016). The pattern of stronger functional connectivity for ACT than OBS might thus reflect the retrieval of actual tool-use experience. The observational learning group instead showed a stronger functional connectivity between the medial orbital frontal gyrus seed ROI and the left cerebellar lobules VIII-IX. As described above, the orbitofrontal cortex is involved in motor imagery (Mizuguchi et al., 2018). The posterior cerebellum is part of the action-observation-network (Casiraghi et al., 2019; Sokolov et al., 2010) and the left cerebellar hemisphere is especially involved in visuo-spatial processing (Stoodley and

Schmahmann, 2018). This functional connectivity might thus reflect the retrieval of the observed manipulation information. The fact that these learning group-specific effects occurred independently of the training condition probably reflects a generalization of manipulation information. If participants spontaneously engaged in manipulation imagery during the visual exploration, this might have led to functional manipulation information available also for VIS objects, albeit probably leading to less vivid mental imagery (see above). In line with this idea, Vingerhoets (2008) found that seeing pictures of tools with unknown function leads to activation in the left hemispheric tool-network.

Lastly, the Type of Word and Learning Group also interacted in their effects on the functional connectivity originating in two regions involved in our lexicality effect. There was a specific increase in functional connectivity for MAN vs. VIS object names in the active, but not the observer group in the precuneus seed ROI, which was more strongly connected with a cluster in the left superior parietal lobule extending into the superior lateral occipital cortex. The left superior parietal lobule is involved in spatial attention (Molenberghs et al., 2007) and is, together with the superior lateral occipital cortex, part of the dorso-dorsal pathway involved in the online control and selection of complex, goal-directed actions (Brandi et al., 2014). Notably, this target region marginally overlaps with the parieto-occipital ROI for real manipulable object processing identified with the functional localizer task. A further interaction effect was found for the left parahippocampal seed ROI, which showed a stronger cross-hemispherical connectivity with the right putamen and insular cortex (again selectively for MAN in the ACT group). Previous research showed that the putamen and insula are involved in the episodic retrieval of temporal sequences (Hsieh and Ranganath, 2015) and egocentric spatial representations (Kenzie et al., 2015; Mijovic-Prelec et al., 2004). It must be noted that, at odds with all the other functional connections discussed above, this one was the only one to cross the two hemispheres. The right hemispheric involvement of the putamen and the insula may be consistent with the right hemispheric dominance for processing spatial information, as shown by (virtual) lesion studies (Fierro et al., 2000; Schintu et al., 2014). Overall, these interaction effects might reflect episodic retrieval of manipulation and (egocentric) visuospatial information supporting the conceptual processing of actively manipulated objects.

Taken together, the results revealed a complex pattern of functional connectivity between, on the one side, multimodal semantic hub areas involved in the lexicalization and, on the other side, distributed cortical, cerebellar and striatal areas known to contribute to the processing of object-specific manipulation, functional and visuospatial information. The results cannot be interpreted in terms of top-down vs. bottom-up influences, as the seed-to-voxel functional analysis does not allow such directional inferences. A further caveat is that these results emerge from a post-hoc analysis that was introduced to cope with the unexpected lack of significant experience-specific activation in the more conventional functional specialization analysis. They nevertheless might be interpreted in favor of a certain degree of experience-specific grounding of the lexicalization of novel object names.

5. Conclusion

The present study in healthy adult human subjects provides evidence that a short training promoting novel object name learning induces functional brain changes that reflect both lexical and semantic processes associated with the encoding of novel concepts in linguistic form. In particular, the processing of the novel names engages brain areas identified to serve as semantic hubs, mirroring real word lexicality effects, as well as brain areas underlying strategic episodic memory processes. To a limited extent, the short training seems to also induce experience-specific brain activity modulations involving sensorimotor areas, as previously observed for processing real words referring to objects for which we already have a consolidated experience. These experience-specific modulations do not appear to emerge as regional activation effects, but rather as functional connectivity increases between semantic hub regions and distributed neocortical, cerebellar and striatal areas coding for object manipulation and related visuospatial information. The emergence of conceptual processing for novel words thus appears to be grounded in functional brain networks specifically coding for the experience with the referred objects.

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Tables

Table 1. Learning performance in the multiple-choice questionnaire.

		Session			
		T1	T2	T3	fMRI
Group	Training	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)
ACT	MAN	72.2 (18.0)	86.7 (11.9)	90.3 (10.3)	83.3 (16.0)
	VIS	71.1 (15.9)	87.2 (14.1)	89.7 (11.4)	86.1 (15.6)
OBS	MAN	68.5 (12.1)	79.4 (19.7)	88.9 (13.6)	76.2 (19.9)
	VIS	64.3 (13.9)	79.6 (20.7)	86.2 (11.6)	75.4 (23.6)

Note. Mean percentage of correct assignments in the multiple-choice questionnaire after the three training sessions (T1-T3) and the fMRI session for the active (ACT) and observational (OBS) group for novel object names from the manipulation (MAN) and visual (VIS) training condition.

Table 2. Training-induced lexicality effects.

Cluster size	Brain Region	*p*	*z*-score	x	y	z
A. Object Names (MAN + VIS) > PWs						
550	L Superior Frontal Gyrus	< .001	5.12	-22	58	0
	L Superior Orbital Frontal Gyrus		5.07	-28	60	-4
	L Middle Frontal Gyrus		5.06	-38	50	8
	L Middle Orbital Frontal Gyrus		4.41	-32	54	-12
540	L Middle Frontal Gyrus	< .001	4.85	-26	18	52
	L Inferior Frontal Gyrus (pars Triangularis)		3.68	-50	30	28
124	L Medial Orbital Frontal Gyrus	.038	4.17	-6	44	-8
2142	L Precuneus	< .001	7.62	-4	-68	36
	L Middle Cingulate Cortex		6.76	-4	-36	40
	L Cuneus		5.46	-16	-58	20
	R Precuneus		4.86	16	-60	28
	R Middle Cingulate Cortex		3.55	14	-46	36
917	L Inferior Parietal Lobule	< .001	6.20	-46	-52	48
	L Angular Gyrus		5.38	-42	-64	48
388	R Inferior Parietal Lobule	< .001	5.54	36	-52	44
	R Angular Gyrus		5.26	36	-66	48
271	L Middle Temporal Gyrus	.001	4.74	-62	-46	-12
	L Inferior Temporal Gyrus		4.37	-50	-34	-24
201	L Parahippocampal Gyrus	.006	5.02	-30	-36	-12
	L Dentate Gyrus (Hippocampus)		4.91	-26	-36	-8
B. PWs > Object Names (MAN + VIS)						
2924	L Precentral Gyrus	< .001	6.95	-60	4	28
	R Postcentral Gyrus		6.28	52	-18	36
	L Postcentral Gyrus		5.87	-58	-22	28
	R Posterior-Medial Frontal Gyrus		5.63	4	0	56
	L Posterior-Medial Frontal Gyrus		5.33	-2	0	56
	R Superior Frontal Gyrus		5.32	30	-10	68
	L Inferior Parietal Lobule		4.99	-44	-28	40

Note. Activations for the lexicality analysis: A. stronger activation for the processing of novel object names (manipulation [MAN] and visual [VIS] training) than pseudowords (PWs). B. vice versa. The significance threshold was set to cluster-level $p < .05$ (FWE corrected), with a $p < .001$cluster-defining threshold.

Table 3. Post-hoc analysis of training-induced functional connectivity

Cluster size	Seed ROIs	*p*	peak coordinates			Target region
			x	y	z	
A. Main Effect Type of Word						
MAN > VIS						
95	L Parahippocampal Gyrus	.017	-56	16	-16	L Temporal Pole
						L (anterior) Middle/Inferior Temporal Gyrus
75		.017	-36	36	-20	L Temporal Pole
						L Frontal Orbital Cortex
						L Frontal Pole
78		.017	-14	46	44	L Frontal Pole
						L Superior Frontal Gyrus
112	L Superior Frontal Gyrus	.008	-10	-78	-56	Cerebellum, Lobule VIIb
B. Main Effect Learning Group						
ACT > OBS						
64	R Inferior Parietal Lobule	.049	6	-100	8	Occipital Pole
101	L Inferior Middle Temporal Gyrus	.030	-4	-68	-28	Cerebellum, Lobules VI-VIII
OBS > ACT						
93	L Medial Orbital Frontal Gyrus	.013	-22	-58	-48	L Cerebellum, Lobules VIII-IX
C. Type of Word x Learning Group Interaction						
73	Precuneus	.049	-28	-56	60	L Superior Parietal Lobule
						L Superior Lateral Occipital Cortex
159	L Parahippocampal Gyrus	.001	28	-4	8	R Putamen
						R Insular Cortex

Note. Enhanced functional connectivity between seed ROIs (left) and target brain regions (right) for: A. Type of Word, B. Learning Group and C. Type of Word x Learning Group interaction. The significance threshold was set to cluster-level $p < .05$ (FDR corrected), with a $p < .001$ cluster-defining threshold.

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The role of experience for abstract concepts: Expertise modulates the electrophysiological correlates of mathematical word processing

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ABSTRACT

Embodied theories assign experience a crucial role in shaping conceptual representations. Supporting evidence comes mostly from studies on concrete concepts, where e.g., motor expertise facilitated action concept processing. This study examined experience-dependent effects on abstract concept processing. We asked participants with high and low mathematical expertise to perform a lexical decision task on mathematical and nonmathematical abstract words, while acquiring event-related potentials. Analyses revealed an interaction of expertise and word type on the amplitude of a fronto-central N400 and a centro-parietal late positive component (LPC). For mathematical words, we found a trend for a lower N400 and a significantly higher LPC amplitude in experts compared to nonexperts. No differences between groups were found for nonmathematical words. The results suggest that expertise affects the processing stages of semantic integration and memory retrieval specifically for expertise-related concepts. This study supports the generalization of experience-dependent conceptual processing mechanisms to the abstract domain.

1. Introduction

In semantic memory, information derived from our individual experience is stored in form of conceptual representations, which make this knowledge available for cognition, language and action. Theories on the neural underpinnings of semantic memory assign different roles to experience in the acquisition and processing of concepts. Theoretical approaches range from amodal/symbolic to grounded and embodied accounts (for reviews see Barsalou, 2008; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). The former postulate that initial experiential information is translated into modality-independent representations. In contrast, strongly embodied theories postulate that conceptual processing reactivates experiential information grounded in modality-specific areas, which were activated during the experience with the concepts' referents (Gallese & Lakoff, 2005; Glenberg, 1997). Theories assuming a weaker form of embodiment additionally include higher order convergence zones mediating such reactivation (Galetzka, 2017; Kiefer & Pulvermuller, 2012; Patterson, Nestor, & Rogers, 2007).

A growing body of research provides evidence for an involvement of experiential information from sensory and motor modalities in the representation of concrete concepts, which also reflects their belonging to a specific category (e.g., animals, tools, actions; Binder & Desai, 2011; Ralph, Jefferies, Patterson, & Rogers, 2017). It is, however, not clear whether the idea of grounding can be applied to abstract concepts (e.g., *justice, algebra, to think*), as they refer to entities that we cannot directly experience through our senses (Binder & Desai, 2011; Ralph et al., 2017). According to longstanding theories on semantic concreteness (e.g., *dual coding theory,* Paivio, 1986; *context availability model*, Schwanenflugel & Shoben, 1983), abstract concepts rely exclusively on linguistic information (for a recent review, see Hoffman, 2016). Recent advances within the grounded and embodied cognition framework emphasize the role of experiential aspects referring to social, introspective, affective and magnitude information for abstract concepts (Desai, Reilly, & van Dam, 2018; Ghio, Vaghi, & Tettamanti, 2013; Hoffman, 2016; Troche, Crutch, & Reilly, 2014; Wilson-Mendenhall, Simmons, Martin, & Barsalou, 2013).

Empirical evidence for the contribution of experiential information to abstract concept representation, however, is scarce. This shortage reflects the difficulty in devising an experimental paradigm that addresses individual experience for abstract concepts. Moreover, previous studies rarely used the category-specific approach applied in the research on concrete concepts to examine fine-grained abstract categories (e.g., social, mathematics, mental states; for an example, see Ghio, Vaghi, Perani, & Tettamanti, 2016). One experimental approach to examine the role of experience for concrete concepts has been, indeed, to compare semantic processing in experts versus nonexperts with

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respect to specific action categories (e.g., Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008; Locatelli, Gatti, & Tettamanti, 2012). The studies applying this method suggest that expertise, which can be defined as greater proficiency derived from experience or training, leads to an augmented recruitment of experiential modality-specific brain areas as resources for conceptual processing, and affects behavioral responses to verbal stimuli referring to the area of expertise.

The approach of comparing the processing of concepts of a specific category in experts versus nonexperts can be extended to the abstract domain. For this purpose, mathematical concepts (e.g., *multiplication*) seem particularly suitable. These can be considered as a specific abstract category, as suggested by the results of a previous psycholinguistic rating study (Ghio et al., 2013). Within the embodied framework, the hypothesis has been put forward that mathematical concepts are grounded in the same brain areas that were activated during mathematical experience such as calculation and number processing (Wilson-Mendenhall et al., 2013). Accordingly, Wilson-Mendenhall et al. (2013) showed that processing the word *arithmetic* (an abstract mathematical concept) compared to *convince* (an abstract social concept) induced greater activations in brain areas that were also activated during a numerical localizer task, including the intraparietal sulcus and the prefrontal cortex. These areas have been repeatedly shown to underlie mathematical cognition in studies on calculation and number perception (Dehaene, Molko, Cohen, & Wilson, 2004; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). The functional network underlying mathematical processing further includes a region in the bilateral inferior temporal cortex, which is more activated by the processing of visually presented Arabic numbers than by the processing of other symbols (i.e., letters or pictures) and has been labeled the visual number form area (Hermes et al., 2017; Shum et al., 2013).

By generalizing from the studies on expertise-induced modulations of action concepts to the mathematical abstract domain, one could hypothesize that the involvement of this mathematics-related prefrontal-intraparietal brain network in processing mathematical concepts would be modulated by individual experience. Evidence for a refinement of parietal areas involved in magnitude-processing by mathematical experience stems from a very recent study on 10–12 year old children (Suarez-Pellicioni & Booth, 2018). Another functional magnetic resonance imaging study examined the processing of advanced mathematical statements (e.g., *A finite left-invariant measure over a compact group is bi-invariant*) in professional mathematicians versus nonmathematicians (Amalric & Dehaene, 2016). In mathematicians, performing semantic judgments on these statements specifically induced activations in prefrontal and intraparietal brain regions involved in number processing and calculation. The study by Amalric and Dehaene (2016) also revealed that activations in the mathematics-related brain regions increased soon after mathematical statement offset and lasted for 15 s.

Previous studies applied event-related potentials (ERPs) to examine more fine-grained temporal dynamics of conceptual category processing (Kiefer, 2001; Lau, Phillips, & Poeppel, 2008). A largely used electrophysiological indicator of semantic processing is the N400 component. It has been associated not only with context-dependent semantic anomalies (Kutas & Hillyard, 1983), but also with the processing of isolated words or pictures (Lau et al., 2008). The N400 has been shown to be sensitive to semantic categories, as it differed between visual and auditory-related concepts (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008), between natural objects and artifacts (Kiefer, 2001), as well as between concrete and abstract concepts (Adorni & Proverbio, 2012; Barber, Otten, Kousta, & Vigliocco, 2013; Holcomb, Kounios, Anderson, & West, 1999; Kounios & Holcomb, 1994). These ERP effects have been interpreted in terms of category-specific access to lexical and semantic information, and are thus thought to reflect how conceptual knowledge is represented and which type of experiential information is being retrieved (Kiefer, 2001; but see Hauk, 2016). Furthermore, the N400 effect has been shown for incongruous vs. congruous arithmetic problems, which suggests that the processing of arithmetic and semantic anomalies relies on at least partly overlapping mechanisms (Niedeggen & Rösler, 1999; Niedeggen, Rösler, & Jost, 1999; for a positive component involved in arithmetic processing in this time window see, e.g., Dehaene, 1996).

Another ERP component that has been found to be sensitive to conceptual category differences, especially for the distinction between abstract and concrete concepts (e.g., Adorni & Proverbio, 2012; Kanske & Kotz, 2007), is a late positive component (LPC). A fronto-central LPC has been interpreted in terms of either mental imagery (Kanske & Kotz, 2007) or top-down control of semantic memory (Adorni & Proverbio, 2012). A more centro-parietal LPC has been suggested to reflect the recollection of individual experience (Strozak, Bird, Corby, Frishkoff, & Curran, 2016) and the retrieval of arithmetic facts involved in solving complex but not simple mathematical problems (Kiefer & Dehaene, 1997). In addition, a recent study demonstrated that the amplitude of the LPC was affected by arithmetic anomalies (Dickson & Federmeier, 2017; 400–600 ms).

In the present study, we specifically aimed to provide evidence for an experience-dependent modulation of mathematical concept processing with respect to mathematical expertise, which we objectively evaluated by administering a math test. We focused on the temporal dynamics of this modulation by measuring ERPs of participants with high versus low mathematical expertise performing a lexical decision task. To avoid a lack of effective comprehension of complex mathematical statements in nonexperts, we used single words instead of sentences (see Amalric & Dehaene, 2016). In a pre-experimental rating with nonexperts, the mathematical words' familiarity ratings did not differ significantly from those of nonmathematical abstract words, which served as a standard of comparison in our ERP study. This design allowed us to test the specificity of mathematical expertise in modulating the processing of words referring to mathematical abstract concepts. We hypothesized that, if mathematical expertise contributes to shaping conceptual representations of mathematical words, its modulatory effect on their conceptual processing might already become apparent in the N400 and in the LPC.

2. Method

2.1. Participants

All 46 participants of the present study were students, between 18 and 30 years old, had normal or corrected-to-normal vision, no history of psychiatric or neurological diseases and were right-handed. One participant had to be excluded due to technical problems during the data acquisition. Two additional participants were excluded from the statistical analysis because their mean LPC amplitudes deviated by more than three standard deviations from the mean of their respective group at three electrode sites (see Section 2.4.2.2 for a detailed description of the ERP analysis). The participants were recruited from different disciplines (mathematics, natural sciences, economics, psychology and humanities) at Heinrich Heine University Düsseldorf, in order to have a heterogeneous sample with respect to the scope of the mathematical education. Each participant completed a math test to quantify his/her mathematical expertise (see Section 2.2.1 for details). Participants with a test score of at least 7 points (total: 12 points) were assigned to the group with high mathematical expertise (HiEx). The HiEx group consisted of 23 participants (14 males, mean age = 22.8 years, *SD* = 3.3). Participants with test scores below 7 points were assigned to the group with low mathematical expertise (LoEx). This group consisted of 20 participants (10 males, mean age = 22.8 years, *SD* = 3.0). In the math test, participants of the HiEx group reached a significantly higher mean score (*M* = 8.4 points, *SD* = 1.0) than the participants of the LoEx group, (*M* = 3.3 points, *SD* = 2.3), as revealed by an independent samples *t*-test, $t(24.816) = 9.305$, $p < .001$, $d = 2.991$.

The study is in line with the declaration of Helsinki and was approved by the ethics committee of the Faculty of Mathematics and Natural Sciences at Heinrich Heine University. All participants gave their written informed consent prior to their participation, for which they received monetary compensation or course credit.

2.2. Material

2.2.1. Assessment of mathematical expertise

A math test assessed the level of mathematical expertise. It contained 12 mathematical problems (four arithmetical, four algebraic and four analytical problems). No time limit was set for completing the test. Two independent raters evaluated the participants' performance on the test. For each of the 12 problems one point was given for the correct solution; half a point if the approach to the problem was correct but the result was incorrect. The first 14 participants (2 HiEx, 12 LoEx) underwent the test after the EEG acquisition. In order to obtain a comparable number of experts and nonexperts, however, we subsequently targeted recruitment towards students of mathematics and natural sciences, and administered the test before the EEG acquisition. The following 29 participants (21 HiEx and 8 LoEx) were tested with this modified order of the procedure. In this second phase of the data acquisition, four volunteers did not undergo the EEG experiment because they did not reach the required score for the HiEx group.

2.2.2. Stimuli

For the lexical decision task (see Section 2.3.1), we used 31 mathematical (MAT) words, 31 nonmathematical (NONMAT) abstract words and 62 pseudo-words (see Table S1 in the supplementary material for the complete list). The MAT words included mathematical terms (e.g., *multiplication* or *mathematics*), but not number words. The NONMAT words mostly referred to mental or emotional states (e.g., *thought* or *fear*). We matched the words for length (number of letters; MAT: $M = 8.42$, $SD = 2.20$; NONMAT: $M = 7.74$, $SD = 2.00$; $t(60) = 1.268$, $p = .210$, $d = 0.323$) and lexical frequency (as assessed via the Wortschatz Lexikon of the University of Leipzig, http://wortschatz.uni-leipzig.de; MAT: $M = 14601.06$, $SD = 76282.49$; NONMAT: $M = 9766.16$, $SD = 17304.96$; $t(60) = 0.344$, $p = .732$, $d = 0.087$). Importantly, we matched MAT and NONMAT words for the psycholinguistic variables concreteness, abstractness, valence, and familiarity based on a pre-experimental rating by an independent sample of 64 German-speaking participants. MAT and NONMAT words differed significantly only in ratings of arousal (see Table 1, left).

To create word-like pseudo-words (e.g., *Hatrip*), we used the pseudo-word generator *Wuggy* (Keuleers & Brysbaert, 2010) with the German language module. The 31 MAT and 31 NONMAT words served as input, from which the program generated one pseudo-word each. The generation parameters restricted the output pseudo-words to match the input words in length of subsyllabic segments, letter length, transition frequencies between letters, and two out of three subsyllabic segments.

2.3. Experimental procedure

2.3.1. Lexical decision task

We applied a lexical decision task, which is a rather implicit task, in order to prevent overt attention to the semantic category manipulation. This task should therefore induce brain activations that reflect aspects of knowledge that are intrinsic to the representation of the concepts. When applied with word-like pseudo-words, as it was done in the present study (see Section 2.2.2), the lexical decision task has been shown to successfully induce semantic processing (Barber et al., 2013; Binder et al., 2003). For each participant, the acquisition took place in a dimly lit, electrically shielded EEG laboratory. Each trial began with a fixation cross that remained for a random interval of 1200–1600 ms, followed by a (pseudo-) word presented on the screen for 800 ms. Then, a blank screen was shown with a duration between 300 ms and 500 ms, followed by a screen prompting the participants' response. The participants' task was to distinguish between words and pseudo-words by pressing a button at the end of each trial. The response buttons (left and right) were randomly assigned to the decision options (word and pseudo-word) between trials. This procedure aimed to avoid motor artifacts caused by preparatory finger movements. If no response was given within 10 s, the next trial started automatically. The inter-trial interval had a duration of 500 ms, throughout which a blank screen was shown. All stimuli were presented on a black background in a white sans-serif font (Arial) of the size 20 pt.

Participants were instructed to look at the fixation cross and to try to avoid any movement. They first completed six practice trials with three words and three pseudo-words not included in the experiment. All

Table 1
Pre- and Post-experimental rating of psycholinguistic variables.

Scale	Word type	Pre-experimental rating				Follow-up rating	
		Independent raters	*df*[a]	*t*	*p*	LoEx	HiEx
Concreteness	MAT	3.51 (0.72)	60	0.939	.351	3.23 (1.83)	2.59 (1.57)
	NONMAT	3.32 (0.88)				2.94 (1.32)	2.24 (0.89)
Abstractness	MAT	5.30 (0.65)	53.130	0.881	.382	5.08 (1.79)	3.97 (1.90)
	NONMAT	5.12 (0.95)				4.55 (1.38)	4.58 (1.59)
Valence[b]	MAT	3.94 (0.29)	32.101	−0.033	.974	3.92 (0.40)	4.08 (0.79)
	NONMAT	3.95 (1.58)				4.10 (0.25)	4.00 (0.63)
Arousal	MAT	2.06 (0.44)	37.961	−9.934	< .001	1.45 (0.48)	2.35 (1.63)
	NONMAT	4.32 (1.19)				3.57 (1.19)	3.39 (1.24)
Familiarity	MAT	4.97 (0.61)	60	−1.140	.259	4.58 (1.87)	5.71 (1.20)
	NONMAT	5.16 (0.70)				5.68 (1.14)	5.04 (1.64)

Note. Means (*SD*) and inferential statistics for the independent samples *t*-tests of the pre-experimental stimulus validation rating are presented on the left side. The right side shows the respective follow-up rating results for participants with low (LoEx, $n = 13$) and high (HiEx, $n = 14$) mathematical expertise. The ratings were performed on 1–7 Likert scales for concreteness, abstractness, valence, arousal and familiarity, for the mathematical (MAT) and nonmathematical (NONMAT) words.

[a] Degrees of freedom were corrected in case of unequal variances.

[b] Valence was rated on a −3 (negative) to +3 (positive) scale, with 0 (neutral). For better comparability, values were transformed to a 1 (negative) to 7 (positive) scale with 4 depicting neutral values.

31 MAT, 31 NONMAT and 62 pseudo-words were presented twice in two separate experimental runs, adding up to 124 trials per run and to a total number of 248 trials. The order of the presentation of the words and pseudo-words was randomized within each run. During each experimental run, participants had the opportunity to take self-paced breaks after every 16 trials. The software Presentation (version 17.0, Neurobehavioral Systems Inc., Albany, CA, USA) was used for stimulus presentation and response recording. We used a Windows 10 Dell Intel Premium PC, a 22″ LED Dell monitor with 1680 * 1050 pixel resolution and a refresh rate of 60 Hz. Responses were given via two response buttons (left/right) on the Cedrus RB-844 response pad (Cedrus Corporation, San Pedro, California).

2.3.2. EEG recording

Twenty-eight Ag/AgCl ring electrodes were used to record electrical potentials on the scalp. They were positioned on a BrainCap textile softcap (Brainproducts GmbH, Germany) following the extended 10–20 system (Chatrian, Lettich, & Nelson, 1985; electrode sites were F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4 and PO8). The ground electrode was attached to site AFz, the linked reference electrodes to the mastoids. Careful scalp preparation kept impedances below 5 kΩ. Four additional electrodes recorded eye movements: one above and one below the left eye, as well as two at the outer canthi of the eyes. The EEG data was recorded with a BrainAmp DC amplifier (Brainproducts GmbH, Germany), a sampling rate of 1000 Hz, a lowpass filter of 1000 Hz and no highpass filter on a Windows 10 Dell Intel Premium PC with the Brain Vision Recorder software (version 1.20.0506, Brain Products GmbH, Germany).

2.4. Data analysis

Statistical analysis was conducted with IBM SPSS statistics (version 23.0, IBM Corporation, USA). For all inferential statistics, an alpha level of .05 was assumed. Degrees of freedom were adjusted according to the Greenhouse-Geisser and Welch-Satterthwaite methods, in the case of violations of sphericity and homogeneity, respectively. Follow-up tests for significant interactions as well as multiple correlations were corrected for the false discovery rate (FDR) with the procedure introduced by Benjamini and Hochberg (1995). Pseudo-words were not considered in the analyses, as we were not interested in lexicality effects. As measures of effect size we report η_p^2 or Cohen's *d* (calculated with JASP, version 0.8.3.1, JASP Team (2018)), where appropriate.

2.4.1. Behavioral data

Accuracy in the lexical decision task was calculated as the percentage of correct responses of all given responses. To analyze accuracy, we applied a 2 × 2 mixed ANOVA with the between-subjects factor Group (HiEx, LoEx) and the within-subjects factor Word Type (MAT, NONMAT).

2.4.2. EEG data

2.4.2.1. Data preprocessing. Data preprocessing was conducted with the Brain Vision Analyzer software (version 2.1, Brainproducts GmbH, Germany). We applied a Butterworth zero phase filter with a low cutoff of 0.1 Hz (time constant: 1.59, slope of 24 dB/Oct) and a high cutoff of 30 Hz, both with a slope of 48 dB/Oct. Additionally, a notch filter for the frequency of 50 Hz was applied to eliminate power supply hum. Then, a fast independent component analysis with classical sphering on a 120 s excerpt of the data of each participant was used to discard one or two components related to blink artifacts. The continuous EEG was then segmented into epochs from 300 ms before to 1200 ms after onset of the presented words. After a baseline correction that subtracted the mean signal of the 200 ms interval prior to stimulus onset from the data, an automatic procedure detected artifacts of non-cerebral origin at the 15 electrodes used in the statistical analyses (see Section 2.4.2.2). The parameters were the following: The maximal allowed voltage step from one data point to the next was 50 µV, the minimal/maximal allowed difference of amplitude values between the highest and the lowest data point within 100 ms intervals was 0.1 µV and 100 µV, respectively, and the minimally/maximally allowed amplitudes were ± 100 µV. Next, all artifact-free trials were averaged for each participant, separately for the two conditions of MAT and NONMAT words. On average, 59.8 MAT (*SD* = 2.9) and 59.6 NONMAT word trials (*SD* = 4.0) were used for the averaged ERPs.

2.4.2.2. ERP data analysis. Visual inspection of the ERP waveforms, averaged across participants, revealed a frontally pronounced N400, in line with the literature on N400 concreteness effects (Adorni & Proverbio, 2012; Barber et al., 2013; Holcomb et al., 1999; Kounios & Holcomb, 1994; Strozak et al., 2016), while the LPC was more positive over posterior electrodes (compare, e.g., Kandhadai & Federmeier, 2010a; Strozak et al., 2016). The N400 was quantified as the mean amplitude in the time window between 350 ms and 450 ms for each of the nine electrodes of a fronto-central cluster (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4). The LPC component, which was quantified as the mean amplitude between 500 ms and 700 ms after stimulus onset, was analyzed for a centro-parietal cluster of nine electrodes (C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4). Notably, a fronto-central P2 preceded the N400 (see Fig. 1A), and seemed to have a slightly higher amplitude in the LoEx group. In order to examine this potential group difference and its potential impact on the subsequent N400 and LPC results, we also extracted the P2 peak amplitude, which was defined as the local maximum between 170 ms and 300 ms at the nine fronto-central electrode sites. The P2, N400 and LPC were then analyzed in separate 2 × 2 × 3 × 3 mixed ANOVAs with the between-subjects factor Group (HiEx, LoEx) and the within-subject factors Word Type (MAT, NONMAT), Frontality (frontal, fronto-central, central for the N400 and P2; central, centro-parietal, parietal for the LPC) and Laterality (left, midline, right). Effects of the topographical factors Frontality and Laterality are reported only if they interacted significantly with at least one of the non-topographical factors.

3. Results

3.1. Behavioral data

Across participants, the mean accuracy in the lexical decision task was very high in all groups and conditions (at least 97.8%). Statistical analysis revealed that the Group did not have a significant effect on accuracy, $F(1, 41) = 4.595$, $p = .194$, $\eta_p^2 = .041$. The effect of the Word Type was significant, $F(1, 41) = 5.476$, $p = .024$, $\eta_p^2 = .118$, with a lower accuracy for MAT ($M = 98.5\%$, $SD = 1.8\%$) than for NONMAT words ($M = 99.1\%$, $SD = 1.3\%$). The Group × Word Type interaction was also significant, $F(1, 41) = 9.574$, $p = .004$, $\eta_p^2 = .189$. Dependent samples *t*-tests revealed that the HiEx group had a similar accuracy for MAT ($M = 99.2\%$, $SD = 1.2\%$) and NONMAT words ($M = 98.9\%$, $SD = 1.3\%$), $t(22) = 0.536$, $p = .598$, $d = 0.112$, while for the LoEx group accuracy was significantly lower for MAT ($M = 97.8\%$, $SD = 2.0\%$) than NONMAT words ($M = 99.4\%$, $SD = 1.3\%$), $t(19) = -3.866$, $p = .002$, $d = -0.864$.

3.2. ERP data

Fig. 1 depicts the ERPs elicited by MAT and NONMAT words, separately for the two groups, at all electrode sites involved in the analyses, as well as pooled across the nine electrodes used for the N400 and P2 analyses (Fig. 1A), and the nine electrodes used for the LPC analysis (Fig. 1B).

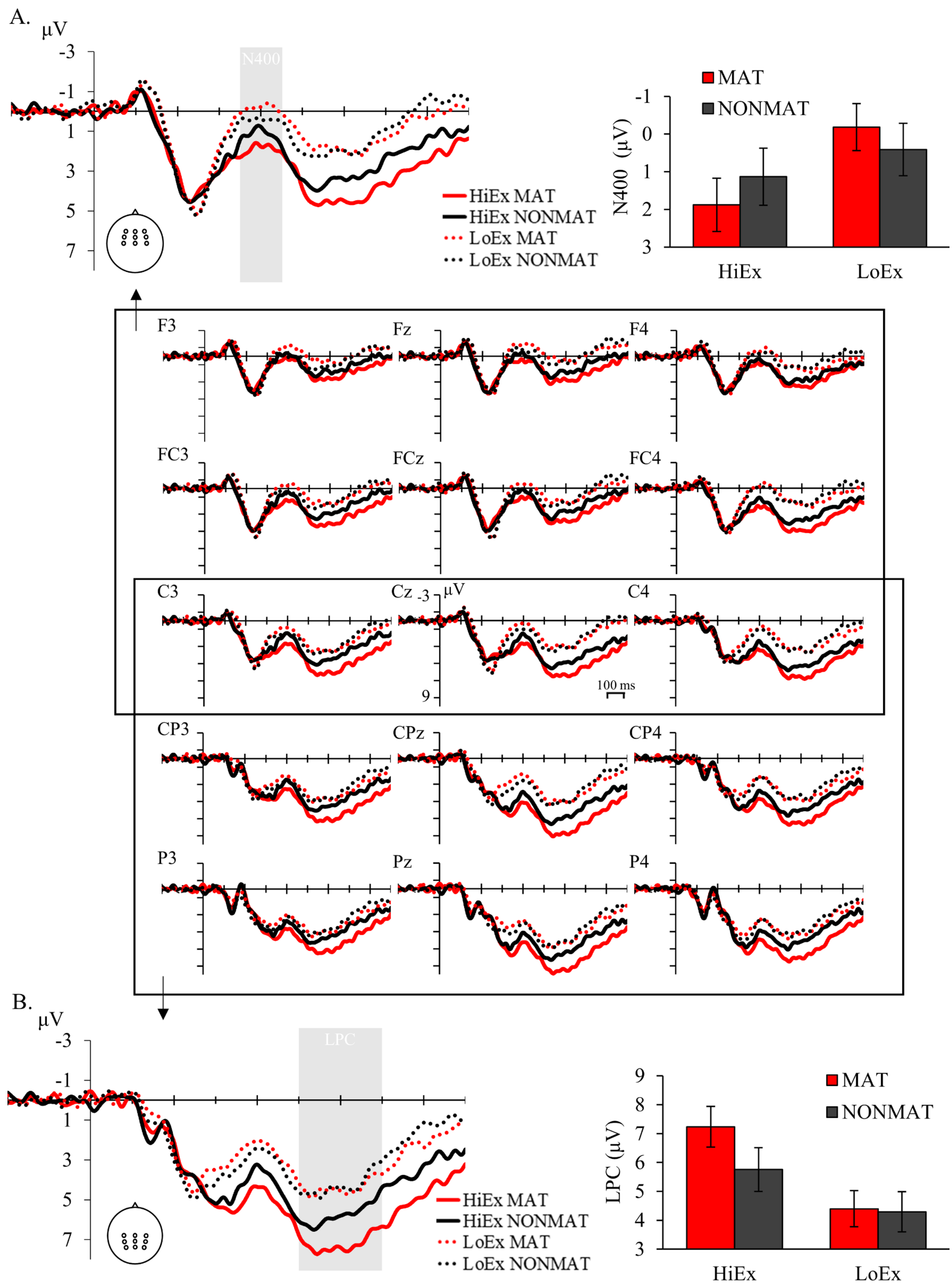

Fig. 1. Group and Word Type effects on N400 and LPC amplitudes. The central part shows the grand average ERPs elicited by mathematical (MAT) and non-mathematical (NONMAT) word processing in the high (HiEx, $n = 23$) and low (LoEx, $n = 20$) expertise group at the electrode sites included, respectively, in the N400 and LPC analyses. A. Left: ERPs pooled over the nine fronto-central electrodes. Shaded area marks the N400 time window (350–450 ms). Right: Mean amplitudes of the N400 separately for the levels of Group and Word Type. B. Left: ERPs pooled over the nine centro-parietal electrodes. Shaded area marks the LPC time window (500–700 ms). Right: Mean amplitudes of the LPC separately for the levels of Group and Word Type. Error bars represent ± one standard error.

3.2.1. P2

In the HiEx group the mean P2 peak amplitude was 6.251 μV (SD = 3.108 μV) for MAT and 6.419 μV (SD = 3.241 μV) for NONMAT words. The LoEx group showed mean amplitudes of 6.513 μV (SD = 2.416 μV) for MAT and 6.703 μV (SD = 3.170 μV) for NONMAT words. Neither Group, $F(1, 41) = 0.098$, $p = .756$, $\eta_p^2 = .002$, nor Word Type, $F(1, 41) = 0.467$, $p = .498$, $\eta_p^2 = .011$, nor the Group × Word Type interaction, $F(1, 41) = 0.003$, $p = .954$,

$\eta_p^2 < .001$, had a significant effect on P2 amplitudes. None of the interactions of the factors Group and Word Type with the topographical factors were significant (all $p \geq .064$). We thus assumed that the results reported in the following were not affected by the P2 component.

3.2.2. N400

Neither Group, $F(1, 41) = 2.070$, $p = .158$, $\eta_p^2 = .048$, nor Word Type, $F(1, 41) = 0.092$, $p = .763$, $\eta_p^2 = .002$, had a significant main effect on the N400 amplitudes. Notably, the Group × Word Type interaction was significant, $F(1, 41) = 6.993$, $p = .012$, $\eta_p^2 = .146$ (for descriptive statistics see the bar graph in Fig. 1A, right). The descriptive pattern showed a cross-over interaction with a reduced N400 for MAT compared to NONMAT words in the HiEx group (*mean difference* = 0.745 μV, *SD* = 1.724 μV) and an enhanced (less positive) N400 for MAT compared to NONMAT words in the LoEx group (*mean difference* = −0.592 μV, *SD* = 1.568 μV). To examine this significant interaction further, we first applied dependent samples *t*-tests to compare the two word types within each group. However, the N400 amplitude difference failed to reach significance in the HiEx group, $t(22) = 2.073$, $p = .100$, $d = 0.432$, as well as in the LoEx group, $t(19) = -1.688$, $p = .108$, $d = -0.377$. Focusing on between-group differences, independent samples *t*-tests revealed a trend towards reduced N400 amplitudes in response to MAT words for the HiEx compared to the LoEx group (*mean difference* = 2.060 μV, *SD* = 3.127 μV), $t(41) = 2.154$, $p = .074$, $d = 0.659$. The groups clearly did not differ regarding the N400 for NONMAT words (*mean difference* = 0.723 μV, *SD* = 3.405 μV), $t(41) = 0.694$, $p = .491$, $d = 0.212$. The three-way interaction Group × Frontality × Laterality was significant, $F(2.914, 119.464) = 3.047$, $p = .033$, $\eta_p^2 = .069$. Independent samples *t*-tests, comparing the two groups at each electrode site, revealed that the differences in N400 amplitudes were largest, albeit not significant, at electrode sites C4 (*mean difference*: 2.246 μV, *SE* = 0.975 μV), $t(41) = 2.303$, $p = .234$, $d = 0.704$, and FC4 (*mean difference*: 2.083 μV, *SE* = 0.944 μV), $t(41) = 2.207$, $p = .149$, $d = 0.675$ (all other $p \geq .374$). Descriptively, amplitudes were lower (more positive) in the HiEx group. No other interactions with the factors Group and Word Type and the topographical factors were significant (all $p \geq .055$).

3.2.3. LPC

The LPC was significantly affected by Group (more positive amplitudes in the HiEx group), $F(1, 41) = 5.419$, $p = .025$, $\eta_p^2 = .117$, as well as by Word Type (more positive amplitudes for MAT words), $F(1, 41) = 6.678$, $p = .013$, $\eta_p^2 = .140$. The Group × Word Type interaction was significant as well, $F(1, 41) = 4.972$, $p = .031$, $\eta_p^2 = .108$ (for descriptive statistics see the bar graph in Fig. 1B, right). Dependent samples *t*-tests revealed that the HiEx group had a significantly more positive LPC amplitude when processing MAT words compared to NONMAT words (*mean difference* = 1.477 μV, *SD* = 2.192 μV), $t(22) = 3.231$, $p = .008$, $d = 0.674$. In the LoEx group, MAT and NONMAT words did not elicit significantly different LPC amplitudes (*mean difference* = 0.109 μV, *SD* = 1.769 μV), $t(19) = 0.275$, $p = .786$, $d = 0.061$. Additional independent samples *t*-tests revealed that the HiEx group showed a significantly higher LPC amplitude than the LoEx group in response to MAT words (*mean difference* = 2.836 μV, *SD* = 2.948 μV), $t(41) = 3.147$, $p = .006$, $d = 0.962$. LPC amplitudes in response to NONMAT words did not differ significantly between groups (*mean difference* = 1.467 μV, *SD* = 2.948 μV), $t(41) = 1.409$, $p = .166$, $d = 0.431$. The Word Type × Frontality interaction also reached significance, $F(1.424, 58.375) = 3.865$, $p = .040$, $\eta_p^2 = 0.086$. In order to explore this interaction, we applied dependent samples *t*-tests comparing the amplitudes elicited by the two word types for each level of Frontality across groups. MAT words elicited significantly higher (more positive) LPC amplitudes than NONMAT words at parietal (*mean difference*: 0.988 μV, *SD* = 2.167 μV) and centro-parietal (*mean difference*: 0.872 μV, *SD* = 2.086 μV) electrode sites, $t(42) = 2.990$, $p = .014$, $d = 0.456$ and $t(42) = 2.742$, $p = .014$, $d = 0.418$, respectively. The comparison was not significant at central electrode sites, $p = .053$. There were no further significant interactions of the factors Word Type and/or Group with the topographical factors (all $p \geq .162$).

3.2.4. Correlation of ERP data with the math test score

To explore the relationship between expertise and ERP indicators of conceptual processing further, we correlated the participants' math test score with the MAT-NONMAT amplitude difference of the N400 and LPC (pooled over the nine electrodes that entered the analysis for each component) by means of two-sided Pearson correlations. N400 ($r = 0.487$, $p = .002$), as well as LPC ($r = 0.442$, $p = .003$) amplitude differences significantly (FDR corrected) correlated with the math test scores.

3.3. Follow-up psycholinguistic rating

To verify whether the degree of mathematical expertise of participants in the HiEx and LoEx group was also reflected by the psycholinguistic evaluation of the MAT and NONMAT words, we collected ratings of the experimental stimuli from the participants in our EEG study in a follow-up online rating. This rating included the same 7-point Likert-scales for concreteness, abstractness, valence, familiarity, and arousal as in the pre-experimental rating performed by a separate sample of participants (see Section 2.2.2). Fourteen participants from the HiEx and 13 from the LoEx group participated in the follow-up rating. Importantly, also in this sub-sample the performance in the math test differed significantly between the HiEx ($M = 8.3$, $SD = 0.7$) and LoEx group ($M = 3.5$, $SD = 2.5$), $t(13.755) = 6.716$, $p < .001$, $d = 2.673$.

3.3.1. Follow-up rating results

Descriptive statistics of the rating results are displayed in Table 1 (right). For each scale, ratings were analyzed by applying a 2 (Group: HiEx, LoEx) × 2 (Word Type: MAT, NONMAT) mixed ANOVA. Consistent with the pre-experimental rating, we did not find any significant main or interaction effects for the concreteness and valence scores (all $p > .160$).

There were no main effects of Group or Word Type on the abstractness and familiarity ratings (all $p \geq .368$). However, we found a significant Group × Word Type interaction for abstractness, $F(1, 25) = 4.484$, $p = .044$, $\eta_p^2 = .152$, and familiarity, $F(1, 25) = 13.144$, $p = .001$, $\eta_p^2 = .345$. Concerning abstractness ratings, the interaction was likely due to the fact that the pattern was descriptively reversed between the two groups. However, dependent samples *t*-tests did neither reveal a significant difference between MAT and NONMAT words in the LoEx group (*mean difference* = 0.531, *SD* = 1.472), $t(12) = 1.301$, $p = .218$, $d = 0.361$, nor in the HiEx group (*mean difference* = −0.615, *SD* = 1.341), $t(13) = -1.716$, $p = .218$, $d = -0.459$. Focusing on differences between the two groups, independent samples *t*-tests comparing the MAT words (*mean difference* = −1.112, *SD* = 1.846) and NONMAT words (*mean difference* = 0.035, *SD* = 1.490) did not reveal any significant differences either, $t(25) = -1.563$, $p = .262$, $d = -0.602$ and $t(25) = 0.060$, $p = .953$, $d = 0.023$, respectively. Concerning the familiarity ratings, dependent samples *t*-tests showed that the LoEx group rated MAT words lower than NONMAT words (*mean difference* = −1.099, *SD* = 1.170), $t(12) = -3.386$, $p = .010$, $d = -0.939$, while in the HiEx group MAT words yielded descriptively higher scores than NONMAT words, although this difference did not reach significance, $t(13) = 1.848$, $p = .087$, $d = 0.494$. Independent samples *t*-tests revealed no significant differences between the two groups for MAT (*mean difference* = 1.124, *SD* = 1.586), $t(20.224) = 1.841$. $p = .160$, $d = 0.721$ and NONMAT words (*mean difference* = −0.636, *SD* = 1.399), $t(23.213) = -1.164$, $p = .250$, $d = -0.448$.

Concerning the arousal ratings, we replicated the main effect of Word Type observed in the pre-experimental rating, $F(1, 25) = 36.402$,

$p < .001$, $\eta_p^2 = .593$, with MAT words receiving a significantly lower mean arousal rating than NONMAT words. Neither the main effect of Group, nor the Group × Word Type interaction was significant, $F(1, 25) = 0.864$, $p = .362$, $\eta_p^2 = .033$ and $F(1, 25) = 4.196$, $p = .051$, $\eta_p^2 = .144$, respectively.

3.3.2. Correlations between follow-up rating and ERP data

The results of the follow-up rating suggested that the degree of mathematical expertise was reflected by abstractness and familiarity ratings of MAT versus NONMAT words. For this reason, we examined whether abstractness and familiarity ratings correlated with the modulations of the ERPs that we observed. Specifically, we performed two-sided Pearson correlations (FDR corrected) for the MAT-NONMAT word rating differences (separately for abstractness and familiarity) with the MAT-NONMAT ERP amplitude differences (separately for N400 and LPC, pooled over nine electrodes). Note that only the sub-sample of the 14 HiEx and 13 LoEx participants who completed the follow-up ratings could be considered in this analysis. The results of the correlation analyses revealed that abstractness and familiarity rating differences neither correlated significantly with the N400 ($r = -0.036$, $p = .903$ and $r = 0.050$, $p = .903$, respectively) nor the LPC amplitude difference ($r = 0.212$, $p = .466$ and $r = 0.314$, $p = .466$, respectively).

4. Discussion

The current study aimed to extend previous evidence for experience-dependent neural representations of concrete concepts (Kiefer & Pulvermuller, 2012) to abstract concepts, by testing whether the individual degree of mathematical expertise (high versus low) specifically modulates the linguistic processing of mathematical concepts. Consistent with our hypotheses, we found a significant interaction of the factors Group and Word Type on the amplitudes of a fronto-central N400 and a centro-parietal LPC. For the N400 component the resolution of the interaction revealed that the processing of MAT words led to a trend-level reduction of the N400 amplitude in participants of the HiEx group compared to the LoEx group, while processing nonmathematical words clearly did not differ between groups. Concerning the LPC component, a significantly more pronounced LPC was found for the processing of mathematical words in the HiEx group compared to the LoEx group, again with no differences between groups for the processing of nonmathematical words. This pattern of results indicates that the degree of expertise with mathematical concepts influenced semantic processing differentially over time.

Single word studies suggest that the N400 amplitude is sensitive to the ease of lexical access and activation of semantic information from long-term memory, and thus reflects aspects of semantic categorization (Kutas & Federmeier, 2000). Specifically, a reduction of the N400 amplitude is considered to reflect either a facilitated activation of semantic features associated with the lexical item, or a reduced need to integrate information from multiple semantic regions (Lau et al., 2008). A higher N400 in response to arithmetic incongruences has been interpreted to reflect a higher processing effort comparable to semantically anomalous sentences (Niedeggen & Rösler, 1999; Niedeggen et al., 1999). Thus, the trend for relatively reduced N400 amplitudes elicited by MAT word processing in the HiEx compared to the LoEx group might be interpreted in terms of a relatively reduced processing effort for MAT words in participants with a high level of mathematical experience. Importantly, however, the N400 amplitude has been sensitive to multiple factors that modulate lexical access (Kutas & Federmeier, 2000; Lau et al., 2008). This raises the question which of the possible factors led to the relatively reduced N400 amplitudes elicited by the processing of mathematical compared to nonmathematical words in the HiEx group. The psycholinguistic rating scores collected in this study can help to exclude some potentially confounding variables, as MAT and NONMAT words were matched for concreteness and valence. Arousal ratings were significantly lower for MAT words in the pre-experimental as well as in the follow-up rating. However, as the arousal ratings for the two word types did not differ between HiEx and LoEx participants, and as arousal has been found to have an impact on word processing only in interaction with valence (Bayer, Sommer, & Schacht, 2010; Yao et al., 2016), an influence of arousal on our ERP results seems unlikely.

Another potentially confounding factor is word familiarity: Studies have shown that less familiar words result in higher N400 amplitudes (Bader & Mecklinger, 2017; Barber, Vergara, & Carreiras, 2004; Lau et al., 2008; Rugg, 1990; Strozak et al., 2016; Vergara-Martinez & Swaab, 2012; Vergara-Martinez, Comesana, & Perea, 2017). Although MAT and NONMAT words were counterbalanced for their frequency of occurrence and familiarity, as measured in a pre-experimental validation rating with an independent sample of nonexperts, a follow-up rating showed that MAT words were indeed rated as less familiar than NONMAT words by LoEx participants, while there was no significant difference to the HiEx participants' familiarity ratings. However, we found that familiarity ratings did not correlate with the N400 amplitude. It can therefore be ruled out that the N400 amplitude modulation by expertise solely reflected differences in word familiarity.

Considering our experimental manipulation, another factor potentially influencing the N400 is the extent of mathematical experience of the participants, which has probably enriched the knowledge they associate with mathematical concepts. We quantified participants' mathematical expertise in terms of their math test performance and showed that it indeed correlated with the N400 amplitude. The HiEx participants' higher mean test score could thus serve as a complementary measure of familiarity with mathematical concepts, providing a more objective, content-based criterion than the merely subjective amount of exposure assessed via familiarity ratings. The test scores might reflect qualitatively different experiences with mathematical concepts, including the successful application of solution strategies. Thus, it seems likely that the HiEx group was more familiar not with the MAT words per se but with the underlying MAT concepts, which reflects the core of their expertise.

To our knowledge, there have not been any ERP studies investigating the role of expertise in conceptual processing of abstract concepts so far. However, indirect evidence that the processing of abstract concepts associated with an experientially enriched content might modulate the N400 amplitude comes from studies on abstract emotional concepts. Stronger experience-dependent emotional content of abstract words facilitated their processing, as reflected in faster reaction times (Kanske & Kotz, 2007; Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011), and reduced N400 amplitudes (Kanske & Kotz, 2007; Trauer, Kotz, & Muller, 2015). Accordingly, the consolidated mathematical experience of the HiEx participants could have enriched their mathematical conceptual representations, leading to the relatively reduced fronto-central N400 amplitude. The current study, however, cannot disentangle whether this effect reflects a facilitated lexical access and feature retrieval, or rather world knowledge integration (Lau et al., 2008). These aspects could be addressed in future research, e.g., by systematically varying a given sentential context for the mathematical words.

Yet another interpretation for the N400 differences between the HiEx and LoEx groups is that the extent of mathematical experience might affect what type(s) of semantic features are associated with mathematical concepts. Category-specific N400 modulation effects have been interpreted as indicative of differences in the type of experience-dependent semantic information (e.g., visual, action) activated by concrete concepts (Adorni & Proverbio, 2009; Kellenbach, Wijers, & Mulder, 2000; Kiefer, 2001, 2005). In studies comparing concrete and abstract concepts, higher N400 amplitudes at frontal electrode sites have been interpreted as indicating stronger sensorimotor integration processes for concepts with a more pronounced inherent multimodality (Adorni & Proverbio, 2012; Barber et al., 2013; Holcomb et al., 1999; Kounios & Holcomb, 1994). In line with these previous studies, we can speculate that the fronto-central N400 modulations we observed for the processing of mathematical concepts reflect a stronger integration of multimodal (i.e., visuospatial and sensorimotor) information in LoEx than HiEx participants. So far, there is only limited evidence for the contribution of multimodal information to the representation of mathematical concepts (Ghio et al., 2013).

However, previous research found abstract number concepts (e.g., *nine*) to be grounded in visuospatial (Spatial Numerical Association of Response Codes [SNARC] effect; Dehaene, Bossini, & Giraux, 1993; Fischer, 2008; Marghetis, Landy, & Goldstone, 2016) and in sensorimotor brain areas, as derived from either spatial number mapping or finger counting habits (Domahs, Moeller, Huber, Willmes, & Nuerk, 2010). Notably, Cipora et al. (2016) found that the SNARC effect was absent in participants with mathematical expertise, which suggests a reduced involvement of multimodal information in abstract numerical representations for mathematical experts (Cipora et al., 2016; but see Sella, Sader, Lolliot, & Cohen Kadosh, 2016). Similarly, the relatively smaller N400 amplitude for MAT words in the HiEx group of this study might be interpreted in terms of such a reduced involvement of multimodal information in mathematical conceptual processing. MAT words received descriptively higher abstractness ratings from LoEx than HiEx participants in the follow-up rating of this study, which seems contradictory at first. However, this might again reflect the actual mathematical experience with the MAT concepts, which made the words seem less abstract to HiEx participants (see also above). Future research might use more fine-grained ratings of abstractness or even a feature production task in order to explore the content that participants with different levels of expertise assign to abstract mathematical concepts.

For the HiEx participants, in turn, mathematical concepts might rely more on mathematics-related semantic information, and therefore activate a brain network specialized on mathematical processing (Wilson-Mendenhall et al., 2013). Intriguingly, an ERP study showed that, when compared to other concrete categories, numerals were the only category that did not elicit a negativity but rather a bilateral parietal positivity (Dehaene, 1995). Such a parietal positivity was also found in number magnitude comparison (Dehaene, 1996) and multiplication (Kiefer & Dehaene, 1997). These results are also consistent with recent findings of the recruitment of number processing and calculation brain areas for the processing of mathematical statements in mathematicians (Amalric & Dehaene, 2016). Although we also observed a descriptively reduced N400 amplitude associated with the processing of mathematical concepts in the HiEx group, a bilateral parietal positivity did not become apparent in that time interval in our data, but in the later one of the LPC.

This later parietal positivity was more pronounced for MAT words in the HiEx group. In addition to this interaction, we also found significant main effects of Group and Word Type. However, as pairwise comparisons resolving the interaction showed that the main effects were driven by the higher LPC amplitudes in response to MAT words in the HiEx group, we will not interpret them separately. The parietal pronunciation of the LPC in the present study might suggest that the mathematical network identified by Amalric and Dehaene (2016), in which parietal structures play a prominent role, was recruited during mathematical conceptual processing in the HiEx group. Kiefer and Dehaene (1997) reported a longer lasting and bilateral instead of only left-hemispheric positivity over parietal areas for complex versus simpler mathematical problems. The authors interpreted this problem size effect as reflecting the retrieval of mathematical knowledge from parietal areas. A recent study with children also found a stronger bilateral parietal activation for a harder (but not easier) magnitude processing task and interpreted it to reflect a refined representation of quantity induced by mathematical experience (Suarez-Pellicioni & Booth, 2018). Such a recall of mathematical knowledge from parietal areas might also have caused the LPC modulation observed in the current study. Our LPC results might thus reflect the stronger reactivation or integration of mathematical knowledge in mathematical experts. This interpretation should be considered with caution, however, given that the spatial information provided by the scalp topography is limited. Furthermore, although there is some evidence that the LPC is sensitive to mathematical stimulus processing, the direction of this modulation in our study is not consistent with an interpretation in terms of ease of retrieval of semantic features (Dickson & Federmeier, 2017; Guthormsen et al., 2016).

Alternatively, the parietal LPC modulation might be interpreted in terms of recollection of individual experience associated with the conceptual content. While a more fronto-central LPC for the processing of concrete versus abstract conceptual categories has been interpreted as indicating mental imagery (Kanske & Kotz, 2007), higher parietal LPC amplitudes have more consistently been linked to strategic, conscious memory processes. This interpretation is based on studies with healthy subjects (Kandhadai & Federmeier, 2010a; Strozak et al., 2016), as well as aphasic (Swaab, Brown, & Hagoort, 1998) and amnestic (Olichney et al., 2000) patients. Usually, LPC modulations depend on tasks explicitly demanding memory recollection (Fischer-Baum, Dickson, & Federmeier, 2014; Kandhadai & Federmeier, 2010b), while the lexical decision task we applied in this study is a rather implicit task. This suggests that rather than being task-related, LPC modulations in our study might be related to the degree of individual experience, with mathematical expertise motivating the recollection of information related to the mathematical concepts. The higher LPC amplitudes elicited by MAT words in the HiEx group might therefore result from explicit, strategic memory retrieval, driven by a stronger recollection of experiential information (Daltrozzo, Wioland, & Kotchoubey, 2007; Guthormsen et al., 2016; Kandhadai & Federmeier, 2010a) or recollection-based reanalysis (Van Petten & Luka, 2012). This recollection of consolidated experiential information might also be required for mental simulations involved in higher level conceptual processing (Barsalou, 2008).

In conclusion, the present study provides evidence for experience-dependent modulations of mathematical concept processing, reflected by specific modulations of mathematical word processing. The relatively reduced N400 amplitudes elicited by mathematical words in the expert group could be the result of a less effortful conceptual processing as well as a reduced reliance on multimodal integration. The more positive LPC elicited by mathematical words in the experts possibly reflects an enhanced retrieval of experiential information in their area of expertise. Taken together, our results speak for a contribution of mathematical experience to shaping and processing mathematical concepts.

5. Statement of significance

This study investigates the role of experience on processing abstract mathematical concepts. By applying event-related potentials, we demonstrate that the level of mathematical expertise (experts vs. non-experts) specifically affects automatic and strategic stages of mathematical word processing. These results provide evidence of experience-dependent mechanisms contributing to abstract concept processing.

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Appendix A. Supplementary material

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