The Neural Basis of Conceptual Knowledge Retrieval

Insights from fMRI & TMS in the Healthy Human Brain

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ABSTRACT

Conceptual knowledge about objects, people and events in the world is central to human cognition, underlying core cognitive abilities such as object recognition and use, and word comprehension. Previous research indicates that concepts consist of perceptual and motor features represented in modality-specific perceptual-motor brain regions. In addition, cross-modal convergence zones integrate modality-specific features into more abstract conceptual representations.

However, several questions remain open: First, to what extent does the retrieval of perceptual-motor features depend on the concurrent task? Second, how do modality-specific and cross-modal regions interact during conceptual knowledge retrieval? Third, which brain regions are causally relevant for conceptually-guided behavior? This thesis addresses these three key issues using functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) in the healthy human brain.

Study 1—an fMRI activation study—tested to what extent the retrieval of sound and action features of concepts, and the resulting engagement of auditory and somatomotor brain regions depend on the concurrent task. 40 healthy human participants performed three different tasks—lexical decision, sound judgment, and action judgment—on words with a high or low association to sounds and actions. We found that modality-specific regions selectively respond to task-relevant features: Auditory regions selectively responded to sound features during sound judgments, and somatomotor regions selectively responded to action features during action judgments. Unexpectedly, several regions (e.g. the left posterior parietal cortex; PPC) exhibited a task-dependent response to both sound and action features. We propose these regions to be “multimodal”, and not “amodal”, convergence zones which retain modality-specific information.

Study 2—an fMRI connectivity study—investigated the functional interaction between modality-specific and multimodal areas during conceptual knowledge retrieval. Using the above fMRI data, we asked (1) whether modality-specific and multimodal regions are functionally coupled during sound and action feature retrieval, (2) whether their coupling depends on the task, (3) whether information flows bottom-up, top-down, or bidirectionally, and (4) whether their coupling is behaviorally relevant. We found that functional coupling between multimodal and modality-specific areas is task-dependent, bidirectional, and relevant for conceptually-guided behavior. Left PPC acted as a connectivity “switchboard” that flexibly adapted its coupling to task-relevant modality-specific nodes.

Hence, neuroimaging studies 1 and 2 suggested a key role of left PPC as a multimodal convergence zone for conceptual knowledge. However, as neuroimaging is correlational, it remained unknown whether left PPC plays a causal role as a multimodal conceptual hub. Therefore, study 3—a TMS study—tested the causal relevance of left PPC for sound and action feature retrieval. We found that TMS over left PPC selectively impaired action judgments on low sound–low action words, as compared to sham stimulation. Computational simulations of the TMS-induced electrical field revealed that stronger stimulation of left PPC was associated with worse performance on action, but not sound, judgments. These results indicate that left PPC causally supports conceptual processing when action knowledge is task-relevant and cannot be compensated by sound knowledge. Our findings suggest that left PPC is specialized for action knowledge, challenging the view of left PPC as a multimodal conceptual hub.

Overall, our studies support “hybrid theories” which posit that conceptual processing involves both modality-specific perceptual-motor regions and cross-modal convergence zones. In our new model of the conceptual system, we propose conceptual processing to rely on a representational hierarchy from modality-specific to multimodal up to amodal brain regions. Crucially, this hierarchical system is flexible, with different regions and connections being engaged in a task-dependent fashion. Our model not only reconciles the seemingly opposing grounded cognition and amodal theories, it also incorporates task dependency of conceptually-related brain activity and connectivity, thereby resolving several current issues on the neural basis of conceptual knowledge retrieval.

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1. GENERAL INTRODUCTION

Imagine you are walking through the woods when suddenly you hear a sound. You quickly identify the sound as the howling of a wolf. Immediately, the image of a wolf appears in your mind: its characteristic shape and size, the color and texture of its fur, and how it moves. You are reminded that wolves are similar to dogs—you briefly think of your heart-warming experiences with dogs—but in contrast to dogs, wolves are dangerous wild animals that you should better not try to pet. Thus, you decide to continue your walk in a different direction than where the sound came from.

This is an example of conceptual knowledge retrieval in action. A concept 'wolf' is stored in your brain that contains all your knowledge about wolves. Much of this knowledge was triggered by the mere sound of a wolf, and you used it to guide your behavior.

1.1 What are concepts?

Concepts are our mental representations of the categories of objects, people, and events in the world (Binder and Desai, 2011; Binder et al., 2009; Kiefer and Pulvermüller, 2012). They comprise our vast knowledge about these categories, which is abstracted away from specific exemplars and situations (Kiefer and Pulvermüller, 2012; Lambon Ralph, 2014). For instance, the concept 'cat'[1] comprises all our knowledge about cats, generalized across different exemplars and experiences of cats.

Conceptual knowledge is crucial for many cognitive abilities. For example, concepts are essential for object recognition, enabling us to recognize superficially distinct entities as part of the same category (e.g. both pears and pineapples as fruit) and distinguish superficially similar entities that belong to different categories (e.g. pears and lightbulbs) (Binder and Desai, 2011; Lambon Ralph, 2014; Lambon Ralph et al., 2010).

Moreover, concepts support object use: Many objects, especially tools like toothbrushes or hammers, have certain actions associated with them (also known as "affordances"; van Elk et al., 2014). Having a concept—a categorical representation—of such objects, which includes these actions, thus allows for more efficient use of these objects (Culham and Valyear, 2006; Johnson-Frey, 2004; Kellenbach et al., 2003).

Finally, concepts underlie the meaning of words (e.g. "cat") and therefore play an essential role in language comprehension and production (Binder and Desai, 2011; Binder et al., 2009; Lambon Ralph, 2014). Hence, as concepts are undoubtedly crucial for human cognition, a central question in cognitive neuroscience has been how concepts are represented and processed in the human brain (for reviews, see Borghesani and Piazza, 2017; Hauk and Tschentscher, 2013; Jefferies, 2013; Kiefer and Pulvermüller, 2012; Lambon Ralph et al., 2016; Meteyard et al., 2012; Pulvermüller, 2013; Thompson-Schill, 2003).

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[1] In this thesis, concepts will be indicated by single quotes, whereas words will be indicated by double quotes in order to distinguish them.

1.2 Amodal theories

According to the traditional view in cognitive science—the “amodal” view—concepts consist of abstract, amodal symbols (Fodor, 1975; Pylyshyn, 1984). These symbols stand in an arbitrary, albeit unique relationship to what they represent in the world. For instance, under this view, the meaning of the word “banana” would be a unique arbitrary symbol like the numeric sequence *4011*—the American grocery store number for bananas (Kemmerer, 2014, pp. 274–275). Importantly, understanding the word “banana” only requires accessing this symbol without the activation of perceptual-motor information about how bananas look, feel, taste, etc. Indeed, according to the amodal view, the conceptual system is completely separate from the modality-specific systems for perception and action (Barsalou, 2008; Meteyard et al., 2012). Perceptual-motor information about concepts is assumed to be transduced into an abstract symbolic format during concept learning (Barsalou, 1999; Pylyshyn, 1984).

However, amodal theories face a severe problem—the “symbol grounding problem” (Harnad, 1990; Searle, 1980): If every concept exclusively consisted of abstract symbols, trying to determine the meaning of a concept would be akin to trying to identify the meaning of a word in a foreign language (e.g. Mandarin Chinese) using a monolingual dictionary in that language (Harnad, 1990). One would go from symbols that are meaningless to oneself (e.g. 好) to other meaningless symbols (e.g. 很,甚,太), and so on, leading to an infinite loop—one would never be able to determine the word’s meaning in this way.

1.3 Grounded cognition theories

The symbol grounding problem inspired so called “grounded cognition” theories which propose concepts to consist of perceptual and motor features (Barsalou, 1999, 2008; Kiefer and Pulvermüller, 2012; Meteyard et al., 2012). For example, the concept ‘dog’ comprises a dog’s typical shape, color, motion, smell and feel, as well as the actions one typically performs with dogs. The key idea is that these perceptual-motor features are represented in the same modality-specific perceptual-motor brain regions that process these modalities during actual perception and action (Barsalou, 1999; Pulvermüller, 1999). For example, visual features of a concept (e.g. shape, color) are represented in visual regions, sound features in auditory regions, action features in somatomotor[2] regions, and so on. Therefore, proponents of the grounded view often posit that concept retrieval (e.g. to understand the word “dog”) involves a “simulation”, i.e. a partial reinstatement of the brain activity during actual perceptual-motor experience (e.g. experiences of dogs; Barsalou, 1999, 2008; Kiefer and Pulvermüller, 2012). Importantly, such simulations need not manifest themselves as vivid and conscious mental imagery, but can be vague or even unconscious (Kiefer and Barsalou, 2013; Trumpp et al., 2014).

1.4 Modality-specific perceptual-motor regions

Evidence for grounded cognition theories mainly comes from neuroimaging studies showing that conceptual processing related to a certain perceptual-motor modality engages the corresponding modality-specific brain regions (for reviews, see Hauk and Tschentscher, 2013;

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[2] Throughout this thesis, the term “somatomotor” will be used to refer to the collective of motor and somatosensory brain regions (cf. Yeo et al., 2011). Both motor and somatosensory regions are involved in real object-directed actions (Hardwick et al., 2018; van Elk et al., 2014) as well as action-related conceptual processing (Desai et al., 2010; Fernandino et al., 2016a).

Kiefer and Pulvermüller, 2012; Meteyard et al., 2012). For instance, studies using functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) have revealed that sound-related conceptual processing activates auditory brain regions (Fernandino et al., 2016a; Goldberg, 2006; Hoenig et al., 2011; Kellenbach et al., 2001; Kiefer et al., 2008), while action-related conceptual processing engages motor and somatosensory areas (Fernandino et al., 2016a; Hauk et al., 2004; Hauk and Pulvermüller, 2004; Martin et al., 1995; Tettamanti et al., 2005). In particular, Kiefer et al. (2008) found that reading sound-related words (e.g. "telephone", "violin") produces stronger activation than non-sound-related words (e.g. "pillow", "flower") in a region within the left posterior superior / middle temporal gyrus (pSTG/MTG) that was also activated during real sound perception (Figure 1.1A). Hauk et al. (2004) showed that reading action verbs engages the motor cortex in a somatotopic fashion (Figure 1.1B): Mouth-related words (e.g. "lick") activate the mouth region, hand-related words activate the hand region, and leg-related words (e.g. "kick") engage the leg region.

Notably, some authors have argued that such modality-specific activations could reflect post-conceptual processes (e.g. mental imagery) that are not *causally* involved in conceptual processing (Mahon and Caramazza, 2008). This is plausible since neuroimaging is correlational and exhibits a low temporal resolution (Walsh and Cowey, 2000). However, studies using methods with a high temporal resolution, such as electroencephalography (EEG) or magnetoencephalography (MEG), have revealed modality-specific effects within 150–200 ms after stimulus onset (e.g. Klepp et al., 2014; Niccolai et al., 2014; Popp et al., 2016; Shtyrov et al., 2004), which is considered too fast to reflect post-conceptual processes (Hauk and Tschentscher, 2013; Kiefer and Pulvermüller, 2012). Early modality-specific activity can occur even when stimuli are unattended (Pulvermüller and Shtyrov, 2006; Shtyrov et al., 2004) or not consciously perceived (Trumpp et al., 2013b, 2014). This suggests that modality-specific perceptual-motor activations during conceptual tasks indeed reflect conceptual feature retrieval (Hauk, 2016; Hauk et al., 2008; Kiefer and Pulvermüller, 2012).

Moreover, studies using methods that allow for causal inferences, such as neuropsychological patient studies or transcranial magnetic stimulation (TMS), indicate a causal role of modality-specific perceptual-motor areas in conceptual processing. Lesions of somatomotor and auditory brain regions are associated with deficits in action-related (Bak et al., 2001, 2006; Grossman et al., 2008; Hillis et al., 2006) and sound-related conceptual processing (Bonner and Grossman, 2012; Trumpp et al., 2013a), respectively. For example, Trumpp et al. (2013a) found that a patient with a focal lesion in the left pSTG/MTG was selectively impaired at conceptual tasks on sound-related, but not non-sound-related, everyday-object concepts. Importantly, the patient also showed an impairment in perceptual sound recognition of the same everyday objects. This is in line with the view that the same brain region is involved in both sound-related conceptual processing and real auditory perception, supporting grounded cognition theories. In addition, several studies indicate that TMS over the motor cortex of healthy volunteers impairs action-related conceptual processing (Lo Gerfo et al., 2008; Pulvermüller et al., 2005; Repetto et al., 2013; Vukovic et al., 2017). However, note that TMS evidence for a causal role of modality-specific perceptual-motor regions is currently scarce for other regions than the motor cortex and for other modalities than action (e.g. sound; Hauk and Tschentscher, 2013).

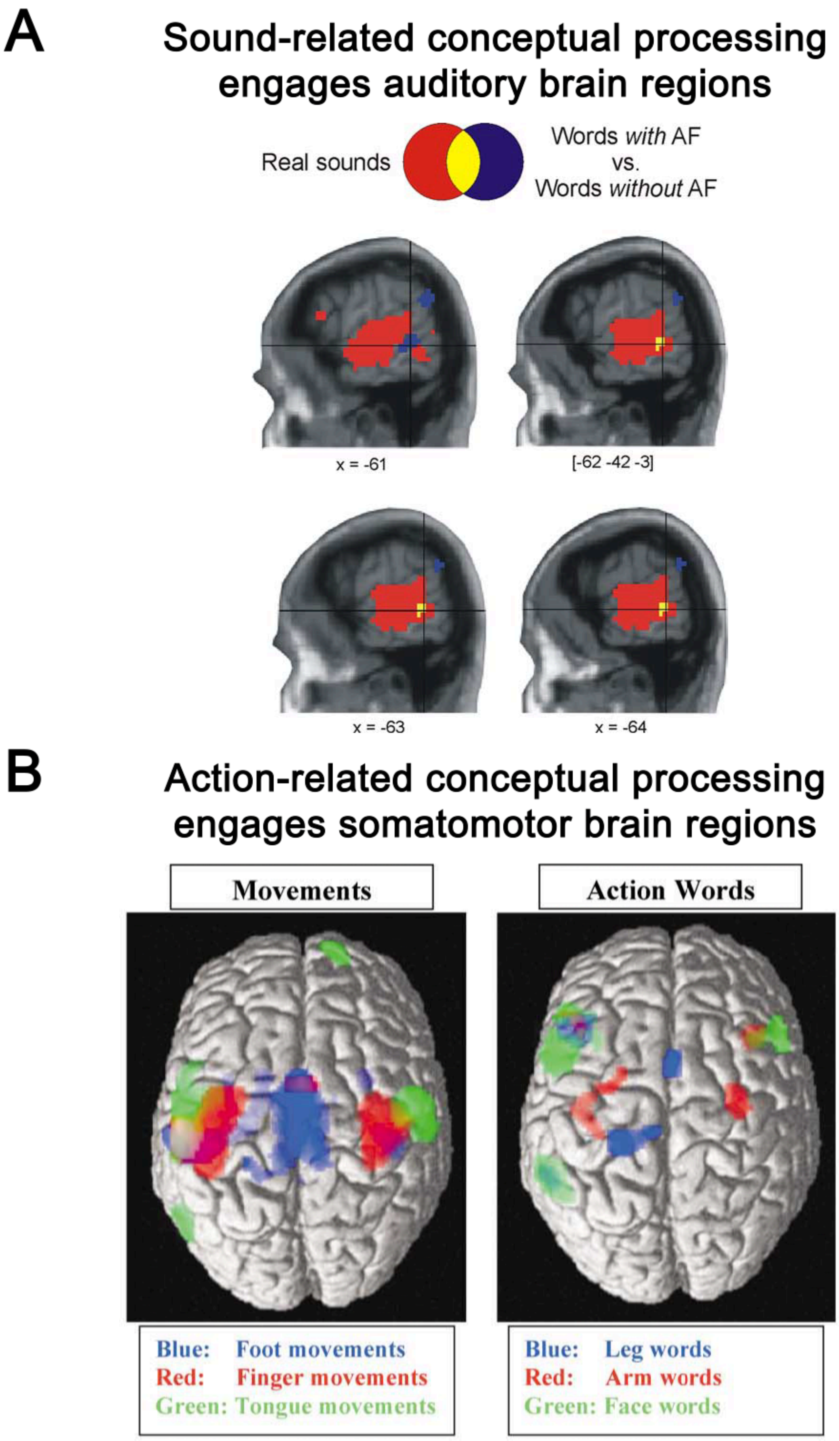

Fig. 1.1: (A) In an fMRI study by Kiefer et al. (2008), functional activation for words with vs. without auditory features (AF; blue) overlapped with real sound perception (red) in a region within the left posterior temporal lobe (yellow). (B) In a study by Hauk et al. (2004), reading action words (right) related to the leg (blue), arm (red), or face (green) activated the motor cortex in a somatotopic fashion, similar to real movements (left) of the foot (blue), fingers (red), and tongue (green).

1.5 Cross-modal convergence zones

In addition to modality-specific perceptual-motor regions, previous studies suggest an involvement of more abstract brain regions in conceptual processing. Pertinent evidence comes from two main sources: (1) semantic dementia, and (2) functional neuroimaging.

Semantic dementia (SD) is a neurodegenerative disorder characterized by the progressive loss of conceptual knowledge across virtually all concept types (e.g. concrete and abstract, living and man-made), input modalities (e.g. written and spoken words, pictures, sounds, smells, and tastes), and output modalities (e.g. speaking, writing, drawing, and using objects) (for reviews, see Jefferies, 2013; Lambon Ralph et al., 2016; Patterson and Lambon Ralph, 2016; Patterson et al., 2007). SD patients typically show a specific-to-general decline, i.e. less familiar, atypical and specific knowledge is affected earlier and more severely than general knowledge shared across many related concepts (Jefferies, 2013; Lambon Ralph et al., 2010; Rogers et al., 2004). For example, an SD patient might correctly recognize a typical house cat, but not a hairless Sphynx cat, as a cat (Lambon Ralph et al., 2010). These characteristics suggest an impairment of central, abstract conceptual representations (Jefferies, 2013; Lambon Ralph et al., 2016, 2010; Patterson et al., 2007).

SD is associated with atrophy and hypometabolism in the bilateral anterior temporal lobes (ATL) (Ding et al., 2020; Galton et al., 2001; Jefferies, 2013; Mion et al., 2010; Mummery et al., 2000). Therefore, many researchers propose the ATL to constitute a central, abstract "hub" for conceptual knowledge (Jefferies, 2013; Lambon Ralph et al., 2016; Patterson et al., 2007; Rogers et al., 2004). A key role of the ATL in conceptual processing is further supported by functional neuroimaging meta-analyses (Rice et al., 2015; Visser et al., 2010), which indicate an engagement of the ATL in a wide variety of conceptual tasks on spoken and written words, or pictures. Moreover, TMS over the ATL of healthy volunteers produces a deficit similar to SD, impairing conceptual processing across various types of concepts and in-/output modalities (e.g. picture naming, semantic judgments on words and pictures; Lambon Ralph et al., 2009; Pobric et al., 2010a,b, 2007).

Note, however, that as SD progresses, damage extends beyond the ATL to posterior temporal and/or inferior frontal cortices (Hodges and Patterson, 2007; Patterson and Lambon Ralph, 2016), which is associated with a worsening of the conceptual processing deficits (Bright et al., 2008; Gorno-Tempini et al., 2004; Martin et al., 2014). This suggests that not only the ATL, but also posterior temporal and inferior frontal regions might constitute key nodes for conceptual processing (Martin et al., 2014). This view is supported by a meta-analysis across 120 fMRI and PET studies that compared functional activation for meaningful vs. meaningless stimuli (e.g. words > pseudowords; conceptual > phonological tasks) (Binder et al., 2009). Strikingly, not only the ATL, but a large set of left-lateralized brain regions showed consistent engagement across studies (Figure 1.2): (1) the lateral temporal cortex, from the ATL to posterior parts of the middle / inferior temporal gyri (pMTG/ITG), (2) the posterior parietal cortex (PPC)[3], (3) the anterior inferior frontal gyrus (aIFG), (4) precuneus / posterior cingulate cortex (PC/PCC), (5) dorso- and ventromedial prefrontal cortex (dmPFC/vmPFC), and (6) medial fusiform / parahippocampal gyri (FG/PH). Therefore, several authors propose that these brain regions might also represent abstract "hubs" contributing to conceptual processing in general (Binder, 2016; Binder and Desai, 2011; Binder and Fernandino, 2015; Fernandino et al., 2016a,b; Price et al., 2015).

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[3] The term "posterior parietal cortex (PPC)" will be used throughout the general introduction and discussion of this thesis. Please note that the PPC includes the posterior inferior parietal lobe (pIPL), which is referenced in studies 1 and 3.

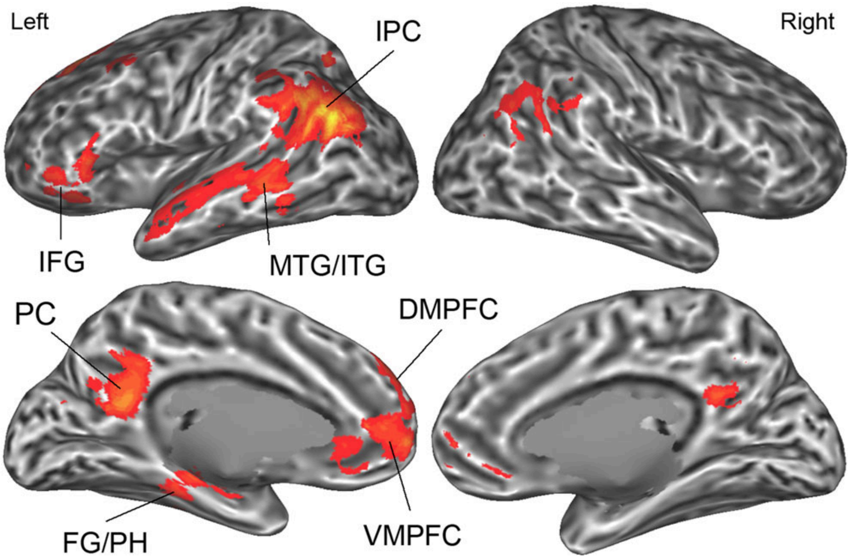

Fig. 1.2: Brain regions showing consistent engagement across functional neuroimaging studies for meaningful vs. meaningless stimuli in the meta-analysis by Binder et al. (2009). IFG = inferior frontal gyrus; IPC = inferior parietal cortex; MTG/ITG = middle / inferior temporal gyri; PC = posterior cingulate / precuneus; FG / PH = fusiform gyrus / parahippocampus; DMPFC = dorsomedial prefrontal cortex; VMPFC = ventromedial prefrontal cortex. Reproduced with permission from Binder (2016).

A crucial question is how the existence of abstract conceptual regions is consistent with grounded cognition theories and does not succumb to the symbol grounding problem (Barsalou, 2016). The consensus answer is that these areas represent "cross-modal convergence zones" that derive their abstract representations through the convergence and integration of distributed modality-specific representations (Barsalou, 2016; Binder, 2016; Damasio, 1989a,b; Fernandino et al., 2016a; Simmons and Barsalou, 2003). In other words, abstract conceptual representations in cross-modal convergence zones are grounded by virtue of being derived from and linked to modality-specific perceptual-motor information (Barsalou, 2016; Binder, 2016). This is supported by the fact that these regions show extensive connectivity with different modality-specific cortices (Margulies et al., 2016; Morán et al., 1987; Seghier, 2013). For example, studies using diffusion tensor imaging (DTI) in the healthy human brain have revealed direct anatomical connections between numerous modality-specific regions and the ATL (Bajada et al., 2017; Binney et al., 2012; Makris et al., 2009) as well as the PPC (Bonner et al., 2013; Seghier, 2013).

Notably, it is currently unclear whether the representations stored in cross-modal convergence zones are "multimodal", i.e. retain modality-specific information, or "amodal", i.e. completely abstracted away from modality-specific content (Binder and Fernandino, 2015). Indeed, it is possible that both multimodal and amodal convergence zones exist, implementing multiple levels of abstraction from modality-specific perceptual-motor features.

1.6 Hybrid theories

Overall, the current evidence seems most consistent with so called "hybrid theories" which propose both modality-specific perceptual-motor regions and cross-modal convergence zones to support conceptual processing (Binder and Desai, 2011; Kemmerer, 2015; Kiefer and Harpaintner, 2020; Kiefer and Pulvermüller, 2012; Lambon Ralph et al., 2016). Two of the most prominent hybrid theories are the "hub-and-spokes" model (Lambon Ralph et al., 2016; Patterson and Lambon Ralph, 2016; Patterson et al., 2007; Rogers et al., 2004) and the "embodied abstraction" model (Binder, 2016; Binder and Desai, 2011; Fernandino et al., 2016a).

The hub-and-spokes model posits that distributed modality-specific "spoke" regions converge onto a central, modality-invariant "hub" in the ATL (Lambon Ralph et al., 2016; Patterson and Lambon Ralph, 2016; Patterson et al., 2007; Rogers et al., 2004). Recent versions of the hub-and-spokes model suggest that the ATL hub exhibits a graded modality specificity, following proximity to and connectivity with different modality-specific cortices (Lambon Ralph et al., 2016): While anterior middle and inferior temporal gyri (aMTG/ITG) appear to be completely modality-invariant, more superior parts (e.g. anterior superior temporal gyrus; aSTG) seem biased towards audition and word semantics, and inferior portions (e.g. anterior fusiform / parahippocampal gyri) seem biased towards vision and picture semantics (Hoffman et al., 2015; Jefferies, 2013; Lambon Ralph et al., 2016; Visser et al., 2012).

The embodied abstraction model proposes that conceptual processing is supported by a hierarchy of brain regions from modality-specific perceptual-motor areas to multiple levels of cross-modal convergence zones (Binder, 2016; Binder and Desai, 2011; Fernandino et al., 2016a). Cross-modal convergence zones integrate the initial modality-specific representations into increasingly abstract representations (Binder, 2016; Binder and Desai, 2011). In contrast to the hub-and-spokes model, the embodied abstraction model posits that cross-modal convergence zones are located not only in the ATL, but also in more posterior parts of the temporal lobe (pMTG/ITG), as well as in the posterior parietal cortex (PPC), posterior cingulate / precuneus (PCC / PC), and medial prefrontal cortex (mPFC) (often with reference to the neuroimaging meta-analysis by Binder et al., 2009).

Both frameworks agree that in addition to modality-specific regions and cross-modal convergence zones—brain regions that *represent* conceptual knowledge—conceptual processing also involves "control regions" that support the retrieval and/or selection of conceptual representations (Binder and Fernandino, 2015; Jefferies, 2013; Lambon Ralph et al., 2016). Particularly the left prefrontal cortex, especially anterior IFG, is implicated in executive control during conceptual tasks by functional neuroimaging (Noonan et al., 2013; Thompson-Schill et al., 1997; Wagner et al., 2001) as well as TMS (Hartwigsen et al., 2016; Whitney et al., 2011, 2012) studies. The role of other regions is more controversial. For example, some authors propose that parts of left pMTG and PPC also support conceptual control (Davey et al., 2015; Jefferies, 2013; Noonan et al., 2013). This view seems to be supported by evidence from semantic aphasia (SA), which is caused by stroke affecting the left prefrontal and/or temporal-parietal cortices (Jefferies, 2013). While SD patients show conceptual impairments across tasks, SA patients exhibit disproportional deficits in conceptual tasks with high executive demands (Jefferies, 2013; Jefferies and Lambon Ralph, 2006; Noonan et al., 2010). In contrast, other authors assume that left PPC and pMTG store conceptual representations (Binder and Desai, 2011; Fernandino et al., 2016a,b; Price et al., 2015). For instance, a recent neuroimaging meta-analysis suggests that left PPC is involved in conceptual representation, not control (Jackson, 2021). This controversy illustrates the fact that it is often highly difficult, if not impossible, to disentangle representation and control experimentally since experiments typically require the controlled retrieval of conceptual representations for them to be observable (Anderson, 1978; Hauk and Tschentscher, 2013; Tune and Asaridou, 2016).

1.7 Open research questions and our studies

Several questions regarding the neural basis of conceptual knowledge retrieval remain open. The studies presented in this thesis address three key issues:
(1) task dependency of perceptual-motor feature retrieval,
(2) functional interaction between modality-specific and cross-modal areas, and
(3) causal relevance.

First, it is unclear to what extent the retrieval of perceptual-motor features of concepts, and the resulting engagement of modality-specific brain regions depend on the concurrent task. This is a crucial issue since some studies have failed to find modality-specific perceptual-motor activity during conceptual processing (e.g. Bedny et al., 2008; Postle et al., 2008; Raposo et al., 2009). For example, Postle et al. (2008) could not identify effector-specific, somatotopic activation of motor regions for action words (as reported by Hauk et al., 2004). Some authors have interpreted such results as evidence against grounded theories (e.g. Bedny et al., 2008; Mahon, 2015; Papeo et al., 2009). In contrast, proponents of grounded theories have argued that the absence of perceptual-motor activity in some tasks could be meaningful and systematic, reflecting the fact that the retrieval of perceptual-motor features occurs flexibly in a task-dependent fashion (Barsalou, 2016; Hoenig et al., 2008; Kemmerer, 2015; Pulvermüller, 2018). For example, Postle et al. merely asked their participants to silently read words, which does not require retrieval of action features of the underlying concepts (Kemmerer, 2015; Willems and Casasanto, 2011). Contrarily, a task that requires the retrieval of a certain perceptual-motor feature (e.g. sound) should engage the corresponding modality-specific areas (e.g. auditory) if the grounded theory is correct. Crucially, however, the task dependency of perceptual-motor feature retrieval has not been systematically tested. This would require a direct comparison of brain activity for different tasks on the same stimuli in the same participants.

Study 1 of this thesis—an fMRI activation study—systematically tested the task dependency of conceptual feature retrieval (Kuhnke et al., 2020b). Specifically, we asked to what extent the retrieval of sound and action features of concepts, and the resulting recruitment of auditory and somatomotor brain regions depend on the concurrent task. We measured brain activity in 40 healthy human participants using fMRI, while they performed three different tasks—lexical decision, sound judgment, and action judgment—on the same words with a high or low association to sounds and actions. We found that the retrieval of sound and action features strongly depended on the task: Selectively during sound judgments, auditory-related regions showed an increased response to sound features of concepts (high > low sound words). Selectively during action judgments, somatomotor regions exhibited increased activity for action features (high > low action words). Crucially, several regions (e.g. left PPC) showed a task-dependent response to both sound and action features. In a new model of the neural architecture underlying conceptual processing, we propose that these regions are “multimodal” and not “amodal”, that is, they retain modality-specific information.

Overall, study 1 revealed a task-dependent engagement of both modality-specific and multimodal regions in sound and action feature retrieval. However, it remains open whether and how modality-specific and multimodal regions work together during conceptual tasks. Indeed, as summarized above, previous research on the neural basis of conceptual processing has mainly focused on *functional segregation*—identifying the distinct brain regions involved in conceptual processing and their functions (Borghesani and Piazza, 2017; Kiefer and Pulvermüller, 2012; Meteyard et al., 2012). In contrast, little is known about *functional integration* in the conceptual system—whether and how different regions interact during conceptual tasks. This is a central question since contemporary theories of conceptual processing, such as the hub-and-spokes and embodied abstraction models, explicitly propose conceptually-guided behavior to be supported by the functional interaction between modality-specific and cross-modal nodes (Binder and Desai, 2011; Fernandino et al., 2016a; Lambon Ralph et al., 2016). Moreover, there is a growing consensus that higher cognitive functions, including conceptual processing, rely on the coordinated activity of large-scale functional neural networks, not isolated brain regions (Bassett and Sporns, 2017; Hartwigsen, 2018; Sporns, 2014).

Therefore, **study 2**—an fMRI connectivity study—investigated the functional integration between modality-specific and multimodal regions during conceptual processing (Kuhnke et al., 2021). Specifically, we asked (1) whether modality-specific and multimodal areas are functionally coupled during sound and action feature retrieval, (2) whether their coupling depends on the task, (3) whether information flows bottom-up, top-down or both, and (4) whether their coupling is relevant for behavior. We found that functional coupling between modality-specific and multimodal areas strongly depended on the task, involved both top-down and bottom-up information flow, and predicted conceptually-guided behavior. In particular, the multimodal region in the left PPC acted as a functional coupling "switchboard", flexibly adapting its connectivity profile to task-relevant modality-specific nodes: Left PPC coupled with auditory regions during sound feature retrieval, and with somatomotor regions during action feature retrieval.

Overall, neuroimaging studies 1 and 2 indicated a key role of the left PPC as a multimodal convergence zone, which seems to guide the retrieval of both action and sound features of concepts via dynamic coupling with somatomotor and auditory cortices, respectively. However, as neuroimaging is correlational, it remains unknown whether left PPC plays a *causal* role as a multimodal conceptual hub. Functional activation in left PPC might be epiphenomenal to behavioral performance (Price and Friston, 2002; Walsh and Cowey, 2000). While there is some evidence for a causal role of left PPC in conceptual processing in general (Hartwigsen et al., 2016; Sliwinska et al., 2015; Stoeckel et al., 2009), no study has tested the functional relevance of left PPC for processing multiple different conceptual features.

Hence, in **study 3**—a TMS study—we asked whether left PPC is causally relevant for both action and sound feature retrieval (Kuhnke et al., 2020a). We applied effective TMS over left PPC, or sham TMS over the vertex, while 26 new participants performed the same tasks as in the fMRI study (lexical decisions, sound judgments, and action judgments on words with a high or low association to sounds and actions). We found that PPC-TMS selectively impaired action judgments on low sound–low action words. For the first time, we directly related computational simulations of the TMS-induced electrical field to behavioral performance, which revealed that stronger stimulation of left PPC is associated with worse performance on action, but not sound, judgments. These results indicate that left PPC causally supports conceptual processing when action knowledge is task-relevant and cannot be compensated by sound knowledge. Our findings suggest that left PPC is specialized for action knowledge, challenging the view of left PPC as a multimodal conceptual hub.

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The following study investigated the task dependency of conceptual knowledge retrieval using fMRI in healthy human participants. Specifically, we tested to what extent the retrieval of sound and action features of concepts and the resulting recruitment of auditory and somatomotor brain regions depend on the task that participants are performing.

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ORIGINAL ARTICLE

Task-Dependent Recruitment of Modality-Specific and Multimodal Regions during Conceptual Processing

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Abstract

Conceptual knowledge is central to cognitive abilities such as word comprehension. Previous neuroimaging evidence indicates that concepts are at least partly composed of perceptual and motor features that are represented in the same modality-specific brain regions involved in actual perception and action. However, it is unclear to what extent the retrieval of perceptual–motor features and the resulting engagement of modality-specific regions depend on the concurrent task. To address this issue, we measured brain activity in 40 young and healthy participants using functional magnetic resonance imaging, while they performed three different tasks—lexical decision, sound judgment, and action judgment—on words that independently varied in their association with sounds and actions. We found neural activation for sound and action features of concepts selectively when they were task-relevant in brain regions also activated during auditory and motor tasks, respectively, as well as in higher-level, multimodal regions which were recruited during both sound and action feature retrieval. For the first time, we show that not only modality-specific perceptual–motor areas but also multimodal regions are engaged in conceptual processing in a flexible, task-dependent fashion, responding selectively to task-relevant conceptual features.

Key words: concepts, embodied cognition, fMRI, language, semantic memory

Introduction

Conceptual knowledge about objects, people, and events in the world is crucial for many cognitive abilities such as recognizing and acting with objects and understanding the meaning of words (Barsalou 1999; Binder and Desai 2011; Kiefer and Pulvermüller 2012; Lambon Ralph 2014). Thus, a central question in cognitive neuroscience has been how concepts are represented and processed in the human brain.

Grounded theories of conceptual representation propose that concepts consist of perceptual and motor features, which are represented in the same modality-specific brain systems engaged during actual perception and action (Barsalou 2008; Kiefer and Pulvermüller 2012; Hauk and Tschentscher 2013; Kiefer and Barsalou 2013). For instance, sound features of concepts are represented in auditory brain regions, while action features are represented in motor-related regions. Evidence for grounded theories is provided by neuroimaging studies demonstrating that processing concepts related to a certain perceptual–motor modality activates the respective modality-specific brain regions (for reviews, see Binder and Desai 2011;

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Kiefer and Pulvermüller 2012; Hauk and Tschentscher 2013; Borghesani and Piazza 2017). For example, processing action verbs engages the motor cortex (Hauk et al. 2004; Hauk and Pulvermüller 2004), while processing sound-related words activates auditory association regions, such as posterior middle temporal gyrus (pMTG; Kiefer et al. 2008, 2012b; Fernandino et al. 2016a). Moreover, lesions of motor or auditory brain regions are associated with deficits in action-related (Bak et al. 2001, 2006; Hillis et al. 2006; Grossman et al. 2008) or sound-related conceptual processing (Bonner and Grossman 2012; Trumpp et al. 2013a), respectively.

In addition to modality-specific areas, previous evidence suggests that conceptual processing involves "convergence zones" (Damasio 1989) at multiple hierarchical levels, which integrate modality-specific representations into increasingly abstract representations (Simmons and Barsalou 2003; Binder et al. 2009; Binder 2016). Therefore, several researchers propose conceptual processing to rely on a hierarchy of functional neural networks from modality-specific to multimodal (i.e., bimodal, trimodal, etc.) up to heteromodal areas (Simmons and Barsalou 2003; Binder and Desai 2011; Kiefer and Pulvermüller 2012; Garagnani and Pulvermüller 2016). Although a common terminology is currently lacking in the field, we call regions "modality-specific" if they represent information related to a single perceptual–motor modality and are located within perceptual–motor systems (following grounded views). We refer to areas as "multimodal" if they integrate information from at least two modalities and remain sensitive to the individual modalities. "Heteromodal" regions are areas that receive input from all modalities. A heteromodal region can be either multimodal itself (i.e., sensitive to individual perceptual-motor modalities) or "amodal" (i.e., insensitive to individual modalities). "Cross-modal" is an overarching term for any region that integrates at least two modalities and thus subsumes multimodal and heteromodal areas. Previous evidence indicates that high-level cross-modal convergence zones are located in the posterior inferior parietal lobe (pIPL), pMTG, medial prefrontal cortex (mPFC) (Binder et al. 2009; Binder 2016), and anterior temporal lobe (ATL; Lambon Ralph et al. 2016).

However, it is unclear to what extent the retrieval of perceptual–motor features and the involvement of modality-specific regions in conceptual processing depend on the concurrent task. According to one view, perceptual–motor features are always activated in a task-independent fashion (Pulvermüller 2005). This view is supported by studies demonstrating activation of modality-specific areas during implicit conceptual tasks (e.g., lexical decision; Pulvermüller et al. 2005; Kiefer et al. 2008, 2012a) or even passive tasks (e.g., Hauk et al. 2004; Hauk and Pulvermüller 2004). Such modality-specific recruitment can occur as early as 200 ms after stimulus onset (Hauk and Pulvermüller 2004; Kiefer et al. 2008), and even when stimuli are unattended (Shtyrov et al. 2004; Pulvermüller and Shtyrov 2006) or not consciously perceived (Trumpp et al. 2013b, 2014).

In contrast, other studies suggest that the retrieval of perceptual–motor features varies with the task. Behavioral studies indicate that even central features of a concept, including perceptual–motor features, can be modulated by the context such as the task (for reviews, see Kiefer et al. 2012b; Lebois et al. 2015). Moreover, evidence from neuroimaging (Bedny et al. 2008; Postle et al. 2008; Raposo et al. 2009), transcranial magnetic stimulation (Papeo et al. 2009, 2015), and lesion studies (Arévalo et al. 2012; Kemmerer et al. 2012) suggests that activation of modality-specific areas does not always occur during conceptual processing.

Some authors have taken the absence of modality-specific activity during some tasks as evidence against grounded theories (e.g., Bedny et al. 2008; Papeo et al. 2009; Mahon 2015). In contrast, proponents of grounded theories have argued that such variability could be meaningful and systematic, reflecting the fact that the retrieval of perceptual–motor features and corresponding recruitment of modality-specific brain regions occurs flexibly in a task-dependent fashion (Hoenig et al. 2008; Kemmerer 2015; Barsalou 2016; Pulvermüller 2018). Specifically, depending on the task explicitness and relevance of perceptual–motor features, different levels of the processing hierarchy may be recruited: An implicit task that does not require perceptual–motor information might only involve high-level convergence zones, whereas a task that explicitly requires retrieval of perceptual–motor features may additionally recruit lower-level perceptual–motor areas (Kemmerer 2015; Popp et al. 2019a). For instance, Binder and colleagues propose that high-level cross-modal areas (e.g., pIPL, pMTG, mPFC, and ATL) are consistently engaged in conceptual processing in a task-independent fashion, whereas the recruitment of modality-specific perceptual–motor areas is assumed to depend on contextual factors such as the task (Binder and Desai 2011; Fernandino et al. 2016a). Tackling the issue of task dependency is therefore crucial to refine theories of conceptual processing and specify how different levels of the processing hierarchy are engaged under different circumstances (Binder and Desai 2011; Willems and Casasanto 2011; Yee and Thompson-Schill 2016).

Although very few neuroimaging studies have directly tested the task dependency of conceptual processing so far, these studies generally support the view that the retrieval of perceptual–motor features and the engagement of modality-specific brain regions depend on the task. For example, Hoenig et al. (2008) found that visual- and motor-related areas showed stronger activity when a nondominant feature had to be verified for a concept. Another study reported several motor-related regions to be more active for words with a high relevance of both action and color features when the task focused on action as opposed to color (van Dam et al. 2012). Hsu et al. (2011) showed that a task which required more detailed color knowledge engaged color-sensitive cortex to a stronger degree. Finally, Borghesani et al. (2019) found areas associated with motion and action processing to exhibit higher activity when two objects are compared for movement than for typical location.

However, these studies have several limitations. Firstly, they exclusively focused on visual and action features, whereas little is known about other modalities such as sound. Moreover, except for Hsu et al., none of the previous studies tested for activation overlap with actual perception and action. Consequently, it remains unknown whether the activated regions were indeed located within perceptual–motor systems. In addition, Hsu et al. and Hoenig et al. confounded their task manipulation with stimulus manipulations, rendering it unclear whether activation differences were due to different tasks, different stimuli, or both. Finally, no previous study independently manipulated the relevance of multiple perceptual–motor features at the same time. It thus remains unknown whether the implicated regions were indeed modality-specific or rather multimodal.

To address these issues and systematically investigate to what extent neural activity for perceptual–motor features of concepts depends on the task, the present functional magnetic resonance imaging (fMRI) study compared different tasks on the same stimuli in the same participants and directly tested for activation overlap with perception and action. Participants performed three different tasks on words that exhibited either a low or high association with sounds and actions, thereby orthogonally varying task and feature relevance. A lexical decision task probed implicit access to action and sound features of concepts, whereas action and sound judgment tasks assessed explicit retrieval of action and sound features, respectively.

Following grounded theories, we hypothesized that retrieval of action features should engage motor-related brain regions, while retrieval of sound features should engage auditory-related regions. Moreover, based on previous work (e.g., Binder and Desai 2011; Fernandino et al. 2016a), we expected that feature-related activity in modality-specific perceptual–motor regions should be increased when the respective feature is task-relevant, whereas activity of high-level cross-modal regions should not be modulated by task.

We found activation for sound or action features exclusively when they were task-relevant. In line with grounded theories, activation for sound or action features overlapped with sound perception or motor action, respectively. However, activation extended beyond auditory or motor areas to higher-level, multimodal regions, which were engaged for both sound and action features. As an unexpected, novel finding, not only modality-specific areas but also multimodal regions showed a flexible, task-dependent recruitment pattern, responding selectively to task-relevant conceptual features. These findings indicate that the task modulates not only which levels of the processing hierarchy (modality-specific, multimodal, up to heteromodal regions) are engaged. The task also influences the neural response to individual perceptual–motor features of concepts at several hierarchy levels, even including high-level cross-modal convergence zones.

Materials and Methods

Subjects

Data from 40 native German speakers (22 females; mean age: 26.6 years; SD: 4.1; range: 19–33) entered the final analysis. A total of 42 subjects were initially recruited, but 2 were excluded due to stopping the experiment or excessive head movement. All subjects were right-handed (mean laterality quotient: 93.7; SD: 9.44; Oldfield 1971). No subject had a history of neurological disorders or head injury or exhibited contraindications to fMRI. All subjects were recruited via the subject database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. Written informed consent was obtained from each subject prior to the experiment. The study was performed according to the guidelines of the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

Experimental Procedures

In two event-related fMRI sessions on separate days, subjects performed three different tasks on the same 192 words that independently varied in their association strength with sounds and actions. The experiment thus followed a 3 × 2 × 2 repeated-measures design with the factors TASK (lexical decision, sound judgment, action judgment), SOUND (low, high relevance for word meaning), and ACTION (low, high relevance for word meaning). All stimuli were presented using the software *Presentation* (Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com; version 17.2). Visual stimuli were back-projected onto a mirror mounted on the head coil. Auditory stimuli were played via MR-compatible in-ear headphones (MR Confon, Magdeburg, Germany).

Session 1. Lexical Decision Task (Implicit)

In the first session, subjects performed a lexical decision task. On each trial, they decided whether the presented stimulus was a word or pseudoword. This implicit conceptual task did not require explicit retrieval of sound or action features. The lexical decision task was always performed before the explicit tasks (see below) to ensure that the subjects' attention was not directed toward the sound or action features of the words.

A total of 384 trials (192 words, 192 pseudowords) were presented in six blocks, separated by 20-s fixation period during which subjects could rest (Fig. 1A). Subjects responded via button press with the index or middle finger of their left hand. They were instructed to respond as quickly and as accurately as possible. Button assignment was counterbalanced across subjects.

The length of the scanning session was ~35 min. Before entering the scanner, subjects practiced the task with 16 trials that were not included in the actual experiment.

Session 2. Sound and Action Judgment Tasks (Explicit)

In the second session, two explicit conceptual tasks were performed. In the sound judgment task, subjects decided whether the presented word was strongly associated with sounds or not. In the action judgment task, subjects judged whether the word was strongly associated with actions. Sound judgments thus explicitly required retrieval of sound features, whereas action judgments required retrieval of action features of concepts. The two tasks were performed in separate mini-blocks to ensure a constant cognitive state during each task and minimize task switching effects.

As in session 1, 384 trials were presented in six blocks of 64 trials each (Fig. 1B). Each of the 192 words was presented in both tasks (counterbalanced across subjects). The order of mini-blocks was pseudo-randomized with the restriction that the same condition could not occur more than twice in succession. Trials were presented in a pseudo-randomized order within blocks with the restriction that all words were presented before any word was repeated and that word repetitions were separated by at least two mini-blocks.

The overall length of the scanning session was ~38 min. Subjects practiced both tasks outside the scanner before the session with 16 trials excluded from the main experiment.

Stimuli

Stimuli were 192 written German nouns denoting concrete objects, which were strongly or weakly associated with sounds and (human) actions, leading to four categories of 48 words each: 1) low sound, low action; 2) low sound, high action; 3) high sound, low action; and 4) high sound, high action (see Fig. 1 for examples).

A total of 163 subjects who did not participate in the fMRI experiment rated an original set of 891 words for their association with sounds, actions, and visual features, as well as their familiarity on a 1-to-6 scale (for a similar procedure, see Kiefer et al. 2008; Bonner et al. 2013; Trumpp et al. 2014; Fernandino et al. 2016b). We selected 48 words for each category such that high and low sound words differed selectively in their sound

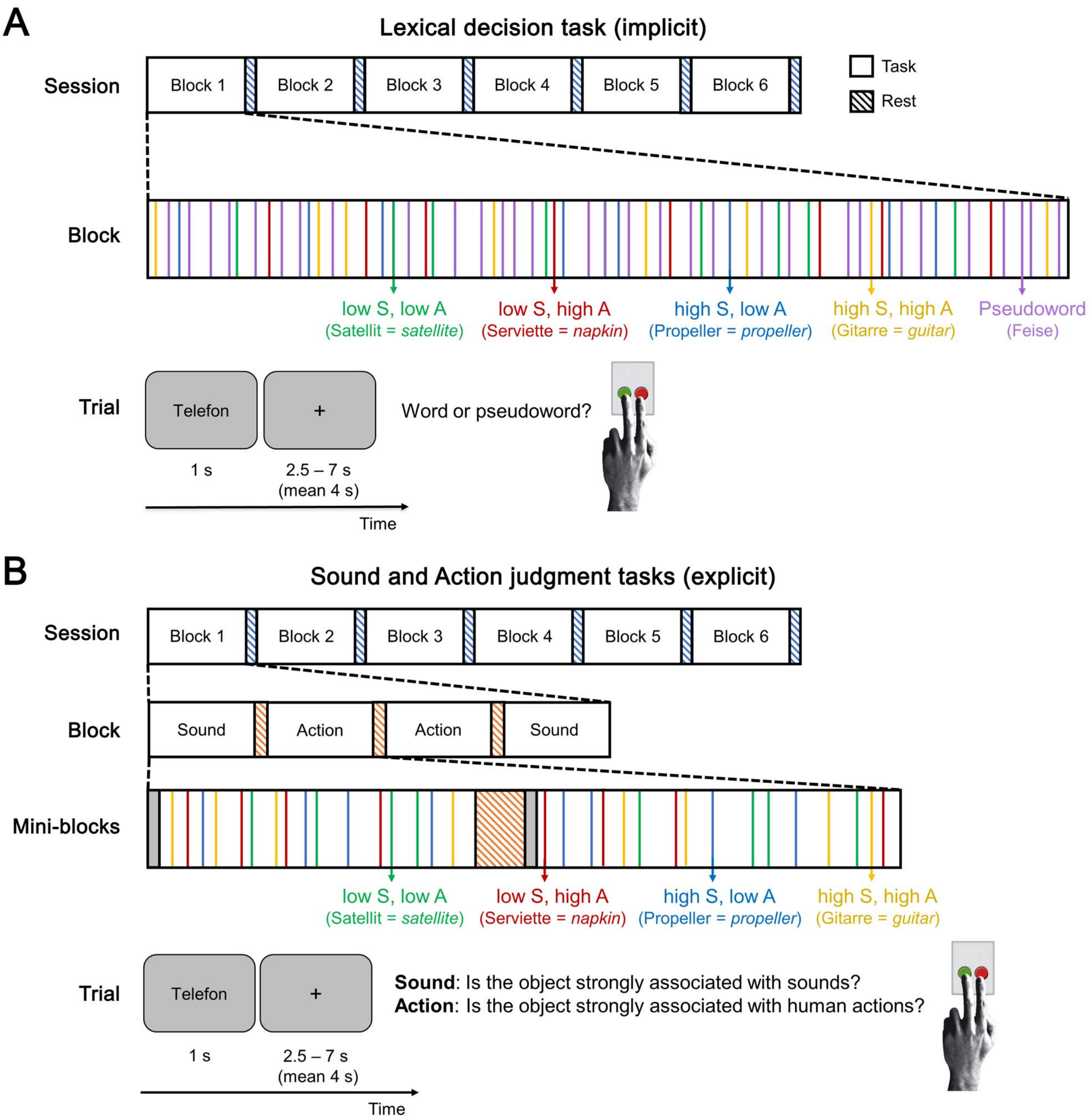

Figure 1. Experimental design. An experimental session consisted of six blocks separated by 20-s rest periods (blue-striped bars). In session 1 (*A*), each block contained 64 trials presented in random order: 32 trials of pseudowords (purple) and 32 trials of real words. These included eight trials for each word category: low sound, low action (green); low sound, high action (red); high sound, low action (blue); high sound, high action (yellow). During each trial, a letter string was shown for 1 s and subjects performed a lexical decision, followed by a jittered inter-trial-interval (ITI) of 2.5–7 s (mean 4 s). In session 2 (*B*), each block included four mini-blocks—two of sound judgments and two of action judgments—which were separated by 12-s rest periods (orange-striped bars). Each mini-block started with a cue indicating the task (gray bars; Supplementary Fig. S1). Then, 16 trials followed, with four trials per word category. In each trial, subjects judged whether the presented word was strongly associated with sounds (sound judgment) or whether it was strongly associated with actions (action judgment).

ratings ($P < 10^{-113}$), while high and low action words differed only in their action ratings ($P < 10^{-103}$). Categories were matched on all other rating criteria and further psycholinguistic measures, including number of letters and syllables, word frequency, bi- and trigram frequencies, and number of orthographic neighbors (all $P > 0.05$; Supplementary Table S1). Note that stimuli for the four word categories were drawn from the same superordinate categories of animals, inanimate natural entities, and man-made objects (cf. Goldberg et al. 2006; Kiefer et al. 2008).

For the lexical decision task, 192 phonologically and orthographically legal pseudowords were created using the software *Wuggy* (Keuleers and Brysbaert 2010; http://crr.ugent.be/Wuggy). For each real word in the experiment, a pseudoword was generated that was matched in length, syllable structure, and transition frequencies between subsyllabic elements.

Functional Localizers

At the end of the second session, two functional localizers were administered to determine auditory and motor brain regions, respectively. Their order was counterbalanced across subjects.

In the auditory localizer, participants were presented with blocks of 1) real object sounds and 2) scrambled versions of the same sounds. Real object sounds should engage high-level auditory representations (e.g., barking of a dog; Bizley and Cohen 2013), whereas scrambled sounds should exclusively recruit low-level acoustic representations (e.g., frequency, loudness). Subjects were instructed to attentively listen to the sounds, while maintaining fixation on a cross (cf. Kiefer et al. 2008; Hoenig et al. 2011). Sounds were presented in 12 blocks (6 real, 6 scrambled) of 18 s each and interspersed with 16-s silence blocks. Block order alternated between real and scrambled sounds. Real sounds included sounds of animals (e.g., elephant), inanimate natural entities (e.g., river), tools (e.g., saw), musical instruments (e.g., violin), and everyday objects (e.g., telephone). Scrambled sounds were created in *Matlab* (version 9.3/2017b) as described by Dormal et al. (2018), yielding sounds that were well-matched to the real sounds for low-level acoustic features but did not have any meaning. All sounds were matched for root mean square intensity, and a 5-ms fade was added at the beginning and end of each sound to avoid click artifacts (Belin et al. 2000; Dormal et al. 2018). The length of the auditory localizer was ~8 min.

In the motor localizer, participants performed three types of movements with their left or right hand in separate blocks, including finger tapping (sequence from thumb to little finger), fist making, and pinching (cf. Bonner et al. 2013). A written cue indicated the type of movement and hand at the beginning of each block. Movement was paced by a fixation cross blinking in a 1 Hz rhythm. Subjects performed 12 movement blocks (2 per movement type per hand) of 18 s, separated by 16-s rest blocks during which the same visual stimulus (blinking cross) was shown but no movements were executed. The motor localizer took ~9 min.

fMRI Data Acquisition and Preprocessing

FMRI data were collected on a 3T Prisma scanner (Siemens, Erlangen, Germany) with a 32-channel head coil. Functional, blood oxygenation level-dependent (BOLD) images were acquired using a multiband (Feinberg et al. 2010) dual gradient-echo EPI sequence (repetition time [TR]: 2 s; echo time [TE]: 12 & 33 ms; flip angle: 90°; field of view [FoV]: 204 mm; voxel size: 2.5 × 2.5 × 2.5 mm; slice gap: 0.25 mm; bandwidth: 1966 Hz/Px; phase encoding direction: A/P; acceleration factor 2). We used a dual-echo sequence to maximize BOLD sensitivity throughout the whole brain, including regions susceptible to signal loss in standard single-echo EPI, such as the ATL (Poser et al. 2006; Halai et al. 2014). To further reduce susceptibility artifacts, slices were tilted 10° up (at anterior edge) from the AC-PC line (Weiskopf et al. 2006). Sixty slices covering the whole brain were recorded in interleaved order and axial orientation. B0 field maps were acquired for susceptibility distortion correction using a gradient-echo sequence (TR: 0.62 s; TE: 4 & 6.46 ms; flip angle: 60°; bandwidth: 412 Hz/Px; other parameters identical to functional sequence). Structural T1-weighted images were acquired for normalization using an MPRAGE sequence (176 slices in sagittal orientation; TR: 2.3 s; TE: 2.98 ms; FoV: 256 mm; voxel size: 1 × 1 × 1 mm; no slice gap; flip angle: 9°; phase encoding direction: A/P).

fMRI analysis was performed using *Statistical Parametric Mapping* (SPM12; Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm/), implemented in *Matlab* (version 9.3/2017b). The two images with a short and long TE were combined using an average weighted by the temporal signal-to-noise ratio (tSNR) of each image at every voxel, which yields optimal BOLD sensitivity at each voxel (Poser et al. 2006). tSNR was calculated based on 30 volumes collected at the beginning of each scanning run, which were excluded from further analyses. Functional images were realigned, distortion corrected (using a B0 field map), slice-timing corrected, normalized to MNI space via unified segmentation of the co-registered structural image (resampling to 2.5 mm^3 isotropic voxels), and smoothed with an 8 mm^3 FWHM Gaussian kernel.

Whole-Brain Analyses

We performed a whole-brain random-effects group analysis based on the general linear model (GLM), using the two-level approach in SPM. At the first level, individual subject data were modeled separately. For the localizers, blocks were modeled using box-car regressors convolved with the canonical hemodynamic response function (HRF). For the conceptual tasks, the GLM included regressors for the 12 experimental conditions, modeling trials as stick functions convolved with the canonical HRF and its temporal derivative. Only correct trials were analyzed, error trials were modeled in a separate regressor-of-no-interest. To account for potential differences in response time (RT) between trials and conditions, a duration-modulated parametric regressor (duration = RT) was included (Grinband et al. 2008). For all tasks, nuisance regressors included the six motion parameters and individual regressors for time points with strong volume-to-volume movement (framewise displacement > 0.9; Siegel et al. 2014). The data were subjected to an AR(1) autocorrelation model to account for temporal autocorrelations and high-pass filtered (cutoff 128 s) to remove low-frequency noise.

Contrast images for each participant were computed at the first level. At the second level, these contrast images were submitted to one-sample or paired *t*-tests (to test for interactions). To identify brain regions sensitive to action or sound features in each task (lexical decision, action judgment, sound judgment), we first compared activation for high > low action words and high > low sound words within each task. Conjunction analyses based on the minimum statistic (testing the conjunction null hypothesis; Nichols et al. 2005) tested for overlap between activation for action or sound features and activation in the motor localizer (hand movements > rest) or auditory localizer (real object sounds > silence; scrambled sounds > silence), respectively.

To localize brain regions whose response to sound or action features depended on the task, we directly compared the activation for high > low action words and high > low sound words between tasks using paired *t*-tests. We contrasted high > low action or sound words within each task first to isolate task-specific activity for action or sound features, while controlling for other potential differences between tasks (such as condition-unspecific differences in response magnitude). To restrict interactions to voxels significant within the task, interactions were inclusively masked by significant voxels of the minuend (cf. Noppeney et al. 2006; Hardwick et al. 2018). We corrected for multiple comparisons at the whole-brain level using false discovery rate (FDR) correction (see below).

Finally, we aimed to localize regions involved in the explicit retrieval of both sound and action features. To this end, a conjunction analysis was performed between [high > low action words during action judgments] and [high > low sound words during sound judgments].

For all second-level analyses, a gray matter mask was applied, restricting statistical tests to voxels with a gray matter probability > 0.3 (SPM12 tissue probability map). All activation maps were thresholded at a voxel-wise FDR of $q < 0.05$ (Benjamini and Hochberg 1995; Genovese et al. 2002), with an additional cluster extent threshold of 20 voxels.

Subject-Specific Functional Region of Interest Analysis

To characterize the response profiles of motor, auditory, and multimodal regions identified in individual subjects, we performed a functional region of interest (fROI) analysis (Fedorenko et al. 2010; Nieto-Castañón and Fedorenko 2012) using the group-constrained subject-specific (GSS) approach (Julian et al. 2012).

We defined three types of fROIs: 1) "Motor fROIs"—motor regions involved in action feature retrieval—using the conjunction [Action judgment: high > low action words] ∩ [Motor localizer: hand movements > rest], 2) "Auditory fROIs"—auditory regions involved in sound feature retrieval—using the conjunction [Sound judgment: high > low sound words] ∩ [Auditory localizer: real sounds > silence], and 3) "Multimodal fROIs"—regions involved in both action and sound feature retrieval—using the conjunction [Action judgment: high > low action words] ∩ [Sound judgment: high > low sound words]. Motor and auditory fROIs were defined via overlap with the motor and auditory localizers to identify grounded conceptual regions, whereas multimodal fROIs could be higher-level areas not involved in basic action or perception. To avoid circularity (Kriegeskorte et al. 2009; Vul et al. 2009), we employed a split-half approach, using half of the data of each subject (blocks 1–3) for fROI definition and the other half (blocks 4–6) for response estimation (cf. Fedorenko et al. 2011, 2013).

fROI definition followed the GSS procedure (Julian et al. 2012): For each fROI type, subject-specific activation maps (5-mm smoothing) were thresholded at $P < 0.05$ and overlaid on top of each other; the resulting overlap map showed how many subjects exhibited activation at each voxel. The overlap map was smoothed (5 mm), thresholded at two subjects (cf. Julian et al. 2012), and parcellated using a watershed algorithm (Meyer 1991) implemented in the spm_ss toolbox (Nieto-Castañón and Fedorenko 2012). We retained only those parcels within which at least 60% of subjects had any suprathreshold voxels or for which we had a priori hypotheses (cf. Fedorenko et al. 2010; Julian et al. 2012). To maximize generalizability to the population, the final analysis included all subjects: fROIs were defined in each individual subject as the 10% most active voxels for the conceptual contrast within each parcel (Fedorenko et al. 2012; Basilakos et al. 2018). Finally, using exclusively the left-out data, percent signal change was estimated for each fROI and condition using the MarsBaR toolbox (Brett et al. 2002).

Statistical inference was performed using a four-way repeated-measures ANOVA (Greenhouse-Geisser corrected) with the factors REGION (all fROIs), TASK (lexical decision, sound judgment, action judgment), SOUND (high, low), and ACTION (high, low). Interactions were resolved using step-down analyses and Bonferroni-Holm corrected post hoc comparisons. We report results for fROIs with significant effects.

Results

Behavioral Results

Mean response time for correct responses was 971.62 ms (SD: 157.10 ms). Mean accuracy was 92.28% (SD: 4.43%), which shows that subjects closely attended to the tasks.

For response accuracy (Fig. 2A), a three-way repeated-measures ANOVA (Greenhouse-Geisser corrected) with factors TASK (lexical decision, sound judgment, action judgment), SOUND (high, low), and ACTION (high, low) identified main effects of TASK ($F(2,78) = 58.11$, $P < 0.001$), SOUND ($F(1,39) = 10.78$, $P = 0.002$), and ACTION ($F(1,39) = 16.11$, $P < 0.001$), as well as interactions between SOUND × ACTION ($F(1,39) = 112.27$, $P < 0.001$), TASK × ACTION ($F(2,78) = 8.43$, $P = 0.003$), TASK × SOUND ($F(2,78) = 40.55$, $P < 0.001$), and TASK × SOUND × ACTION ($F(2,78) = 35.05$, $P < 0.001$). Step-down analyses revealed no significant effects during lexical decisions, whereas SOUND × ACTION interactions occurred during sound judgments ($F(1,39) = 93.49$, $P < 0.001$) and action judgments ($F(1,39) = 47.48$, $P < 0.001$). During sound judgments, we found higher accuracy for high sound words with a high than low action association ($t(39) = 9.26$, $P < 0.001$) and the opposite pattern for low sound words ($t(39) = 4.7$, $P < 0.001$). In addition, a main effect of SOUND ($F(1,39) = 34.52$, $P < 0.001$) reflected higher accuracy for low than high sound words and a main effect of ACTION ($F(1,39) = 57.01$, $P < 0.001$) reflected higher accuracy for high than low action words. During action judgments, high action words with a high versus low sound association were more accurate ($t(39) = 4.0$, $P < 0.001$) and the opposite pattern for low action words ($t(39) = 7.58$, $P < 0.001$). Moreover, a main effect of SOUND ($F(1,39) = 24.40$, $P < 0.001$) indicated higher accuracy for high than low sound words.

Response times for correct trials (Fig. 2B) also showed main effects of TASK ($F(2,78) = 148.434$, $P < 0.001$), SOUND ($F(1,39) = 6.550$, $P = 0.014$), and ACTION ($F(1,39) = 26.038$, $P < 0.001$), as well as interactions between SOUND × ACTION ($F(1,39) = 169.427$, $P < 0.001$), TASK × ACTION ($F(2,78) = 7.761$, $P = 0.005$), and TASK × SOUND × ACTION ($F(2,78) = 71.26$, $P < 0.001$). All three tasks exhibited a SOUND × ACTION interaction (lexical decision: $F(1,39) = 18.02$, $P < 0.001$; sound judgment: $F(1,39) = 139.65$, $P < 0.001$; action judgment: $F(1,39) = 79.33$, $P < 0.001$). During lexical decisions, we observed faster responses for low action words with a high than low sound association ($t(39) = 5.72$, $P < 0.001$) and for low sound words with a high than low action association ($t(39) = 4.11$, $P < 0.001$). In addition, a main effect of SOUND ($F(1,39) = 12.76$, $P < 0.001$) indicated faster responses for high than low sound words. During sound judgments, high sound words with a high versus low action association lead to faster responses ($t(39) = 11.51$, $P < 0.001$) and vice versa for low sound words ($t(39) = 5.58$, $P < 0.001$). Moreover, a main effect of ACTION ($F(1,39) = 31.794$, $P < 0.001$) reflected shorter responses for high than low action words. During action judgments, low action words with a low versus high sound association were faster ($t(39) = 3.98$, $P < 0.001$) and vice versa for high action words ($t(39) = 6.69$, $P < 0.001$). A main effect of ACTION ($F(1,39) = 13.07$, $P < 0.001$) indicated faster response times for high than low action words and a main effect of SOUND ($F(1,39) = 5.797$, $P = 0.021$) indicated faster responses for high than low sound words.

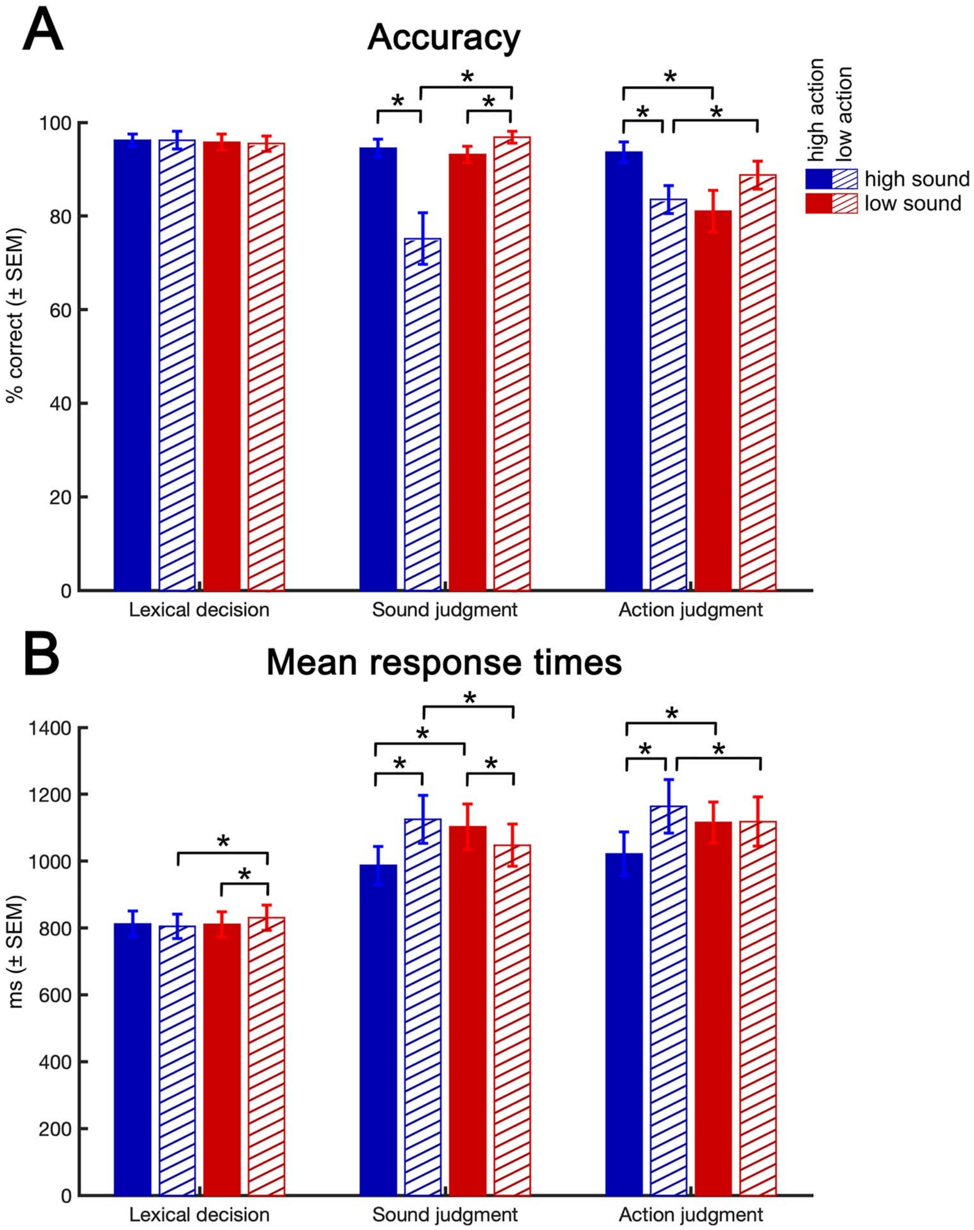

Figure 2. Behavioral results. (*A*) Accuracy is shown in percent correct responses. (*B*) Mean response times for correct trials are given in ms. Error bars represent standard error of the mean (SEM). $^*P < 0.05$ (Bonferroni-Holm corrected).

These behavioral results illustrate the interaction between the relevance of a certain perceptual–motor feature for a concept and the concurrent task, supporting the notion that the retrieval of perceptual–motor features is task-dependent. To account for potential influences of differences in accuracy or reaction times on brain activation, only correct trials were analyzed, and response times were entered into the subject-level GLM as a duration-modulated parametric regressor (Grinband et al. 2008).

Localizer Activations

The motor localizer (hand movements > rest) engaged bilateral primary, pre-, and supplementary motor cortices, somatosensory cortices, anterior supramarginal gyrus (aSMG) extending into inferior parietal sulcus (IPS), cerebellum, as well as the lateral temporal–occipital junction (LTO) at the border of pMTG to anterior occipital cortex (Supplementary Table S2).

In the auditory localizer, scrambled sounds (> silence) activated bilateral early auditory cortex, brainstem, cerebellum, and right inferior frontal gyrus (IFG). Real sounds (>silence) engaged a broader region of bilateral auditory cortex extending into the superior and middle temporal gyri (STG/MTG), as well as dorsomedial prefrontal cortex (dmPFC), left middle frontal gyrus (MFG), IFG, IPS, and middle cingulate cortex (MCC) (Supplementary Table S3).

Within-Task Activations for Sound and Action Features of Concepts

We first tested for activation increases for sound features (high > low sound words) and action features of concepts (high > low action words) within each task.

Action Features

In the lexical decision task, high as compared to low action words did not elicit significant activation in any voxel (at $q < 0.05$ FDR-corrected). Even when reducing the statistical threshold to $P < 0.001$ uncorrected, only the left ventromedial prefrontal cortex (vmPFC)—a high-level, heteromodal region (Binder et al. 2009)—showed activity, whereas no motor-related regions were engaged.

Similarly, in the sound judgment task, we observed no significant activation for action-related words (at $q < 0.05$ FDR-corrected). At $P < 0.001$ uncorrected, the left angular gyrus (AG), SMG, precuneus, and right vmPFC were activated. Most of these regions (AG, precuneus, vmPFC) represent heteromodal regions involved in conceptual processing (Binder et al. 2009; Binder 2016).

In contrast, in the action judgment task, action-related words produced widespread activation in both hemispheres (Fig. 3A; Supplementary Table S4). This activation overlapped with brain activity in the motor localizer in bilateral cerebellum, premotor cortex (PMC), aSMG/IPS, somatosensory cortex, supplementary motor area (SMA), MCC, and pMTG/LTO (Fig. 3B; Supplementary Table S5). However, activation for action-related conceptual processing was also present *outside* regions activated by the motor localizer (as determined by exclusive masking), namely in bilateral posterior cingulate cortex (PCC), posterior inferior temporal gyrus (pITG; extending into posterior fusiform gyrus (FG) in the left hemisphere), more posterior parts of SMG/IPS (extending into the superior parietal lobe [SPL] in the left hemisphere), left dmPFC, anterior IFG (aIFG), AG, and more anterior parts of MTG.

Sound Features

An analogous pattern emerged for sound features of concepts. In the lexical decision task, no significant activation was found for high versus low sound words, even when reducing the statistical threshold to $P < 0.001$ uncorrected.

Also in the action judgment task, no voxel was significantly activated (at $q < 0.05$ FDR-corrected). An exploratory analysis at $P < 0.001$ uncorrected (extent > 20 voxels) revealed activation in bilateral precuneus/PCC and left posterior IPS.

In the sound judgment task, however, sound-related words elicited widespread activation (Fig. 4A; Supplementary Table S6). This activation did not overlap with brain activity during the perception of scrambled sounds (i.e., sounds that lacked any meaning and mainly engaged early auditory cortices; Supplementary Fig. S3). In contrast, activation for sound-related words during sound judgments overlapped with activity for the perception of real object sounds in left IFG (extending into insula), MFG/precentral sulcus (PreCS), pIPS, pMTG, dmPFC, vmPFC, and right cerebellum (Fig. 4B; Supplementary Table S7). However, sound-related words also engaged regions that were not activated during real sound perception, including left AG, posterior SMG (pSMG), and other portions of IFG, MFG/PreCS, pMTG, dmPFC, vmPFC, and right cerebellum.

Task Dependency of Conceptual Feature Activation

The above-described results suggest that neural activity for a certain conceptual feature is strongly task-dependent: We selectively observed activity for a specific feature in a task that explicitly required that feature. To further investigate the task dependency of activation for action or sound features, we performed several whole-brain interaction analyses.

Action Features

Several regions showed significantly stronger activation for high as compared to low action words in the action judgment task than in both other tasks (as determined by the conjunction of the TASK × ACTION interactions). These areas included left aIFG, SMG/IPS (extending into SPL), pITG (extending into FG), caudate nucleus, ventral PMC (PMv), and right cerebellum (Fig. 5; Supplementary Table S10). Additionally, left SMA, dmPFC, and bilateral cingulate cortex were more active during action judgments as compared to sound judgments (Supplementary Table S8). Finally, left pMTG/LTO showed stronger activation during action judgments than lexical decisions (Supplementary Table S9).

Among these regions, left PMv, anterior SMG/IPS, pMTG/LTO, SMA, and right cerebellum overlapped with the motor localizer (Fig. 5C). In contrast, no overlap was found in left aIFG, pITG/FG, dmPFC, caudate nucleus, more anterior parts of pMTG, and more posterior parts of SMG/IPS.

Sound Features

The strongest evidence for task-dependent activation for sound features of concepts was found in left aIFG and dmPFC. These regions showed significantly stronger activation for high versus low sound words in the sound judgment task than in both other tasks (Fig. 6; Supplementary Table S13). Moreover, the left pIPL (including AG, pSMG, pIPS), MFG/PreCS, vmPFC, and pMTG were more strongly engaged for high versus low sound words in the sound judgment task relative to the lexical decision task (Supplementary Table S12).

Clusters in left pIPS, aIFG, and dmPFC overlapped with real sound perception, whereas clusters in left AG, pSMG, MFG/PreCS, and pMTG did not (Fig. 6C).

Multimodal Conceptual Regions

Finally, we tested for regions that were commonly engaged during the explicit retrieval of action features (high > low action words during action judgments) and sound features (high > low sound words during sound judgments). Such multimodal activation was found in left posterior IPL (AG, pSMG, IPS), pMTG, aIFG, dmPFC, vmPFC, and right cerebellum (crus I/II) (Fig. 7A; Supplementary Table S14).

These regions were located largely *outside* auditory and motor systems (Fig. 7B): Left AG, pSMG, vmPFC, anterior-most IFG, as well as parts of left pMTG, dmPFC, and right cerebellum overlapped with neither the auditory nor motor localizer. A small cluster in left anterior IPS (aIPS) overlapped with the motor localizer, while overlap with the auditory localizer was found in left pIPS, more posterior parts of IFG (extending into insula), and portions of pMTG, dmPFC, and right cerebellum.

Subject-Specific fROI Analyses

To characterize the complete response profiles of motor, auditory, and multimodal regions involved in conceptual processing, we performed a subject-specific fROI analysis. In contrast to standard group analyses that aggregate responses from the same location in standard space across subjects, fROI analyses aggregate responses from the same *functional* region across subjects, resulting in higher sensitivity and functional resolution (i.e., the ability to separate adjacent but functionally distinct regions) (Fedorenko and Kanwisher 2009, 2011; Nieto-Castañón and Fedorenko 2012). fROI analyses are thus complementary to

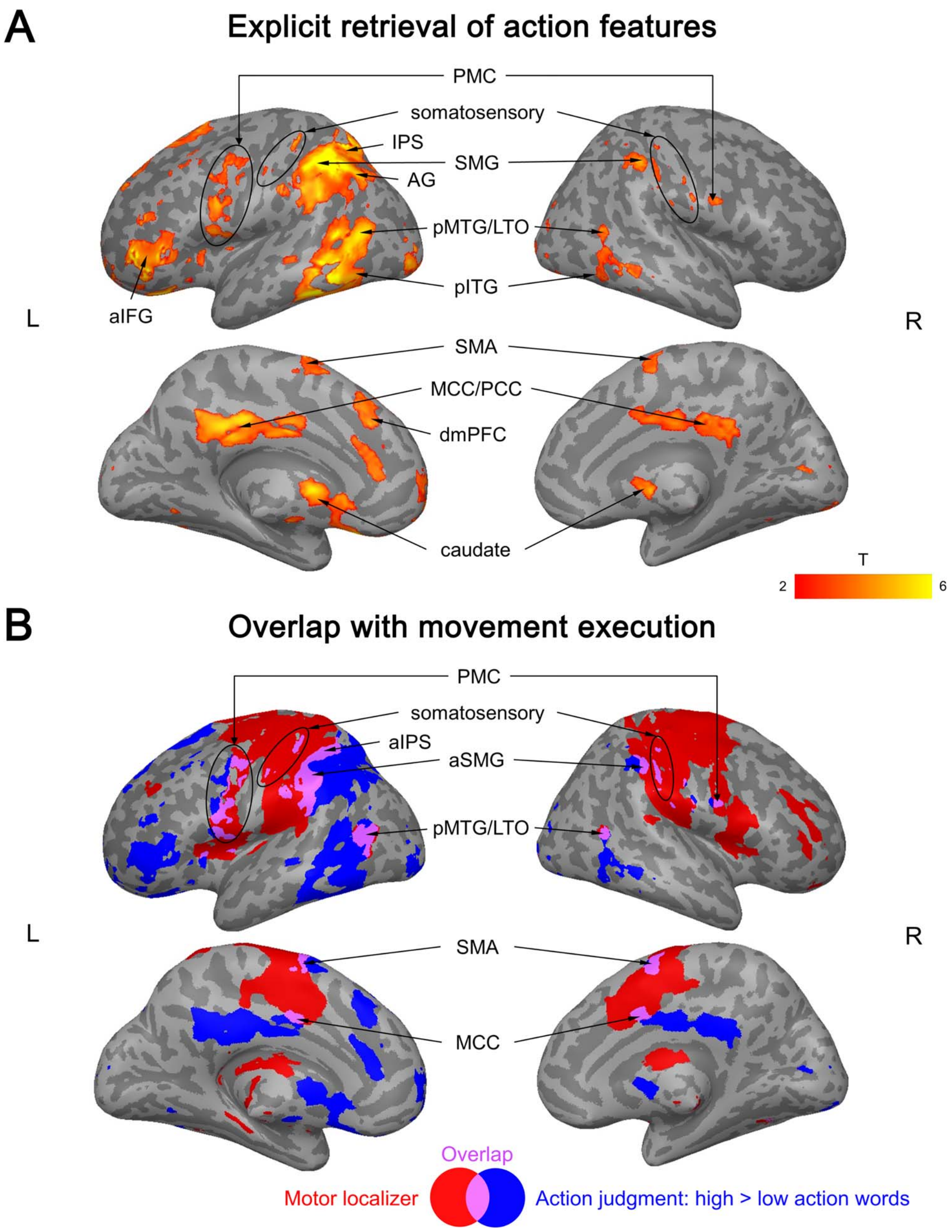

Figure 3. (*A*) Activation for action features (high > low action words) in the action judgment task. (*B*) Overlap (purple) between the activation for action features in the action judgment task (blue) and the motor localizer (hand movements > rest; red). All activation maps were thresholded at $q < 0.05$ FDR-corrected (extent > 20 voxels).

our whole-brain analyses: They allow us to determine whether regions defined functionally in individual subjects are indeed specific to action or sound features, or multimodal, and to what extent their feature-related activity is task-dependent. Different data of each subject were used for fROI definition and response estimation.

We identified motor fROIs (subject-specific regions engaged for action feature retrieval and the motor localizer) in left aSMG/IPS, pMTG/LTO, and left and right PMv (Fig. 8A); auditory fROIs (subject-specific regions engaged for sound feature retrieval and the auditory localizer) in left aIFG, MFG, PreCS, pIPS, pSTG/MTG, and dmPFC (Fig. 8B); and multimodal fROIs (subject-specific regions engaged for both sound and action feature retrieval) in left aIFG, pIPL, and pMTG (Fig. 8C).

A repeated-measures ANOVA revealed a REGION × TASK × SOUND × ACTION interaction ($F(32,543) = 2.074$, $P = 0.01$). We resolved this interaction using step-down ANOVAs within each fROI.

Motor fROIs

Motor fROIs in left aSMG/IPS and pMTG/LTO showed significant TASK × ACTION interactions, which were driven by a high > low ACTION effect during action judgments but not the other tasks (Fig. 8A; Supplementary Table S15 for statistics). Right PMv exhibited a similar, albeit nonsignificant, response pattern. Left PMv also showed a significant TASK × ACTION interaction, but this was driven by trends toward a high > low ACTION effect during action judgments and a low > high

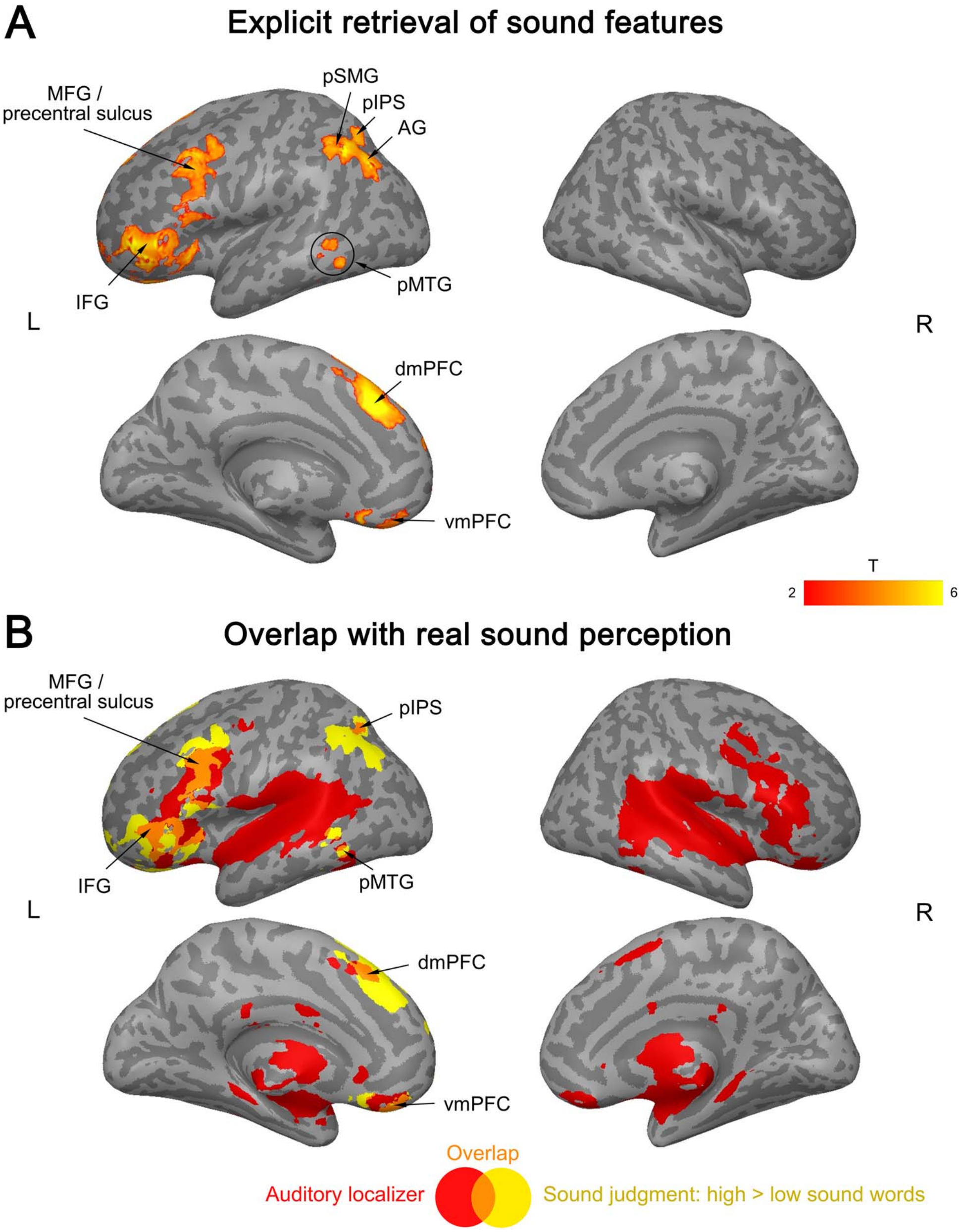

Figure 4. (*A*) Activation for sound features of concepts (high > low sound words) in the sound judgment task. (*B*) Overlap (orange) between activation for sound features in the sound judgment task (yellow) and the auditory localizer (real object sounds > silence; red). All activation maps were thresholded at $q < 0.05$ FDR-corrected (extent > 20 voxels).

ACTION effect during sound judgments, potentially reflecting suppression of action-related activity when action features are irrelevant. Direct between-task comparisons revealed that all motor fROIs showed stronger activity for action features (high > low ACTION) during action judgments than during sound judgments and/or lexical decisions.

These results indicate that left aSMG/IPS, pMTG/LTO, and bilateral PMv are specific to action features in a task-dependent fashion, responding selectively to action features (not sound features) exclusively during action judgments.

Auditory fROIs

Auditory fROIs in left aIFG, PreCS, and dmPFC all showed TASK × SOUND × ACTION interactions, driven by a SOUND × ACTION interaction during sound judgments and no effects during the other tasks (Fig. 8*B*; Supplementary Table S16 for statistics). This interaction occurred as high sound–low action words produced stronger activity than the other conditions (which did not differ between each other). Left MFG showed a TASK × SOUND interaction, driven by a high > low SOUND effect during sound judgments but not during the other tasks. All of these regions were more strongly engaged for sound features (high > low SOUND) during sound judgments than during action judgments and/or lexical decisions.

These results indicate that auditory-related areas within left aIFG, PreCS, dmPFC, and MFG are specific to sound features in a task-dependent manner, responding to high (vs. low) sound words (MFG) or even only to high sound–low

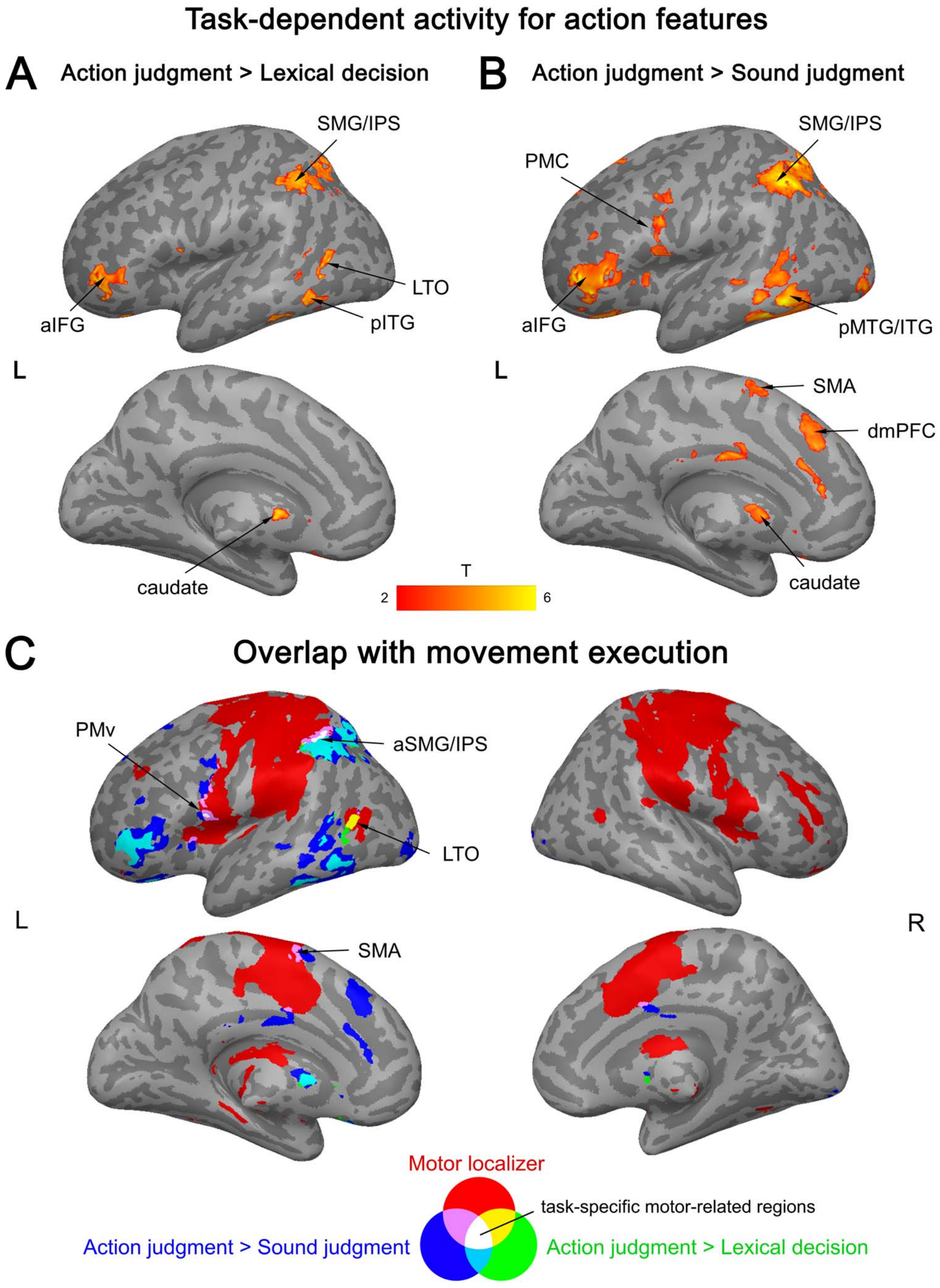

Figure 5. Interaction between activation for action features (high > low action words) and task. (*A*) Stronger activation during action judgments than lexical decisions. (*B*) Stronger activation during action judgments than sound judgments. (*C*) Activation overlap between the interaction and movement execution. All activation maps were thresholded at $q < 0.05$ FDR-corrected (extent > 20 voxels).

action words (aIFG, PreCS, dmPFC) selectively during sound judgments.

Left pIPS and pSTG/MTG showed a distinct response profile: Both regions exhibited significant TASK × SOUND and TASK × ACTION interactions, which were driven by a high > low SOUND effect during sound judgments, a high > low ACTION effect during action judgments, and no effects during lexical decisions. Activity for sound features (high > low SOUND) was significantly stronger during sound judgments than action judgments or lexical decisions, and activity for action features (high > low ACTION) was higher during action judgments than sound judgments or lexical decisions. This suggests that these areas are not specific to sound features but indeed multimodal, responding to both sound and action features when they are task-relevant, respectively (see below).

Multimodal fROIs

Both left pIPL and pMTG showed significant TASK × SOUND and TASK × ACTION interactions, which were driven by a high > low SOUND effect during sound judgments, a high > low

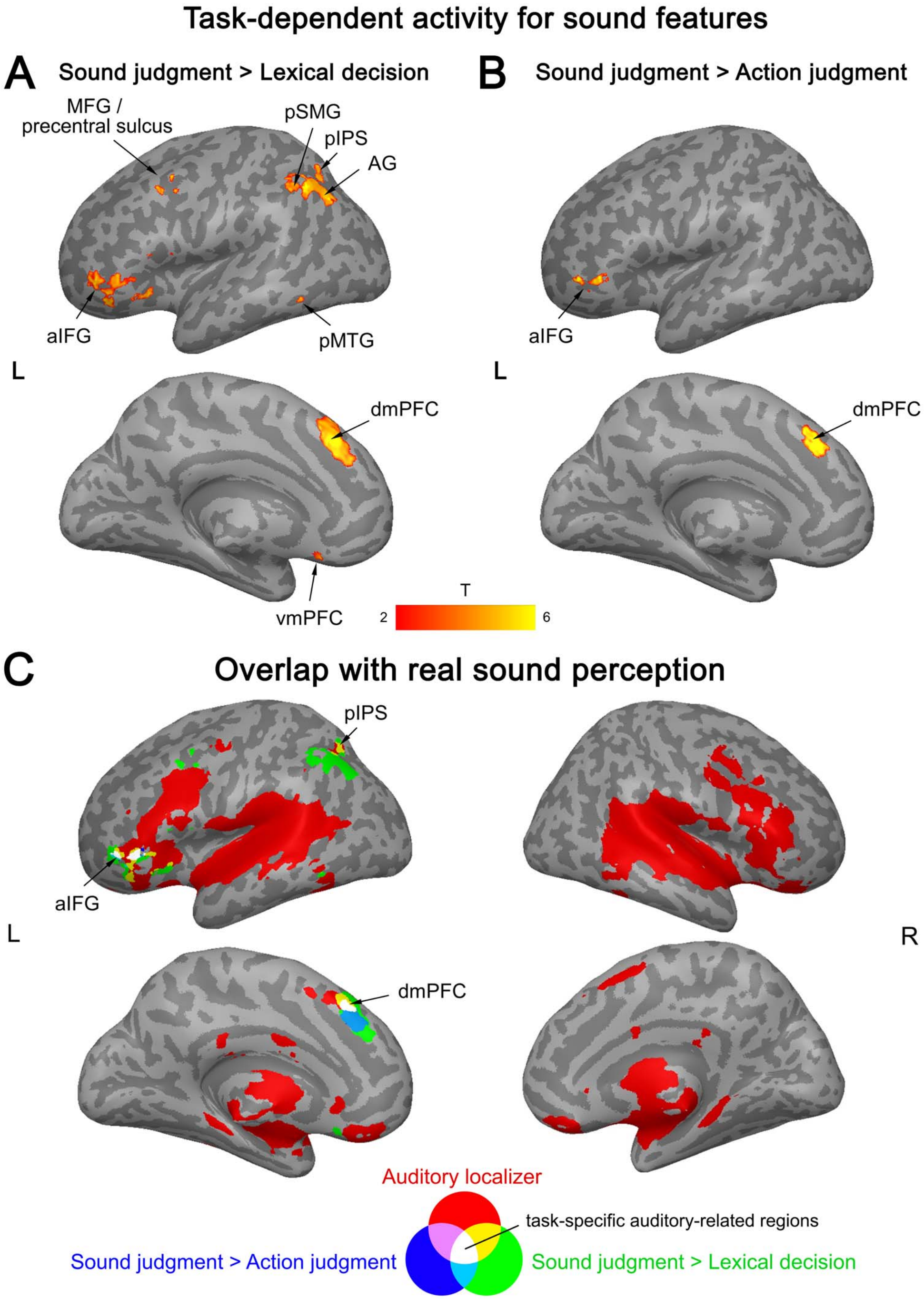

Figure 6. Interaction between activation for sound features (high > low sound words) and task. (A) Stronger activation during sound judgments than lexical decisions. (B) Stronger activation during sound judgments than action judgments. (C) Activation overlap between the interaction and real sound perception. All activation maps were thresholded at $q < 0.05$ FDR-corrected (extent > 20 voxels).

ACTION effect during action judgments, and no effects during lexical decisions (Fig. 8C; Supplementary Table S17 for statistics). Left aIFG showed a slightly different response profile with a TASK × SOUND × ACTION interaction, driven by a SOUND × ACTION interaction during sound judgments which occurred as high sound–low action words produced stronger activity than all other conditions (which did not significantly differ). Like pIPL and pMTG, left aIFG showed a high > low ACTION effect during action judgments and no effects during lexical decisions. All three regions showed significantly stronger activation for sound features (high > low SOUND) during sound judgments than during both action judgments and lexical decisions and stronger activation for action features (high > low ACTION) during action judgments than during sound judgments and lexical decisions.

These findings provide strong evidence that left aIFG, pIPL, and pMTG contain multimodal and task-dependent areas involved in conceptual processing in individual subjects,

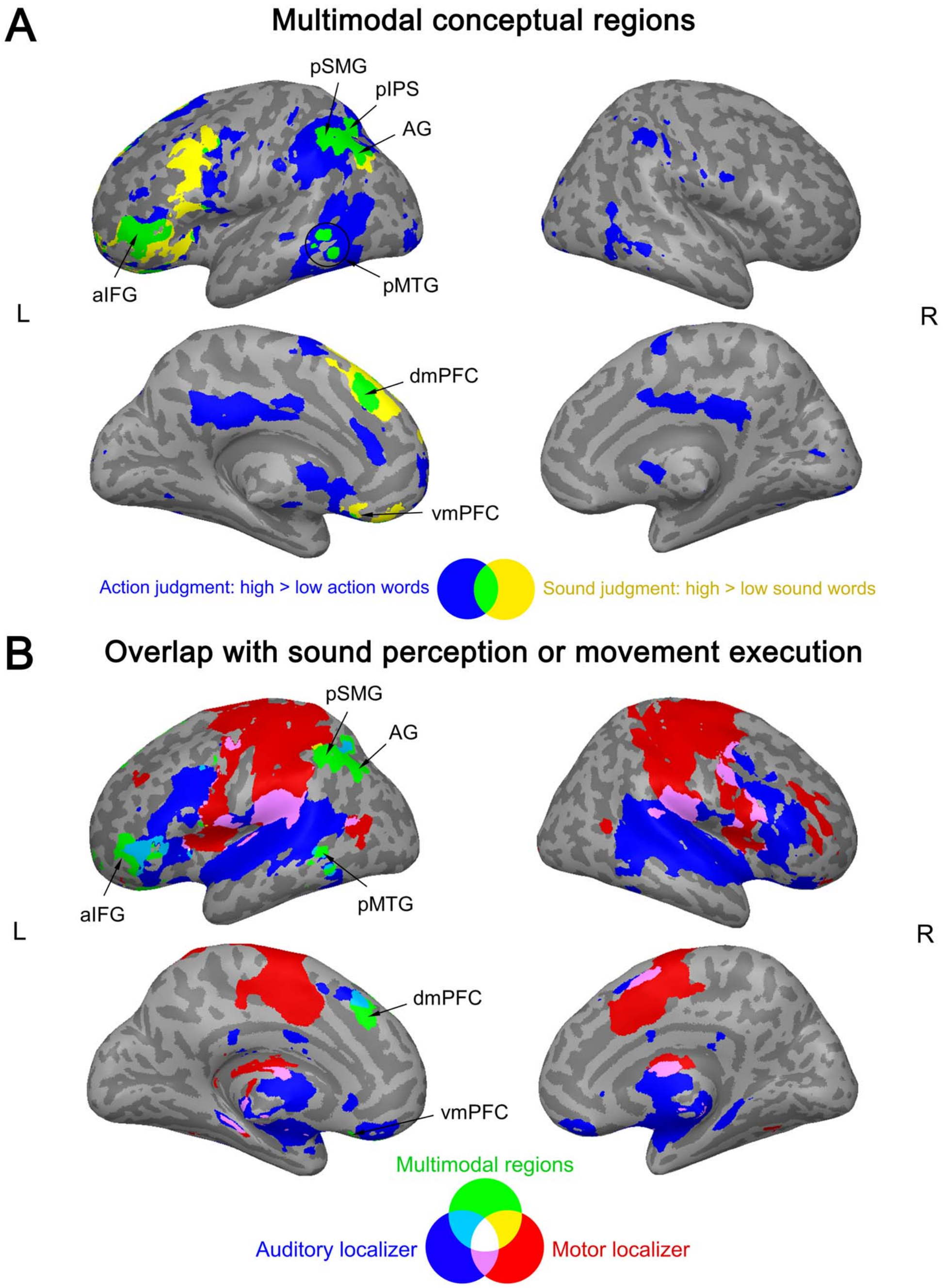

Figure 7. (*A*) Multimodal conceptual regions. Activation overlap (green) between the explicit retrieval of action features (blue) and sound features (yellow). (*B*) Overlap between multimodal regions (green) and the auditory localizer (blue) or motor localizer (red). All activation maps were thresholded at $q < 0.05$ FDR-corrected (extent > 20 voxels).

responding to both action and sound features selectively when these are task-relevant.

Discussion

In this study, we investigated the neural correlates of conceptual processing and their modulation by task. We found neural activation for action and sound features of concepts selectively when they were task-relevant in motor- and auditory-related areas, respectively, as well as in higher-level, multimodal regions. Both modality-specific and multimodal regions showed significantly stronger activity for a certain feature when that feature was task-relevant. These results provide strong evidence that the retrieval of conceptual features and recruitment of modality-specific perceptual–motor areas depend on the task. As an unexpected, novel finding, not only modality-specific, but also multimodal areas exhibited a task-dependent response to perceptual-motor features of concepts.

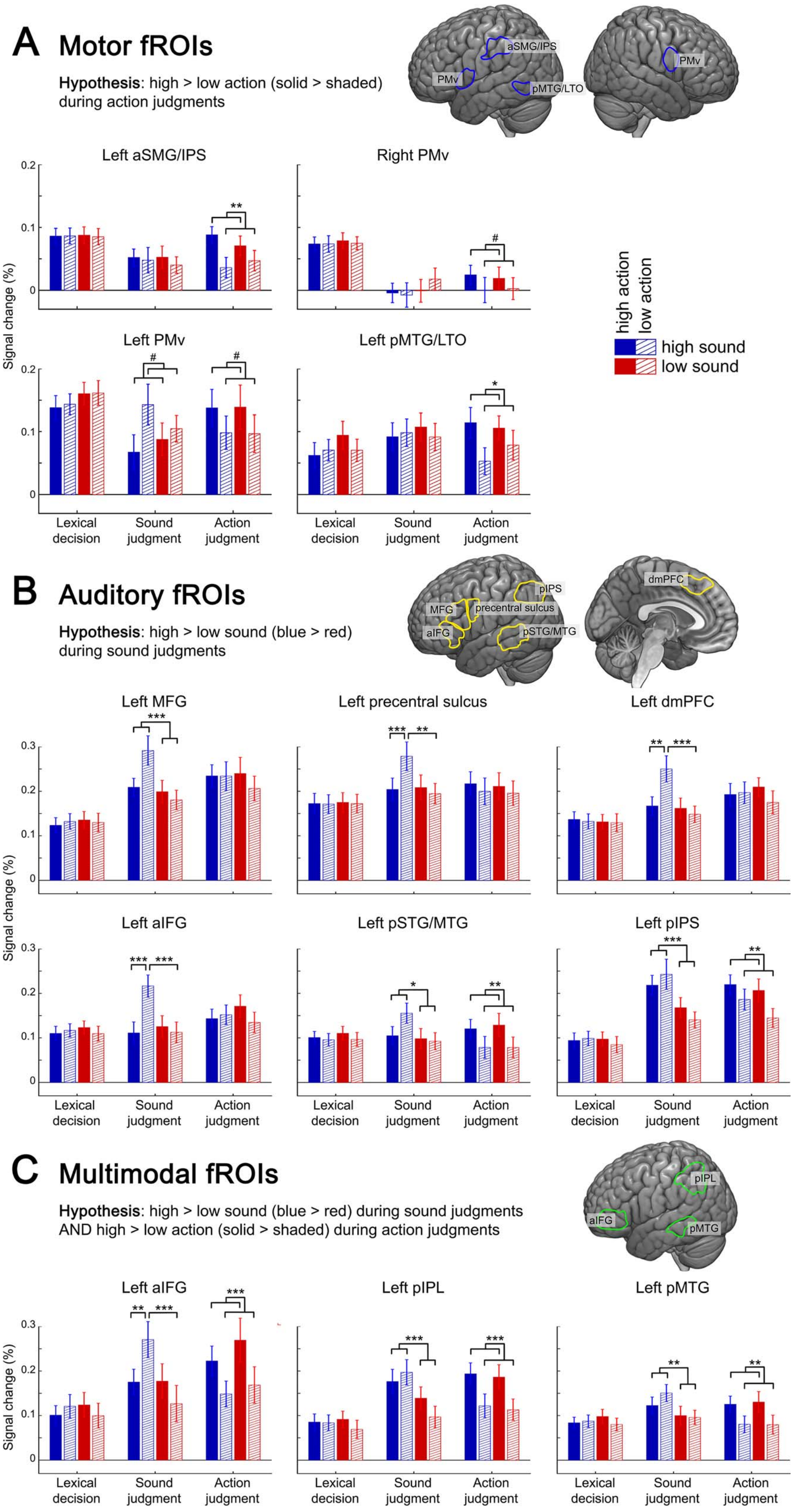

Figure 8. Response profiles for (*A*) motor fROIs, subject-specific regions engaged for action feature retrieval and the motor localizer; (*B*) auditory fROIs, subject-specific regions engaged for sound feature retrieval and the auditory localizer; and (C) multimodal fROIs, subject-specific regions engaged for both sound and action feature retrieval. Mean signal change (in %) is shown for each experimental condition; error bars represent standard error of the mean. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{\#}P < 0.1$/did not survive multiple comparisons correction.

Action Feature Retrieval Involves Motor-Related and Multimodal Regions

Exclusively during action judgments, action features of concepts produced widespread activation, which partially overlapped with the motor localizer in bilateral PMC, SMA, somatosensory areas, aSMG/IPS, pMTG/LTO, and cerebellum.

These regions represent secondary or association regions of the motor system, which are not involved in movement per se, but support movement planning or preparation (for reviews, see van Elk et al. 2014; Hardwick et al. 2018). PMC is associated with actions in the environment (Rizzolatti et al. 1988; Davare et al. 2009), whereas SMA is linked to actions that require little monitoring of the environment, such as self-generated actions (Deecke and Kornhuber 1978; Halsband et al. 1994; Debaere et al. 2003). The cerebellum controls the timing, strength, and precision of movement (Haggard et al. 1995; Wolpert et al. 1998; Ohyama et al. 2003) and contains somatotopic motor representations in its anterior and posterior lobes (Buckner 2013). aSMG/IPS is involved in the visual–motor control of object-directed actions (Haaland et al. 2000; Turella and Lingnau 2014), and pMTG/LTO represents different types of hand actions during execution, observation, and imagery (Lewis 2006; Oosterhof et al. 2010). The subject-specific fROI analysis revealed that action-related areas in left aSMG/IPS, pMTG/LTO, and bilateral PMv indeed specifically respond to action features when these are task-relevant and never respond to sound features.

Several of these regions have previously been implicated in action-related conceptual processing. For instance, Fernandino et al. (2016a) found that the relevance of action features to word meaning correlated with activation during concreteness judgments in bilateral aSMG, pMTG/LTO, and somatosensory areas. A meta-analysis by Binder et al. (2009) showed that left pMTG/LTO and SMG were the only regions with consistent activation across neuroimaging studies for processing of words referring to manipulable artifacts as compared to living things and retrieval of action knowledge relative to other types of knowledge. Similarly, another meta-analysis found that only left pMTG/LTO, extending into SMG, was consistently activated across neuroimaging studies of action-related conceptual processing on words or pictures (Watson et al. 2013).

Overall, it seems that pMTG/LTO and SMG are more consistently engaged during action feature processing than PMC, SMA, somatosensory cortex, and cerebellum (Watson et al. 2013; van Elk et al. 2014). One intriguing hypothesis is that these latter areas, which arguably represent lower-level regions of the motor system, only come into play during tasks that require highly explicit or deep processing of action features, such as our action judgment task (cf. Watson et al. 2013). This notion is supported by a previous study that did *not* find activation for action features in PMC, SMA, or cerebellum during concreteness judgment (Fernandino et al. 2016a), a task that does not require the same extent of action feature processing as action judgment.

Note that our motor localizer was restricted to hand movements and therefore might not have engaged all brain regions involved in the complex object-directed actions associated with our high-action words. However, the localizer involved pinching and fist-making, which arguably resemble object-directed hand movements more closely than low-level motor tasks like finger tapping. Indeed, our motor localizer engaged pMTG/LTO and aSMG/IPS, two relatively high-level motor-related regions that are usually not engaged in finger tapping (Mostofsky et al. 2006; Gountouna et al. 2010).

Crucially, retrieval of action features also engaged regions *outside* motor-related areas. These included areas that have previously been proposed to constitute heteromodal regions involved in conceptual processing (left AG, pSMG, aIFG, and mPFC; Binder et al. 2009)—a crucial result we will return to below.

Sound Feature Retrieval Involves Auditory-Related and Multimodal Regions

Sound features selectively elicited significant activation during sound judgments. This activation did not overlap with the perception of scrambled sounds; thus, we found no evidence for an involvement of early auditory cortex. However, activation overlapped with the perception of real object sounds in regions implicated in high-level auditory processing, including left IFG, MFG/PreCS, and pMTG. These areas respond more strongly to recognized environmental sounds than unrecognized time-reversed versions of the same sounds (Lewis et al. 2004). Moreover, left IFG and MFG are more strongly engaged during the recall of sounds than pictures (Wheeler et al. 2000). The homologue region in the monkey (left ventrolateral prefrontal cortex) contains neurons representing abstract sound categories (for a review, see Romanski and Averbeck 2009).

Notably, the subject-specific fROI analysis showed that the response of some auditory fROIs (left aIFG, PreCS, dmPFC) was mainly driven by sound judgments on high sound–low action words. This is striking since this condition was also associated with the lowest response accuracy, which might reflect that sound features of high sound–low action words are not associated with corresponding actions, making them more demanding to retrieve due to a lack of action–sound coupling (Lemaitre et al. 2018). One might wonder whether activity of these regions could solely reflect task demands, that is, domain-general executive control processes. Several arguments speak against this view. Firstly, we controlled for difficulty differences between trials and conditions by removing error trials from the analysis and including a response time regressor. Secondly, auditory fROIs were defined via overlap with the auditory localizer, in which subjects merely listened to sounds—a simple task that required little executive processing. The overlap instead suggests that activation reflected engagement of auditory representations. Thirdly, the implicated regions have previously been associated with both high-level auditory processing (Wheeler et al. 2000; Lewis et al. 2004; Romanski and Averbeck 2009) and sound-related conceptual processing (Kellenbach et al. 2001; Kiefer et al. 2008; Fernandino et al. 2016a)—results that cannot be accounted for by task difficulty alone. Finally, the response profile of auditory fROIs was not a mirror image of behavioral performance: Performance differences were also seen during action judgments (see Fig. 2), but auditory fROIs responded selectively during sound judgments. Auditory fROIs thus showed modality- and task-specificity for sound features.

However, it is possible that some of the regions engaged during sound feature retrieval support the controlled retrieval of sound feature representations, rather than sound feature representation per se. A region representing sound features would be expected to activate not only for high sound–*low* action words but also for high sound–*high* action words. A selective response when conceptual retrieval demands are high seems more consistent with a role in conceptual-semantic control than representation (Jefferies 2013; Noonan et al. 2013; Lambon Ralph et al. 2016). The fact that activation for sound feature retrieval overlapped with perception of real object sounds, but not scrambled sounds, is consistent with the engagement of more abstract conceptual processes (Simanova et al. 2014). This is corroborated by the fact that especially left aIFG (Thompson-Schill et al. 1997; Wagner et al. 2001) and sometimes dmPFC (Alexander et al. 1989; Binder and Desai 2011) have previously been implicated in the controlled retrieval and/or selection of conceptual representations.

Several previous studies have implicated left pMTG in sound feature processing. In a lexical decision task, Kiefer et al. (2008) found that words with a high versus low relevance of sound features activate a region in left pMTG that was also engaged during real sound perception and overlaps with the pMTG region activated for sound features in our study. This sound-related pMTG subregion can be dissociated from a more posterior subregion that is engaged for action-related, but not sound-related concepts (Kiefer et al. 2012b) and overlaps with the pMTG/LTO area activated for action features in our study. Finally, a patient with a focal lesion in left pSTG/MTG was selectively impaired at processing sound-related, but not non-sound-related concepts, suggesting that this area is indeed causally relevant for processing sound features of concepts (Trumpp et al. 2013a; see Bonner and Grossman 2012 for corroborating evidence). However, in our study, the entire left pMTG region activated during the retrieval of sound features was also engaged during the retrieval of action features. This converges with previous evidence that the same region in left pMTG is modulated by both sound features and visual–motion features of concepts (Fernandino et al. 2016a). Moreover, left pMTG previously showed greater activity for both sound and action verbs as compared to pseudowords in a lexical decision task (Popp et al. 2019b). This area might therefore represent a multimodal, rather than sound-specific, region involved in conceptual processing. Indeed, the subject-specific fROI analysis revealed that even the portion of pMTG that overlapped with the auditory localizer was engaged for both sound and action feature retrieval. A similar multimodal response profile was found in left pIPS.

Crucially, activation for sound feature retrieval extended *beyond* the auditory localizer to left AG, pSMG, aIFG, and mPFC. Note that these regions were also engaged during the explicit retrieval of action features and did not overlap with the motor localizer, suggesting that they represent high-level, multimodal regions involved in conceptual processing.

Overall, the observed overlap of modality-specific activity patterns for conceptual feature retrieval and core regions for auditory or motor processing supports grounded theories of conceptual processing, which assume the retrieval of conceptual knowledge to involve a partial reinstatement of activity in perceptual–motor areas during actual perception and action (Pulvermüller 1999; Barsalou 2008; Kiefer and Pulvermüller 2012). However, our results are inconsistent with the view that conceptual processing relies *exclusively* on modality-specific perceptual-motor regions (e.g., Allport 1985) because the retrieval of sound or action features also involved higher-level, multimodal areas.

Recruitment of Multimodal Regions during Conceptual Processing

Notably, several regions were engaged both during the explicit retrieval of action features and sound features, including left posterior IPL (AG, pSMG, pIPS), pMTG (anterior to LTO), aIFG, mPFC, and right cerebellum. These areas largely did not overlap with either the motor or auditory localizers, suggesting that they support more abstract representations than perceptual–motor areas.

Except for the right cerebellum, all of these regions have previously been described as "heteromodal" regions involved in conceptual processing, that is, regions engaged in the processing of all concepts, irrespective of their perceptual–motor content (Bonner et al. 2013; Binder 2016; Fernandino et al. 2016a, 2016b). This is supported by a meta-analysis of functional neuroimaging studies which showed that, among other regions, left posterior IPL, MTG, aIFG, and mPFC consistently show stronger activation for meaningful as compared to meaningless stimuli (Binder et al. 2009). It has been proposed that posterior IPL and parts of MTG act as heteromodal "convergence zones" at the top of a hierarchy integrating modality-specific representations into increasingly abstract representations (Binder and Desai 2011; Price et al. 2015). In contrast, prefrontal areas—especially left aIFG—appear to support the controlled retrieval and/or selection of conceptual representations (Thompson-Schill et al. 1997; Wagner et al. 2001; Jefferies 2013; Hartwigsen et al. 2016).

Crucially, the fact that these regions were sensitive to both action and sound features individually suggests that their representations are not amodal (i.e., completely abstracted away from modality-specific perceptual-motor information), but multimodal, that is, they retain modality-specific information about the individual features they integrate (cf. Barsalou 2016; Binder 2016; Fernandino et al. 2016a, 2016b). Note that this does not preclude the additional contribution of amodal regions to conceptual processing. For instance, it has been proposed that the ATL constitutes such an amodal "hub" (Lambon Ralph et al. 2016). In line with this view, the ATL was activated for words versus pseudowords in the lexical decision task (see Supplementary Fig. S2), indicating that it contributes to conceptual processing in general (cf. Binder et al. 2009).

Surprisingly, the right cerebellum also emerged as one of the regions engaged during the retrieval of both action and sound features. While the cerebellum is not included in contemporary models of conceptual processing (e.g., Binder and Desai 2011; Lambon Ralph et al. 2016), increasing evidence suggests that it contributes to higher cognitive processes and not just to movement planning and execution (for reviews, see Strick et al. 2009; Buckner 2013). Indeed, the subregion of the cerebellum activated during action and sound feature retrieval in the present study shows selective resting-state functional connectivity with *all* other multimodal conceptual regions identified here, that is, posterior IPL, pMTG, aIFG, and mPFC (Krienen and Buckner 2009; Buckner et al. 2011). The fact that this area did not overlap with the motor localizer further strengthens the view that it constitutes a nonmotor, higher-level subregion of the cerebellum.

Notably, the subject-specific fROI analysis identified two distinct functional subregions within the left aIFG: a sound-specific and a multimodal subregion. This illustrates the advantages of subject-specific fROI analyses, which yield higher sensitivity and functional resolution (i.e., the ability to separate adjacent but functionally distinct areas) than standard group analyses (Fedorenko et al. 2010; Nieto-Castañón and Fedorenko 2012). Importantly, this analysis confirmed that multimodal conceptual regions (sets of voxels activated during both sound and action feature retrieval) exist in individual subjects.

Overall, our results support theories that assume conceptual processing to rely on both modality-specific perceptual–motor

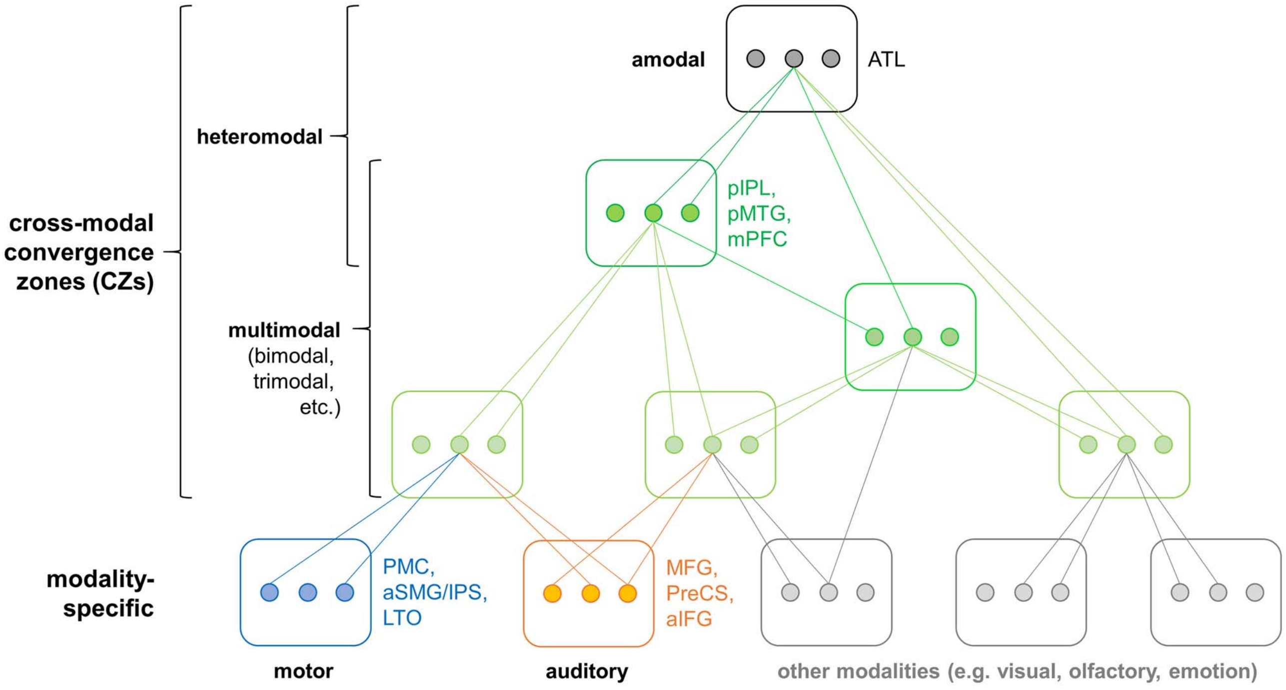

Figure 9. A new model of the neural architecture underlying conceptual representation. *Modality-specific* representations are integrated into increasingly abstract representations via multiple levels of cross-modal CZs. Heteromodal CZs, which receive input from all modalities, can be subdivided into *multimodal* regions that retain modality-specific information and *amodal* regions that do not. Boxes represent brain regions and dots represent individual representational units that converge onto a more abstract representation at a higher level. Note that this is merely a simplified schema and more hierarchy levels probably exist. The model is a synthesis of our current results and previous theories (Binder and Desai 2011; Lambon Ralph et al. 2016; Fernandino et al. 2016a).

regions and cross-modal[1] convergence zones (CZs), such as the "embodied abstraction" (Binder and Desai 2011; Fernandino et al. 2016a) and "hub-and-spokes" (Patterson et al. 2007; Lambon Ralph et al. 2016) models. Whereas the hub-and-spokes model singles out the ATL as the main "hub" for conceptual knowledge, the embodied abstraction view proposes a hierarchy of cross-modal CZs in the inferior parietal, temporal, and medial prefrontal cortices. Our results support the embodied abstraction view as we found evidence for multimodal conceptual processing in left pIPL, pMTG, and mPFC (among other regions). While recent versions of the hub-and-spokes view propose the ATL to be "graded," with subregions closest to modality-specific cortices preferring the respective modalities (Lambon Ralph et al. 2016), we found no modality-specific effects in the ATL. However, as mentioned above, the ATL might constitute an amodal region supporting conceptual processing. Therefore, our results seem consistent with a theory that combines both the embodied abstraction and hub-and-spokes views (Fig. 9): Conceptual processing may rely on a representational hierarchy from modality-specific perceptual–motor regions to multiple levels of cross-modal CZs, including multimodal (bimodal, trimodal, etc.) up to heteromodal CZs, which receive input from all modalities (cf. Damasio 1989; Mesulam 1998; Simmons and Barsalou 2003; Binder and Desai 2011; Margulies et al. 2016). As a novel distinction, we subdivide heteromodal CZs into two classes: 1) Heteromodal CZs that are *multimodal* themselves, that is, retain modality-specific information and 2) *amodal* regions that completely abstract away from modality-specific input. Amodal regions thus occupy the top of the hierarchy with the highest level of abstraction. Together with previous evidence, our data suggest that high-level *multimodal* CZs include left pIPL, pMTG, and mPFC (Binder et al. 2009; Binder 2016), and the ATL functions as an *amodal* hub (Jefferies 2013; Lambon Ralph et al. 2016). In addition to the representational hierarchy, control regions (especially left aIFG) support the controlled retrieval and/or selection of conceptual representations (Thompson-Schill et al. 1997; Wagner et al. 2001; Noonan et al. 2013).

Task Dependency of Conceptual Feature Retrieval

Many of the regions that were engaged during the retrieval of action or sound features were more strongly activated when the respective feature was task-relevant. These included both modality-specific perceptual-motor areas and multimodal regions.

Together with the finding that action or sound features only produced significant activity when they were explicitly required by the task, these results suggest that perceptual–motor features are selectively retrieved when they are task-relevant. Moreover, they support the view that the engagement of modality-specific perceptual–motor areas in conceptual processing strongly depends on the task (Hoenig et al. 2008; Binder and Desai 2011; Willems and Casasanto 2011; Kemmerer 2015; Yee and Thompson-Schill 2016). For example, Hoenig et al. (2008) found that visual- and motor-related areas showed stronger activity when a nondominant conceptual feature (i.e., visual for artifacts; action for natural items) than a dominant

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[1] The term "cross-modal" denotes any region that integrates multiple modalities and thus subsumes multimodal and heteromodal areas.

feature had to be verified for an object noun. Van Dam et al. (2012) found left IPL, pIPS, and pMTG to be more active for words with a high relevance of both action and color features during a task focusing on action than a task focusing on color. Another study reported that a color-sensitive region in left fusiform gyrus responded more strongly when the task required more detailed color knowledge (Hsu et al. 2011). Finally, Borghesani et al. (2019) showed that a similar set of brain regions as those engaged for action feature retrieval in our study (bilateral SMG/IPS, pMTG/LTO, and aIFG) exhibits higher activity when two object pictures are compared for movement than for typical location, regardless of object category (animals, tools, non-tool artifacts).

The results of these studies corroborate our findings of task-dependent engagement of modality-specific perceptual–motor regions for conceptual feature retrieval. In line with our conclusions, van Dam et al. infer from their results that motor-related regions show stronger activity for action-related concepts when action features are task-relevant. At first sight, Hoenig et al.'s and Borghesani et al.'s findings might seem at odds with our result of increased activity for high versus low action words during action judgments: Hoenig et al. found stronger activity for nondominant than dominant features, and Borghesani et al. failed to detect an interaction with stimulus category. However, this may merely reflect differences in the experimental design. In Hoenig et al.'s study, a feature had to be verified for a subsequently presented object concept on every trial, which seemed to require increased processing in modality-specific areas when the feature was nondominant. Similarly, Borghesani et al.'s movement task required retrieval of motion features for all stimuli. In contrast, our action judgment task exclusively required retrieval of action feature representations for high action words; low action words only necessitated confirmation that they lacked a (strong) action feature representation. Therefore, in all cases, increased activity in perceptual–motor regions seems to reflect increased activation of modality-specific conceptual features when they are task-relevant.

However, except for Hsu et al., none of these previous studies tested for activation overlap with perception and action. It was thus unclear whether the task-dependent regions were indeed located within perceptual–motor systems. This is especially crucial for regions like left IPL or pMTG where modality-specific and higher-level multimodal regions lie side by side (see Figs 7 and 8). Secondly, Hoenig et al. and Hsu et al. confounded their task manipulation with stimulus differences, rendering it ambiguous whether activation differences were due to different tasks, different stimuli, or both. Thirdly, none of the previous studies independently manipulated the relevance of multiple perceptual–motor features at the same time, preventing the investigation of modality-specificity. While van Dam et al. manipulated the relevance of both action and color features, activation was not compared directly, but only against abstract words. In Hoenig et al.'s study, manipulation of visual and action relevance was nonorthogonal and confounded with stimulus category.

We addressed these limitations by directly comparing neural activity during different tasks on the same stimuli, allowing us to unambiguously attribute activation differences to task, and not stimulus, differences. Moreover, we directly tested for activation overlap with perception and action, which enabled us to determine which of the task-dependent regions were located within perceptual–motor cortices. Finally, we independently manipulated the relevance of both action and sound features for a concept, which allowed us to test whether a brain region was specific to action or sound features, or multimodal.

Surprisingly, not only modality-specific areas but also higher-level, multimodal regions showed a task-dependent response to sound or action features. Modality-specific areas are selectively sensitive to the single feature they represent when it is task-relevant, while multimodal areas seem selectively sensitive to any of the multiple features they bind when these are task-relevant. These findings suggest that the task modulates not just which levels of the processing hierarchy are engaged. Rather, the task modulates activity for individual perceptual–motor features at several, possibly all, levels of the hierarchy.

It should be noted that some studies found modality-specific activations even during shallow tasks, that is, implicit (Pulvermüller et al. 2005; Kiefer et al. 2008, 2012b; Sim et al. 2015) or passive tasks (Hauk et al. 2004; Hauk and Pulvermüller 2004), or when the stimulus was unattended (Shtyrov et al. 2004; Pulvermüller and Shtyrov 2006) or not consciously perceived (Trumpp et al. 2013b, 2014). These findings seem to contradict the proposal that perceptual–motor features are selectively retrieved when task-relevant. However, such effects have largely been observed when the pertinent feature was central to the concept. For instance, action verbs (e.g., “lick,” “kick,” or “pick”) engaged the motor cortex during shallow tasks (Hauk et al. 2004; Hauk and Pulvermüller 2004; Tettamanti et al. 2005). As action knowledge is crucial to the meaning of action verbs, activation of motor regions might be required even for shallow comprehension of action verbs. These findings are thus consistent with the view that perceptual–motor features are only activated when relevant in the current context.

Importantly, the fact that perceptual–motor features are not always activated during conceptual tasks does *not* entail that they are not essential components of a concept or that modality-specific brain regions are not functionally relevant for conceptual processing (Kemmerer 2015; Barsalou 2016). Instead, it implies that we need to abandon models of conceptual processing that assume a rigid, task-independent architecture and move to models that allow for task-dependent flexibility of the retrieval of different conceptual features and engagement of the brain systems that represent them (Hoenig et al. 2008; Binder and Desai 2011; Kiefer and Pulvermüller 2012; Kemmerer 2015).

Some authors have argued that perceptual–motor activations during conceptual tasks may be epiphenomenal (e.g., reflect post-conceptual mental imagery) and not *causally* relevant for conceptual processing (Mahon and Caramazza 2008). This issue cannot be addressed with correlative neuroimaging methods but requires methods that allow for causal inferences such as lesion or noninvasive brain stimulation studies (Walsh and Cowey 2000; Hartwigsen et al. 2015). Causal evidence for the involvement of perceptual–motor areas in conceptual processing is currently scarce and equivocal (Willems and Casasanto 2011; Hauk and Tschentscher 2013; Papeo et al. 2013). Hence, an important avenue for future research will be to investigate whether, and crucially, under which circumstances perceptual–motor regions causally support conceptual processing.

Conclusions

In conclusion, our results support theories that assume conceptual processing to rely on a flexible, multi-level architecture grounded in the perceptual–motor systems. Firstly, conceptual processing involves both modality-specific perceptual–

motor areas and higher-level, multimodal regions. Secondly, the retrieval of a certain perceptual–motor feature and engagement of modality-specific areas are strongly task-dependent. Crucially, we show for the first time that not only modality-specific areas but also multimodal regions are sensitive to a certain conceptual feature exclusively when this feature is task-relevant. These findings indicate that the task modulates conceptual feature processing throughout the hierarchy of functional neural networks.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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Conflict of Interest

None declared.

References

Alexander MP, Benson DF, Stuss DT. 1989. Frontal lobes and language. *Brain Lang*. 37:656–691.

Allport DA. 1985. Distributed memory, modular subsystems and dysphasia. In: Newman SK, Epstein R, editors. *Current perspectives in dysphasia*. Churchill Livingstone, Edinburgh.

Arévalo AL, Baldo JV, Dronkers NF. 2012. What do brain lesions tell us about theories of embodied semantics and the human mirror neuron system? *Cortex*. 48:242–254.

Bak TH, O'Donovan DG, Xuereb JH, Boniface S, Hodges JR. 2001. Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*. 124:103–120.

Bak TH, Yancopoulou D, Nestor PJ, Xuereb JH, Spillantini MG, Pulvermüller F, Hodges JR. 2006. Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*. 129:321–332.

Barsalou LW. 1999. Perceptual symbol systems. *Behav Brain Sci*. 22:577–609 discussion 610–60.

Barsalou LW. 2008. Grounded cognition. *Annu Rev Psychol*. 59:617–645.

Barsalou LW. 2016. On staying grounded and avoiding quixotic dead ends. *Psychon Bull Rev*. 23:1122–1142.

Basilakos A, Smith KG, Fillmore P, Fridriksson J, Fedorenko E. 2018. Functional characterization of the human speech articulation network. *Cereb Cortex*. 28:1816–1830.

Bedny M, Caramazza A, Grossman E, Pascual-Leone A, Saxe R. 2008. Concepts are more than percepts: the case of action verbs. *J Neurosci*. 28:11347–11353.

Belin P, Zatorre RJ, Lafaille P, Ahad P, Pike B. 2000. Voice-selective areas in human auditory cortex. *Nature*. 403:309–312.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Ser B*. 57:289–300.

Binder JR. 2016. In defense of abstract conceptual representations. *Psychon Bull Rev*. 23:1096–1108.

Binder JR, Desai RH. 2011. The neurobiology of semantic memory. *Trends Cogn Sci*. 15:527–536.

Binder JR, Desai RH, Graves WW, Conant LL. 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*. 19:2767–2796.

Bizley JK, Cohen YE. 2013. The what, where and how of auditory-object perception. *Nat Rev Neurosci*. 14:693–707.

Bonner MF, Grossman M. 2012. Gray matter density of auditory association cortex relates to knowledge of sound concepts in primary progressive aphasia. *J Neurosci*. 32:7986–7991.

Bonner MF, Peelle JE, Cook PA, Grossman M. 2013. Heteromodal conceptual processing in the angular gyrus. *Neuroimage*. 71:175–186.

Borghesani V, Piazza M. 2017. The neuro-cognitive representations of symbols: the case of concrete words. *Neuropsychologia*. 105:4–17.

Borghesani V, Riello M, Gesierich B, Brentari V, Monti A, Gorno-Tempini ML. 2019. The neural representations of movement across semantic categories. *J Cogn Neurosci*. 31: 791–807.

Brett M, Anton J-L, Valabregue R, Poline J-B. 2002. Region of interest analysis using an SPM toolbox [abstract]. Presented at the 8th International Conferance on Functional Mapping of the Human Brain. Available on CD-ROM in NeuroImage, Vol. 16, No. 2, abstract 497. Sendai, Japan.

Buckner RL. 2013. The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. *Neuron*. 80:807–815.

Buckner RL, Krienen FM, Castellanos A, Diaz JC, Yeo BTT. 2011. The organization of the human cerebellum estimated by intrinsic functional connectivity. *J Neurophysiol*. 106:2322–2345.

Damasio AR. 1989. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition*. 33:25–62.

Davare M, Montague K, Olivier E, Rothwell JC, Lemon RN. 2009. Ventral premotor to primary motor cortical interactions during object-driven grasp in humans. *Cortex*. 45: 1050–1057.

Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP. 2003. Internal vs. external generation of movements: differential neural pathways involved in bimanual coordination performed in the presence or absence of augmented visual feedback. *Neuroimage*. 19:764–776.

Deecke L, Kornhuber HH. 1978. An electrical sign of participation of the mesial "supplementary" motor cortex in human voluntary finger movement. *Brain Res*. 159:473–476.

Dormal G, Pelland M, Rezk M, Yakobov E, Lepore F, Collignon O. 2018. Functional preference for object sounds and voices in the brain of early blind and sighted individuals. *J Cogn Neurosci*. 30:86–106.

Fedorenko E, Behr MK, Kanwisher N. 2011. Functional specificity for high-level linguistic processing in the human brain. *Proc Natl Acad Sci*. 108:16428–16433.

Fedorenko E, Duncan J, Kanwisher N. 2013. Broad domain generality in focal regions of frontal and parietal cortex. *Proc Natl Acad Sci*. 110:16616–16621.

Fedorenko E, Hsieh P-J, Nieto-Castañón A, Whitfield-Gabrieli S, Kanwisher N. 2010. New method for fMRI investigations of language: defining ROIs functionally in individual subjects. *J Neurophysiol*. 104:1177–1194.

Fedorenko E, Kanwisher N. 2009. Neuroimaging of language: why hasn't a clearer picture emerged? *Lang Linguist Compass*. 3:839–865.

Fedorenko E, Kanwisher N. 2011. Functionally localizing language-sensitive regions in individual subjects with fMRI: a reply to Grodzinsky's critique of Fedorenko and Kanwisher (2009). *Lang Linguist Compass*. 5:78–94.

Fedorenko E, McDermott JH, Norman-Haignere S, Kanwisher N. 2012. Sensitivity to musical structure in the human brain. *J Neurophysiol*. 108:3289–3300.

Feinberg DA, Moeller S, Smith SM, Auerbach E, Ramanna S, Glasser MF, Miller KL, Ugurbil K, Yacoub E. 2010. Multiplexed echo planar imaging for sub-second whole brain fMRI and fast diffusion imaging. *PLoS One*. 5:e15710.

Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS. 2016a. Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb Cortex*. 26:2018–2034.

Fernandino L, Humphries CJ, Conant LL, Seidenberg MS, Binder JR. 2016b. Heteromodal cortical areas encode sensory-motor features of word meaning. *J Neurosci*. 36:9763–9769.

Garagnani M, Pulvermüller F. 2016. Conceptual grounding of language in action and perception: a neurocomputational model of the emergence of category specificity and semantic hubs. *Eur J Neurosci*. 43:721–737.

Genovese CR, Lazar NA, Nichols T. 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*. 15:870–878.

Goldberg RF, Perfetti CA, Schneider W. 2006. Perceptual knowledge retrieval activates sensory brain regions. *J Neurosci*. 26:4917–4921.

Gountouna VE, Job DE, McIntosh AM, Moorhead TWJ, Lymer GKL, Whalley HC, Hall J, Waiter GD, Brennan D, McGonigle DJ *et al*. 2010. Functional magnetic resonance imaging (fMRI) reproducibility and variance components across visits and scanning sites with a finger tapping task. *Neuroimage*. 49: 552–560.

Grinband J, Wager TD, Lindquist M, Ferrera VP, Hirsch J. 2008. Detection of time-varying signals in event-related fMRI designs. *Neuroimage*. 43:509–520.

Grossman M, Anderson C, Khan A, Avants B, Elman L, McCluskey L. 2008. Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*. 71:1396–1401.

Haaland KY, Harrington DL, Knight RT. 2000. Neural representations of skilled movement. *Brain*. 123:2306–2313.

Haggard P, Miall RC, Wade D, Fowler S, Richardson A, Anslow P, Stein J. 1995. Damage to cerebellocortical pathways after closed head injury: a behavioural and magnetic resonance imaging study. *J Neurol Neurosurg Psychiatry*. 58:433–438.

Halai AD, Welbourne SR, Embleton K, Parkes LM. 2014. A comparison of dual gradient-echo and spin-echo fMRI of the inferior temporal lobe. *Hum Brain Mapp*. 35:4118–4128.

Halsband U, Matsuzaka Y, Tanji J. 1994. Neuronal activity in the primate supplementary, pre-supplementary and premotor cortex during externally and internally instructed sequential movements. *Neurosci Res*. 20:149–155.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP. 2018. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosci Biobehav Rev*. 94: 31–44.

Hartwigsen G, Bergmann TO, Herz DM, Angstmann S, Karabanov A, Raffin E, Thielscher A, Siebner HR. 2015. Modeling the effects of noninvasive transcranial brain stimulation at the biophysical, network, and cognitive level. *Prog Brain Res*. 222:261–287.

Hartwigsen G, Weigel A, Schuschan P, Siebner HR, Weise D, Classen J, Saur D. 2016. Dissociating parieto-frontal networks for phonological and semantic word decisions: a condition-and-perturb TMS study. *Cereb Cortex*. 26: 2590–2601.

Hauk O, Johnsrude I, Pulvermüller F. 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron*. 41:301–307.

Hauk O, Pulvermüller F. 2004. Neurophysiological distinction of action words in the fronto-central cortex. *Hum Brain Mapp*. 21:191–201.

Hauk O, Tschentscher N. 2013. The body of evidence: what can neuroscience tell us about embodied semantics? *Front Psychol*. 4:1–14.

Hillis AE, Heidler-Gary J, Newhart M, Chang S, Ken L, Bak TH. 2006. Naming and comprehension in primary progressive aphasia: the influence of grammatical word class. *Aphasiology*. 20:246–256.

Hoenig K, Müller C, Herrnberger B, Sim E-J, Spitzer M, Ehret G, Kiefer M. 2011. Neuroplasticity of semantic representations for musical instruments in professional musicians. *Neuroimage*. 56:1714–1725.

Hoenig K, Sim E-J, Bochev V, Herrnberger B, Kiefer M. 2008. Conceptual flexibility in the human brain: dynamic recruitment of semantic maps from visual, motor, and motion-related areas. *J Cogn Neurosci*. 20:1799–1814.

Hsu NS, Kraemer DJM, Oliver RT, Schlichting ML, Thompson-Schill SL. 2011. Color, context, and cognitive style: variations in color knowledge retrieval as a function of task and subject variables. *J Cogn Neurosci*. 23:2544–2557.

Jefferies E. 2013. The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex*. 49:611–625.

Julian JB, Fedorenko E, Webster J, Kanwisher N. 2012. An algorithmic method for functionally defining regions of interest in the ventral visual pathway. *Neuroimage*. 60: 2357–2364.

Kellenbach ML, Brett M, Patterson K. 2001. Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cogn Affect Behav Neurosci*. 1:207–221.

Kemmerer D. 2015. Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible multilevel architecture for conceptual knowledge. *Psychon Bull Rev*. 22:1068–1075.

Kemmerer D, Rudrauf D, Manzel K, Tranel D. 2012. Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex*. 48:826–848.

Keuleers E, Brysbaert M. 2010. Wuggy: a multilingual pseudoword generator. *Behav Res Methods*. 42:627–633.

Kiefer M, Adams SC, Zovko M. 2012a. Attentional sensitization of unconscious visual processing: top-down influences on masked priming. *Adv Cogn Psychol*. 8:50–61.

Kiefer M, Barsalou LW. 2013. Grounding the human conceptual system in perception, action, and internal states. In: Prinz W, Beisert M, Herwig A, editors. *Tutorials in action science*. The MIT Press, Cambridge, pp. 381–407.

Kiefer M, Pulvermüller F. 2012. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*. 48:805–825.

Kiefer M, Sim E-J, Herrnberger B, Grothe J, Hoenig K. 2008. The sound of concepts: four markers for a link between auditory and conceptual brain systems. *J Neurosci*. 28:12224–12230.

Kiefer M, Trumpp N, Herrnberger B, Sim E-J, Hoenig K, Pulvermüller F. 2012b. Dissociating the representation of action- and sound-related concepts in middle temporal cortex. *Brain Lang*. 122:120–125.

Kriegeskorte N, Simmons WK, Bellgowan PS, Baker CI. 2009. Circular inference in neuroscience: the dangers of double dipping. *Nat Neurosci*. 12:535–540.

Krienen FM, Buckner RL. 2009. Segregated fronto-cerebellar circuits revealed by intrinsic functional connectivity. *Cereb Cortex*. 19:2485–2497.

Lambon Ralph MA. 2014. Neurocognitive insights on conceptual knowledge and its breakdown. *Philos Trans R Soc B Biol Sci*. 369:20120392.

Lambon Ralph MA, Jefferies E, Patterson K, Rogers TT. 2016. The neural and computational bases of semantic cognition. *Nat Rev Neurosci*. 18:42–55.

Lebois LAM, Wilson-Mendenhall CD, Barsalou LW. 2015. Are automatic conceptual cores the gold standard of semantic processing? The context-dependence of spatial meaning in grounded congruency effects. *Cogn Sci*. 39:1764–1801.

Lemaitre G, Pyles JA, Halpern AR, Navolio N, Lehet M, Heller LM. 2018. Who's that knocking at my door? Neural bases of sound source identification. *Cereb Cortex*. 28:805–818.

Lewis JW. 2006. Cortical networks related to human use of tools. *Neurosci*. 12:211–231.

Lewis JW, Wightman FL, Brefczynski JA, Phinney RE, Binder JR, DeYoe EA. 2004. Human brain regions involved in recognizing environmental sounds. *Cereb Cortex*. 14:1008–1021.

Mahon BZ. 2015. What is embodied about cognition? *Lang Cogn Neurosci*. 30:420–429.

Mahon BZ, Caramazza A. 2008. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J Physiol*. 102:59–70.

Margulies DS, Ghosh SS, Goulas A, Falkiewicz M, Huntenburg JM, Langs G, Bezgin G, Eickhoff SB, Castellanos FX, Petrides M *et al*. 2016. Situating the default-mode network along a principal gradient of macroscale cortical organization. *Proc Natl Acad Sci*. 113:12574–12579.

Mesulam MM. 1998. From sensation to cognition. *Brain*. 121:1013–1052.

Meyer F. 1991. Un algorithme optimal de ligne de partage des eaux. Paper Presented at the Dans 8me congrès de reconnaissance des formes et intelligence artificielle, Lyon, France.

Mostofsky SH, Rimrodt SL, Schafer JGB, Boyce A, Goldberg MC, Pekar JJ, Denckla MB. 2006. Atypical motor and sensory cortex activation in attention-deficit/hyperactivity disorder: a functional magnetic resonance imaging study of simple sequential finger tapping. *Biol Psychiatry*. 59:48–56.

Nichols T, Brett M, Andersson J, Wager T, Poline JB. 2005. Valid conjunction inference with the minimum statistic. *Neuroimage*. 25:653–660.

Nieto-Castañón A, Fedorenko E. 2012. Subject-specific functional localizers increase sensitivity and functional resolution of multi-subject analyses. *Neuroimage*. 63: 1646–1669.

Noonan KA, Jefferies E, Visser M, Lambon Ralph MA. 2013. Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *J Cogn Neurosci*. 25:1824–1850.

Noppeney U, Price CJ, Penny WD, Friston KJ. 2006. Two distinct neural mechanisms for category-selective responses. *Cereb Cortex*. 16:437–445.

Ohyama T, Nores WL, Murphy M, Mauk MD. 2003. What the cerebellum computes. *Trends Neurosci*. 26:222–227.

Oldfield RC. 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*. 9:97–113.

Oosterhof NN, Wiggett AJ, Diedrichsen J, Tipper SP, Downing PE. 2010. Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *J Neurophysiol*. 104: 1077–1089.

Papeo L, Lingnau A, Agosta S, Pascual-Leone A, Battelli L, Caramazza A. 2015. The origin of word-related motor activity. *Cereb Cortex*. 25:1668–1675.

Papeo L, Pascual-Leone A, Caramazza A. 2013. Disrupting the brain to validate hypotheses on the neurobiology of language. *Front Hum Neurosci*. 7:148.

Papeo L, Vallesi A, Isaja A, Rumiati RI. 2009. Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One*. 4:e4508.

Patterson K, Nestor PJ, Rogers TT. 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci*. 8:976–987.

Popp M, Trumpp NM, Kiefer M. 2019a. Processing of action and sound verbs in context: an FMRI study. *Transl Neurosci*. 10:200–222.

Popp M, Trumpp NM, Sim E, Kiefer M. 2019b. Brain activation during conceptual processing of action and sound verbs. *Advances in Cognitive Psychology*, 15:236–255.

Poser BA, Versluis MJ, Hoogduin JM, Norris DG. 2006. BOLD contrast sensitivity enhancement and artifact reduction with multiecho EPI: parallel-acquired inhomogeneity-desensitized fMRI. *Magn Reson Med*. 55:1227–1235.

Postle N, McMahon KL, Ashton R, Meredith M, de Zubicaray GI. 2008. Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *Neuroimage*. 43:634–644.

Price AR, Bonner MF, Grossman M. 2015. Semantic memory: cognitive and neuroanatomical perspectives. In: Arthur W. Toga, editor. *Brain mapping an encyclopedic reference*. Academic Press: Elsevier, Amsterdam, 3, pp. 529–536.

Pulvermüller F. 1999. Words in the brain's language. *Behav Brain Sci*. 22:253–279, S0140525X9900182X.

Pulvermüller F. 2005. Brain mechanisms linking language and action. *Nat Rev Neurosci*. 6:576–582.

Pulvermüller F. 2018. Neurobiological mechanisms for semantic feature extraction and conceptual flexibility. *Top Cogn Sci*. 10:590–620.

Pulvermüller F, Hauk O, Nikulin VV, Ilmoniemi RJ. 2005. Functional links between motor and language systems. *Eur J Neurosci*. 21:793–797.

Pulvermüller F, Shtyrov Y. 2006. Language outside the focus of attention: the mismatch negativity as a tool for studying higher cognitive processes. *Prog Neurobiol*. 79: 49–71.

Raposo A, Moss HE, Stamatakis EA, Tyler LK. 2009. Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia*. 47:388–396.

Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M. 1988. Functional organization of inferior area 6 in the macaque monkey. *Exp Brain Res*. 71:491–507.

Romanski LM, Averbeck BB. 2009. The primate cortical auditory system and neural representation of conspecific vocalizations. *Annu Rev Neurosci*. 32:315–346.

Shtyrov Y, Hauk O, Pulvermüller F. 2004. Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. *Eur J Neurosci*. 19:1083–1092.

Siegel JS, Power JD, Dubis JW, Vogel AC, Church JA, Schlaggar BL, Petersen SE. 2014. Statistical improvements in functional magnetic resonance imaging analyses produced by censoring high-motion data points. *Hum Brain Mapp*. 35: 1981–1996.

Sim E-J, Helbig HB, Graf M, Kiefer M. 2015. When action observation facilitates visual perception: activation in Visuomotor areas contributes to object recognition. *Cereb Cortex*. 25:2907–2918.

Simanova I, Hagoort P, Oostenveld R, Van Gerven MAJ. 2014. Modality-independent decoding of semantic information from the human brain. *Cereb Cortex*. 24:426–434.

Simmons WK, Barsalou LW. 2003. The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cogn Neuropsychol*. 20:451–486.

Strick PL, Dum RP, Fiez JA. 2009. Cerebellum and nonmotor function. *Annu Rev Neurosci*. 32:413–434.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D. 2005. Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci*. 17:273–281.

Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci*. 94: 14792–14797.

Trumpp NM, Kliese D, Hoenig K, Haarmeier T, Kiefer M. 2013a. Losing the sound of concepts: damage to auditory association cortex impairs the processing of sound-related concepts. *Cortex*. 49:474–486.

Trumpp NM, Traub F, Kiefer M. 2013b. Masked priming of conceptual features reveals differential brain activation during unconscious access to conceptual action and sound information. *PLoS One*. 8:e65910.

Trumpp NM, Traub F, Pulvermüller F, Kiefer M. 2014. Unconscious automatic brain activation of acoustic and action-related conceptual features during masked repetition priming. *J Cogn Neurosci*. 26:352–364.

Turella L, Lingnau A. 2014. Neural correlates of grasping. *Front Hum Neurosci*. 8:1–8.

van Dam WO, van Dijk M, Bekkering H, Rueschemeyer SA. 2012. Flexibility in embodied lexical-semantic representations. *Hum Brain Mapp*. 33:2322–2333.

van Elk M, van Schie H, Bekkering H. 2014. Action semantics: a unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. *Phys Life Rev*. 11:220–250.

Vul E, Harris C, Winkielman P, Pashler H. 2009. Puzzlingly high correlations in fMRI studies of emotion, personality and social cognition. *Perspect Psychol Sci*. 4:274–290.

Wagner AD, Paré-Blagoev EJ, Clark J, Poldrack RA. 2001. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron*. 31:329–338.

Walsh V, Cowey A. 2000. Transcranial magnetic stimulation and cognitive neuroscience. *Nat Rev Neurosci*. 1:73–80.

Watson CE, Cardillo ER, Ianni GR, Chatterjee A. 2013. Action concepts in the brain: an activation likelihood estimation meta-analysis. *J Cogn Neurosci*. 25:1191–1205.

Weiskopf N, Hutton C, Josephs O, Deichmann R. 2006. Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: a whole-brain analysis at 3 T and 1.5 T. *Neuroimage*. 33:493–504.

Wheeler ME, Petersen SE, Buckner RL. 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc Natl Acad Sci*. 97:11125–11129.

Willems RM, Casasanto D. 2011. Flexibility in embodied language understanding. *Front Psychol*. 2:1–11.

Wolpert DM, Miall RC, Kawato M. 1998. Internal models in the cerebellum. *Trends Cogn Sci*. 2:338–347.

Yee E, Thompson-Schill SL. 2016. Putting concepts into context. *Psychon Bull Rev*. 23:1015–1027.

3. FMRI CONNECTIVITY STUDY

The study presented in this chapter has been published as:

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Study 1 revealed that sound and action knowledge retrieval involve both modality-specific perceptual-motor and multimodal brain regions in a task-dependent fashion. However, it remains unknown whether and how modality-specific and multimodal regions *interact* during conceptual knowledge retrieval. The study presented in the following chapter investigated the functional interaction between modality-specific and multimodal areas using fMRI.

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ORIGINAL ARTICLE

Task-Dependent Functional and Effective Connectivity during Conceptual Processing

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Abstract

Conceptual knowledge is central to cognition. Previous neuroimaging research indicates that conceptual processing involves both modality-specific perceptual-motor areas and multimodal convergence zones. For example, our previous functional magnetic resonance imaging (fMRI) study revealed that both modality-specific and multimodal regions respond to sound and action features of concepts in a task-dependent fashion (Kuhnke P, Kiefer M, Hartwigsen G. 2020b. Task-dependent recruitment of modality-specific and multimodal regions during conceptual processing. Cereb Cortex. 30:3938–3959.). However, it remains unknown whether and how modality-specific and multimodal areas interact during conceptual tasks. Here, we asked 1) whether multimodal and modality-specific areas are functionally coupled during conceptual processing, 2) whether their coupling depends on the task, 3) whether information flows top-down, bottom-up or both, and 4) whether their coupling is behaviorally relevant. We combined psychophysiological interaction analyses with dynamic causal modeling on the fMRI data of our previous study. We found that functional coupling between multimodal and modality-specific areas strongly depended on the task, involved both top-down and bottom-up information flow, and predicted conceptually guided behavior. Notably, we also found coupling between different modality-specific areas and between different multimodal areas. These results suggest that functional coupling in the conceptual system is extensive, reciprocal, task-dependent, and behaviorally relevant. We propose a new model of the conceptual system that incorporates task-dependent functional interactions between modality-specific and multimodal areas.

Key words: DCM, grounded cognition, language, PPI, semantic memory

Introduction

Conceptual knowledge is crucial for many cognitive abilities, such as object recognition and use, as well as word comprehension (Lambon Ralph 2014; van Elk et al. 2014). Therefore, a central question in cognitive neuroscience has been how concepts are represented and processed in the human brain.

Research on the neural basis of conceptual processing has largely focused on functional segregation—identifying the different brain regions involved in conceptual processing and their functions. These studies have suggested that conceptual processing relies on both modality-specific perceptual-motor regions and cross-modal convergence zones (for reviews, see Kiefer and Pulvermüller 2012; Meteyard et al. 2012; Borghesani and Piazza 2017). Modality-specific regions represent perceptual-motor features of concepts. For example, action features are represented in motor and somatosensory regions (Hauk et al. 2004; Fernandino et al. 2016; Vukovic et al. 2017), whereas sound features are represented in auditory regions (Kiefer et al. 2008; Bonner and Grossman 2012). These findings support grounded cognition theories, which propose a functional-anatomical overlap between conceptual processing and real perceptual-motor experience (Barsalou 2008; Kiefer and Barsalou 2013). Cross-modal convergence zones, on the other hand, integrate modality-specific features into increasingly abstract representations (Damasio 1989; Simmons and Barsalou 2003; Binder 2016).

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A common terminology is still lacking in the field and key terms (e.g., "modality", "modality-specific", and "cross-modal") are widely used but rarely explicitly defined. However, these terms are useful to distinguish brain regions based on their representational abstraction from direct perceptual-motor experience (Binder 2016; Margulies et al. 2016). Therefore, we propose the following working definitions for this article: We refer to "perceptual-motor modalities" as the brain's major input and output channels of perception and action (e.g., motor, somatosensory, auditory, visual, etc.). Note that these modalities do not simply correspond to the senses (hence the term "perceptual-motor" and not "sensory") as they include channels of internal perception (e.g., emotion, proprioception) as well as motor action (Barsalou 2008; Kiefer and Barsalou 2013). Within the modalities, several dimensions can be further distinguished. For example, the visual modality includes the dimensions shape, color, motion, etc., which are processed by specialized neural circuits within the visual system (Van Essen and Maunsell 1983; Felleman and Van Essen 1991). We call brain regions "modality-specific" if they represent information related to a single perceptual-motor modality (Kiefer and Pulvermüller 2012). Regions are called "cross-modal" if they integrate information from at least two modalities into more abstract, cross-modal representations (Binder 2016).

We recently proposed a distinction among cross-modal convergence zones between "multimodal" areas that retain modality-specific information, and "amodal" areas that do not (Kuhnke et al. 2020b). That is, "amodal" regions contain the most abstract, modality-invariant conceptual representations, and are relevant for processing all types of conceptual information, regardless of perceptual-motor content (Jefferies 2013; Lambon Ralph et al. 2016). Previous evidence suggests that the left posterior parietal cortex (PPC) represents a "multimodal" convergence zone (Fernandino et al. 2016; Kuhnke et al. 2020b), whereas the anterior temporal lobe (ATL) acts as an "amodal" hub (Jefferies 2013; Lambon Ralph et al. 2016). For example, the left PPC responds to both sound and action features of concepts, whereas the ATL responds to general conceptual information (words > pseudowords) but not to modality-specific features (Kuhnke et al. 2020b; for similar results, see Fernandino et al. 2016). The amodal ATL appears to represent an abstract conceptual similarity structure that transcends individual modalities (Lambon Ralph et al. 2010; Patterson and Lambon Ralph 2016). Such an amodal conceptual representation seems necessary to explain the emergence of coherent conceptual categories (Lambon Ralph et al. 2010). In support of this view, evidence from semantic dementia (Patterson et al. 2007; Jefferies 2013), functional neuroimaging (Visser et al. 2010; Rice et al. 2015), transcranial magnetic stimulation (TMS; Pobric et al. 2010a, 2010b), and computational modeling (Rogers et al. 2004; Chen et al. 2017; Jackson et al. 2021) indicates a crucial role of the ATL in conceptual processing across virtually all types of concepts, regardless of their perceptual-motor content.

Overall, current evidence seems most consistent with "hybrid theories" that propose conceptual processing to rely on a representational hierarchy from modality-specific regions to multiple levels of cross-modal convergence zones (Binder and Desai 2011; Fernandino et al. 2016; Kiefer and Harpaintner 2020; Kuhnke et al. 2020b). Crucially, this hierarchical system is flexible, with different regions being recruited dynamically depending on the task (Hoenig et al. 2008; Kemmerer 2015; Popp et al. 2019b). For instance, both modality-specific and multimodal areas selectively respond to sound and action features when these are task-relevant (Kuhnke et al. 2020b).

However, little is known about functional integration within the conceptual system, that is, whether and how different regions interact during conceptual processing. Although some studies have investigated functional coupling between amodal ATL and modality-specific areas (Jackson et al. 2016; Chiou and Lambon Ralph 2019), it remains unknown whether and how multimodal areas (e.g., left PPC) interact with modality-specific regions. Here, we asked whether modality-specific and multimodal areas are coupled during conceptual processing, whether their coupling depends on the task, whether information flows bottom-up, top-down or bidirectionally, and whether their coupling is relevant for behavior.

We combined whole-brain, data-driven psychophysiological interaction (PPI) analyses with dynamic causal modeling (DCM) on the functional magnetic resonance imaging (fMRI) data of Kuhnke et al. (2020b). A total of 40 healthy participants performed three different tasks—lexical decision, sound judgment, and action judgment—on the same words with a high or low association to sounds and actions. PPI tested for task-dependent changes in functional coupling between modality-specific and multimodal seed regions with the rest of the brain (Friston et al. 1997; McLaren et al. 2012). As seed regions, we chose the somatomotor, auditory, and multimodal brain regions that exhibited the strongest functional activation for action knowledge retrieval, sound knowledge retrieval, or both, respectively (Kuhnke et al. 2020b). The results informed a DCM analysis that assessed the direction of information flow between multimodal and modality-specific areas (Kahan and Foltynie 2013; Zeidman et al. 2019a).

We hypothesized that modality-specific and multimodal areas interact in a task-dependent manner during conceptual processing. Multimodal regions should interact with somatomotor regions selectively during action feature retrieval and with auditory regions during sound feature retrieval. Based on previous work, we expected information to flow top-down (Damasio 1989; Fernandino et al. 2016) and bottom-up (Kiefer et al. 2011; Sim et al. 2015). Crucially, task-dependent functional coupling between modality-specific and multimodal areas should predict behavior in a modality-specific fashion: Interindividual differences in coupling between multimodal and somatomotor or auditory regions should correlate with personal action and sound associations, respectively.

Materials and Methods

Subjects

Data from 40 native German speakers [22 female; mean age: 26.6 years; standard deviation (SD): 4.1; range: 19–33] were analyzed. A total of 42 participants were initially recruited, but two were excluded due to strong head movement or aborting the experiment. All participants were right-handed (mean laterality quotient: 93.7; SD: 9.44; Oldfield 1971) and had no history of neurological disorders or head injury, or exhibited contraindications to fMRI. They were recruited via the subject database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. Written informed consent was obtained from each subject prior to the experiment. The study was performed according to the guidelines of the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

Experimental Procedures

The experimental procedure is reported in detail in Kuhnke et al. (2020b) and summarized here. The study employed a 3 × 2 × 2 within-subject design with the factors TASK (lexical decision, sound judgment, action judgment), SOUND (high, low association), and ACTION (high, low association). In two event-related fMRI sessions, participants performed three different tasks on 192 words with a high or low association to sounds and actions (Fig. 1). In the first session, participants performed a lexical decision task, in which they decided whether the presented stimulus was a real word or pseudoword. In the second session, participants performed sound and action judgment tasks. In the sound judgment task, participants judged whether the object denoted by the word was strongly associated with sounds. In the action judgment task, participants judged whether the object was strongly associated with actions. Whereas the lexical decision task acted as a control task that did not require sound or action knowledge, the sound and action judgment tasks explicitly required sound and action knowledge, respectively.

High and low sound words selectively differed in their association with sounds, whereas high and low action words differed only in their association with actions, as determined by the ratings of a different group of 163 volunteers (cf. Trumpp et al. 2014; Fernandino et al. 2016). Experimental conditions were matched on ratings of visual conceptual associations and familiarity, number of letters and syllables, word frequency, bi- and trigram frequencies, and number of orthographic neighbors (see the Supplementary Material of Kuhnke et al. 2020b). Stimuli for all conditions were selected from the same superordinate categories of animals, inanimate natural entities, and man-made objects (Goldberg 2006; Kiefer et al. 2008). For the lexical decision task, a pseudoword was generated for each word matched in length, syllable structure, and transition frequencies using the "Wuggy" software (Keuleers and Brysbaert 2010; http://crr.ugent.be/Wuggy).

At the end of the second session, we administered functional localizers for brain regions involved in auditory perception and somatomotor action. In the auditory localizer, participants attentively listened to 18-s blocks of real sounds, interspersed with 16-s silence blocks (cf. Kiefer et al. 2008; Hoenig et al. 2011). In the somatomotor localizer, participants performed different types of hand movements (finger tapping, fist making, pinching) in 18-s blocks, separated by 16-s rest blocks (cf. Bonner et al. 2013). Note that these localizers were designed to identify brain regions involved in real sound perception and somatomotor action, which may include areas beyond modality-specific circuits (see Discussion). Despite these limitations, the localizers allowed us to test the basic prediction of grounded cognition theories of a functional-anatomical overlap between conceptual processing and real perceptual-motor experience (cf. Kiefer et al. 2008; Hoenig et al. 2011; Hsu et al., 2011; Bonner et al. 2013).

fMRI Data Acquisition and Preprocessing

fMRI data were collected on a 3 T Prisma scanner (Siemens, Erlangen, Germany) equipped with a 32-channel head coil. Functional, blood oxygenation level dependent (BOLD) images were acquired using a multiband dual gradient-echo echo-planar imaging (EPI) sequence [repetition time (TR): 2 s; echo times (TE): 12 and 33 ms; flip angle: 90°; field of view (FoV): 204 mm; voxel size: 2.5 × 2.5 × 2.5 mm; slice gap: 0.25 mm; bandwidth: 1966 Hz/Px; phase encoding direction: A/P]. A total of 60 slices covering the whole brain were recorded in interleaved order and axial orientation. We combined a multiband factor of 2 with in-plane GRAPPA acceleration of 2x (Feinberg et al. 2010), which exhibits a very low probability for false-positive activation due to slice leakage (Todd et al. 2016). We used a dual-echo sequence (Poser et al. 2006; Halai et al. 2014) and tilted slices 10° up (at the anterior edge) from the anterior commissure-posterior commissure line (Weiskopf et al. 2006) to minimize susceptibility artifacts and maximize BOLD sensitivity throughout the entire brain, including in regions suffering from signal loss in single-echo EPI such as the ATL (Devlin et al. 2000). B0 field maps were acquired for susceptibility distortion correction using a gradient-echo sequence (TR: 0.62 s; TE: 4 and 6.46 ms; flip angle: 60°; bandwidth: 412 Hz/Px; other parameters identical to functional sequence). Structural T1-weighted images were acquired for normalization using an MPRAGE sequence (176 slices in sagittal orientation; TR: 2.3 s; TE: 2.98 ms; FoV: 256 mm; voxel size: 1 × 1 × 1 mm; no slice gap; flip angle: 9°; phase encoding direction: A/P).

fMRI analysis was performed using Statistical Parametric Mapping (SPM12; Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm/) implemented in Matlab (version 9.3). The two images with a short and long TE were combined using an average weighted by the temporal signal-to-noise ratio (tSNR) at each voxel, which yields optimal BOLD sensitivity (Poser et al. 2006). tSNR was calculated based on 30 volumes collected at the beginning of each scanning run, which were excluded from further analyses. Functional images were realigned, distortion corrected, slice-timing corrected, normalized to Montreal Neurological Institute (MNI) space, and smoothed with a 5 mm^3 FWHM Gaussian kernel. An analysis of mean tSNR in anatomical regions-of-interest indicated satisfactory signal quality across the brain, including in the ATL (Supplementary Table 1).

Psychophysiological Interactions

We leveraged the PPI approach to identify brain regions that show task-dependent functional coupling with auditory, somatomotor, and multimodal regions during conceptual processing. PPI reveals regions that exhibit task-dependent functional connectivity with a seed region-of-interest (ROI), above and beyond their task-independent connectivity (correlation), and task-related activation (O'Reilly et al. 2012). We employed generalized PPI (gPPI) that extends the PPI approach to experimental designs with more than two conditions (like the present one) for which standard SPM PPI is invalid (McLaren et al. 2012).

We used the group-constrained subject-specific approach (Julian et al. 2012) to define seed ROIs based on subject-specific functional activation (Fedorenko et al. 2010; Nieto-Castañón and Fedorenko 2012). This approach yields higher sensitivity and functional resolution (i.e., the ability to separate adjacent but functionally distinct regions) than the classical approach of defining ROIs based on the same location in standard space (Fedorenko and Kanwisher 2009, 2011; Nieto-Castañón and Fedorenko 2012). We defined three seed ROIs: 1) a "somatomotor seed"—the somatomotor region most strongly engaged in action feature retrieval—using the conjunction [Action judgment: high > low action words] ∩ [Somatomotor localizer: hand movements > rest]; 2) an "auditory seed"—the auditory region most strongly engaged in sound feature retrieval—using the conjunction [Sound judgment: high > low sound words] ∩ [Auditory localizer: real sounds > silence]; and 3) a "multimodal seed"—the brain

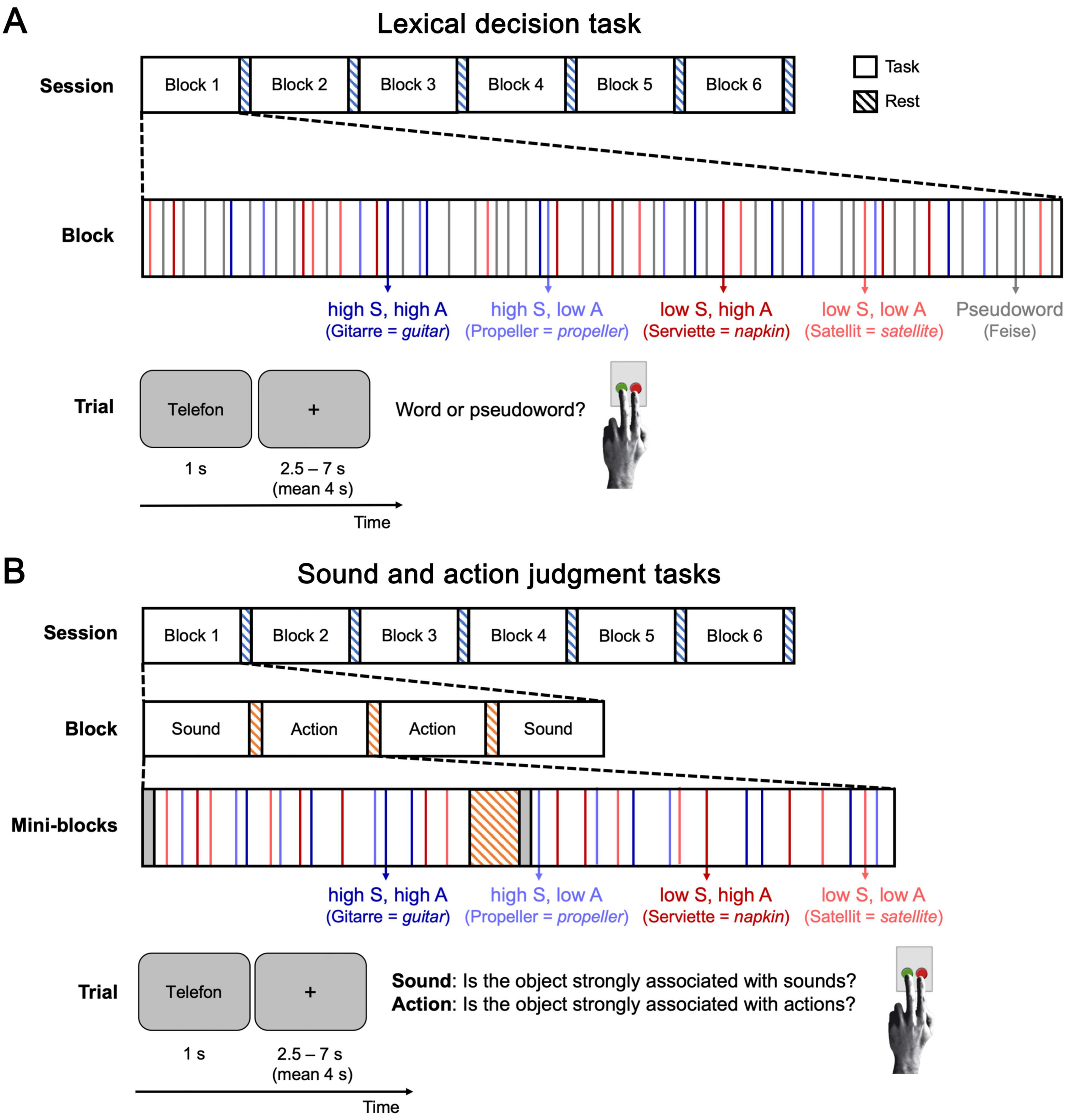

Figure 1. Experimental procedure. In two fMRI sessions, participants performed a lexical decision task (*A*), and sound and action judgment tasks (*B*). Trials for the four word types high sound–high action (dark blue), high sound–low action (light blue), low sound–high action (dark red), and low sound–low action (light red) were presented in random order within six blocks (64 trials each). Blocks were separated by 20-s rest periods (blue-striped bars). Sound and action judgment tasks were performed in mini-blocks of 16 trials, separated by 12-s rest periods (orange-striped bars). On each trial, a word was shown for 1 s, followed by an intertrial interval (fixation cross) of 2.5-7 s. Participants responded via button press.

region most strongly engaged in both action and sound feature retrieval—using the conjunction [Action judgment: high > low action words] ∩ [Sound judgment: high > low sound words] (for details on the activation analyses, see Kuhnke et al. 2020b). For each seed type, subject-specific activation maps were thresholded at $P < 0.05$ and overlaid on top of each other. The resulting overlap map was smoothed (5 mm), thresholded at two subjects, and parcellated using a watershed algorithm (Meyer 1991) implemented in the spm_ss toolbox (Nieto-Castañón and Fedorenko 2012). We retained the parcel with the strongest activation at the group level. Seed ROIs were then defined in each individual subject as the 10% most active voxels for the conceptual contrast within the parcel (Fedorenko et al. 2012; Basilakos et al. 2018).

We performed a whole-brain random-effects group analysis based on the general linear model (GLM), using the standard two-level approach. At the first level, individual participant data were modeled separately using the gPPI toolbox (version

13.1; https://www.nitrc.org/projects/gppi). The participant-level GLM included: 1) "Psychological" regressors for all experimental conditions, that is, stick functions at trial onsets convolved with the canonical hemodynamic response function (HRF). Only correct trials were included; error trials were modeled in a separate regressor of no interest. 2) A "physiological" regressor formed by the first eigenvariate of the seed ROI time series (i.e., the first principle component of the multivariate time series across all voxels in the ROI). 3) PPI regressors for each experimental condition created by multiplying the deconvolved BOLD signal of the seed ROI with the condition onsets and convolving with the canonical HRF (Gitelman et al. 2003; McLaren et al. 2012). 4) Nuisance regressors, including the six head motion parameters, individual regressors for time points with strong volume-to-volume movement (framewise displacement > 0.9; Siegel et al. 2014), and a duration-modulated parametric regressor accounting for response time differences between trials and conditions (Grinband et al. 2008).

Contrast images were computed for each participant and submitted to *t*-tests at the group level. To test for functional coupling during sound and action feature retrieval, we compared the connectivity for high > low sound words, and high > low action words within each task (lexical decision, sound judgment, action judgment). Conjunction analyses based on the minimum statistic (testing the conjunction null hypothesis; Nichols et al. 2005) tested for overlap between functional coupling for action or sound feature retrieval and activation in the somatomotor localizer (hand movements > rest) or auditory localizer (real sounds > silence), respectively. Finally, interaction analyses tested for task dependency in functional coupling by directly comparing the coupling increase for action features (high vs. low action words) or sound features (high vs. low sound words) between tasks (using paired *t*-tests). Interactions were inclusively masked by the minuend (within-task) contrast (Noppeney et al. 2006; Hardwick et al. 2018; Kuhnke et al. 2020b). For all group-level analyses, a gray matter mask was applied, restricting statistical tests to voxels with a gray matter probability > 0.3 (SPM12 tissue probability map). All activation maps were thresholded at a voxel-wise $P < 0.001$ and a cluster-wise $P < 0.05$ family-wise error (FWE) corrected for multiple comparisons.

To investigate whether task-dependent functional coupling between modality-specific and multimodal regions is relevant for behavior, we performed several PPI–behavior correlation analyses. To this end, we extracted the mean connectivity *t*-value of each participant from group-level PPI clusters (see Results section). We then performed Bayesian linear correlations between participants' connectivity values and their personal action or sound ratings for the respective words. Ratings were collected outside the scanner after the fMRI measurements and reflected how strongly a participant personally associated each word with actions or sounds (on a 1-to-6 scale). A control analysis tested whether interindividual differences in sound or action ratings also correlated with response times in the sound and action judgment tasks for the same words. Bayesian correlation analyses were performed using the "JASP" program (https://jasp-stats.org/; Wagenmakers et al. 2018), and tested whether the data were better predicted by the null hypothesis (i.e., no correlation) or alternative hypothesis (i.e., positive correlation between functional coupling strength and individual ratings). BF_{10} denotes the Bayes Factor in favor of the alternative hypothesis, whereas BF_{01} refers to the Bayes Factor in favor of the null hypothesis (where $BF_{01} = 1/BF_{10}$). For example, $BF_{10} = 3$ means that the data were three times more likely under the alternative hypothesis than under the null hypothesis (Lakens et al. 2020).

Dynamic Causal Modeling

Although PPI can reveal task-dependent changes in functional coupling between a seed region and the rest of the brain, it cannot assess the direction of information flow between brain regions. Consequently, we additionally performed DCM (Friston et al. 2003) to assess directed causal influences between the network nodes identified in our PPI analyses. DCM estimates a model of effective connectivity between brain regions to predict a neuroimaging time series. A DCM consists of three types of parameters: 1) "intrinsic" (i.e., task-independent) directed connections between brain regions, 2) "modulatory inputs" that change connection strengths during a certain experimental manipulation, and 3) "driving inputs" that drive activity in the network. The goal of DCM is to optimize a tradeoff between model fit (of the predicted to observed time series) and complexity (i.e., deviation of model parameters from their prior expectations), measured by the model evidence (Kahan and Foltynie 2013; Zeidman et al. 2019a).

We performed a two-level analysis using parametric empirical bayes (PEB) and Bayesian model reduction (BMR)—the current "standard practice for group DCM studies" (Friston et al. 2016). At the first level, a "full model" was specified and estimated for each participant (see Results section). Regions included in the model were the left PPC (corresponding to the multimodal PPI seed), left auditory association cortex (AAC; group cluster from PPI analysis for sound feature retrieval), and left motor/somatosensory cortex (M1/S1; group cluster from PPI analysis for action feature retrieval). The first eigenvariate of the BOLD time series of each region was extracted and adjusted for effects-of-interest (all experimental conditions) using a GLM that modeled all trials as stick functions convolved with the canonical HRF, and regressed out the six motion parameters, high-movement time points (framewise displacement > 0.9; Siegel et al. 2014), and response time differences (Grinband et al. 2008). DCM inputs were mean-centered, so that the intrinsic connections reflected the mean connectivity across experimental conditions (Zeidman et al. 2019a).

At the second level, DCM parameters of individual participants were entered into a GLM—the PEB model—that decomposed interindividual variability in connection strengths into group effects and random effects (Zeidman et al. 2019b). BMR then compared the full model against numerous reduced models that had certain parameters "switched off" (i.e., prior mean and variance set to 0) (Friston et al. 2016). Finally, we computed the Bayesian model average (BMA), the average of parameter values across models weighted by each model's posterior probability (*Pp*) (Penny et al. 2007). This approach is preferred over exclusively assessing the parameters of the "best" model as it accommodates uncertainty about the true underlying model (Friston et al. 2016; Dijkstra et al. 2017). The BMA was thresholded to only retain parameters with a *Pp* $> 95\%$ (Zeidman et al. 2019b). For each modulatory input, we calculated the resulting connectivity value (in Hz) using formula 3 in Zeidman et al. (2019a). Finally, to determine whether one experimental condition modulated a certain connection more strongly than another, we directly compared different modulatory inputs on the same connection using Bayesian contrasts (Dijkstra et al. 2017).

Results

Psychophysiological Interactions

We performed a PPI analysis to investigate task-dependent changes in functional coupling between modality-specific and multimodal "seed" regions with the rest of the brain during conceptual processing. We defined three seed regions: 1) a "somatomotor seed"—the motor region most strongly engaged in action feature retrieval, 2) an "auditory seed"—the auditory region most strongly engaged in sound feature retrieval, and 3) a "multimodal seed"—the brain region most strongly engaged in both action and sound feature retrieval. We identified the "somatomotor seed" in the left anterior inferior parietal lobe (aIPL)/primary somatosensory cortex (S1), the "auditory seed" in the left middle frontal gyrus (MFG)/precentral sulcus (PreCS), and the "multimodal seed" in the left PPC.

Somatomotor Seed (Left aIPL/S1)

During action judgments, retrieval of action features (high > low action words) increased functional coupling between the somatomotor seed (left aIPL/S1) and the left ATL (including anterior middle and inferior temporal gyri) (Fig. 2*A*; Supplementary Table 2). The ATL region did not overlap with the somatomotor localizer (Fig. 2*B*), suggesting that it represents a higher-level, cross-modal area.

Functional coupling with the somatomotor seed was task-specific for action judgments. During sound judgments or lexical decisions, we found no increased coupling for action features (high > low action words) between the somatomotor seed and any other brain region. In addition, interaction analyses revealed a TASK × ACTION interaction in functional coupling with the somatomotor seed: Left ATL showed a stronger coupling increase for action features (high vs. low action words) during action judgments than during lexical decisions (Fig. 2*C*; Supplementary Table 3).

Moreover, the functional connectivity change was specific to action features: No region showed significant functional coupling with the somatomotor seed for sound features (high > low sound words) in any task.

Auditory Seed (Left MFG/PreCS)

During sound judgments, retrieval of sound features (high > low sound words) increased functional connectivity between the auditory seed (left MFG/PreCS) and the thalamus, left fusiform gyrus (FG), and right superior parietal lobe (SPL) (Fig. 3*A*; Supplementary Table 4*A*). The thalamus cluster partially overlapped with the auditory localizer (Fig. 3*B*; Supplementary Table 4*B*), indicating that it is involved in real sound perception. FG and SPL did not overlap with the auditory localizer.

Functional coupling with the auditory seed was task-specific for sound judgments. During action judgments or lexical decisions, we found no significant coupling changes between the auditory seed and any other brain region. In addition, interaction analyses revealed a TASK × SOUND interaction in functional coupling with the auditory seed: All three regions (thalamus, FG, SPL) showed a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during lexical decisions and/or action judgments (Fig. 3*C*; Supplementary Table 5).

Moreover, functional coupling with the auditory seed was specific to sound features. The auditory seed did not show increased coupling for action features (high > low action words) with any other brain area in any task.

Multimodal Seed (Left PPC)

The multimodal seed (left PPC) showed a double dissociation in its functional connectivity profile. During action judgments, retrieval of action features (high > low action words) selectively increased functional connectivity between the multimodal seed and left primary motor/somatosensory cortex (M1/S1; extending into SPL), as well as the right posterior superior temporal sulcus (pSTS) (Fig. 4*A*; Supplementary Table 6*A*). Left M1/S1 overlapped with the somatomotor localizer, whereas right pSTS did not (Fig. 4*B*; Supplementary Table 6*B*). Interaction analyses showed that both areas exhibited a TASK × ACTION interaction, driven by a larger coupling increase for action features (high vs. low action words) during action judgments than during lexical decisions and/or sound judgments (Fig. 4*C*; Supplementary Table 7). Sound features (high > low sound words) did not induce significant functional connectivity changes during action judgments.

Conversely, during sound judgments, sound feature retrieval (high > low sound words) increased functional connectivity between the multimodal seed and an extensive network of other brain regions (Fig. 5*A*; Supplementary Table 8*A*). Several of these regions overlapped with the auditory localizer (Fig. 5*B*; Supplementary Table 8*B*), including left AAC (extending into inferior frontal gyrus), right IPL, as well as bilateral dorsomedial prefrontal cortex (dmPFC) and thalamus. However, we also found increased functional coupling between the multimodal seed and several regions outside the auditory system, including bilateral precuneus, middle cingulate cortex, early visual cortex, and left somatosensory cortex. Most of these areas exhibited a TASK × SOUND interaction, driven by a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during lexical decisions and/or action judgments (Fig. 5*C*; Supplementary Table 9). No coupling changes were found for action features (high > low action words) during sound judgments.

During lexical decisions, we did not identify significant coupling changes with the multimodal seed, neither for action features (high > low action words) nor for sound features (high > low sound words).

Amodal seed (Left ATL)

As the ATL is widely considered a central, amodal hub of the conceptual system, we performed a supplementary PPI analysis seeding in the ATL (see Supplementary Material). This "amodal seed" (left ATL) showed a similar task-dependent double dissociation in functional coupling as the multimodal PPC. During sound judgments, left ATL showed increased coupling for sound features with the bilateral precuneus/posterior cingulate cortex (PC/PCC) (Supplementary Fig. 1; Supplementary Tables 10 and 11). During action judgments, left ATL exhibited increased coupling for action features with the left dmPFC (Supplementary Fig. 2; Supplementary Tables 12 and 13). Neither of these regions overlapped with the relevant perceptual-motor localizers. Therefore, whereas multimodal PPC interacted with modality-specific perceptual-motor regions, amodal ATL was functionally coupled with other high-level cross-modal convergence zones in a task-dependent fashion.

Functional Coupling between Multimodal and Modality-Specific Areas Is Relevant for Behavior

The PPI analyses identified networks of brain regions that interact with each other in a task-dependent manner during conceptual processing. Most strikingly, the multimodal region

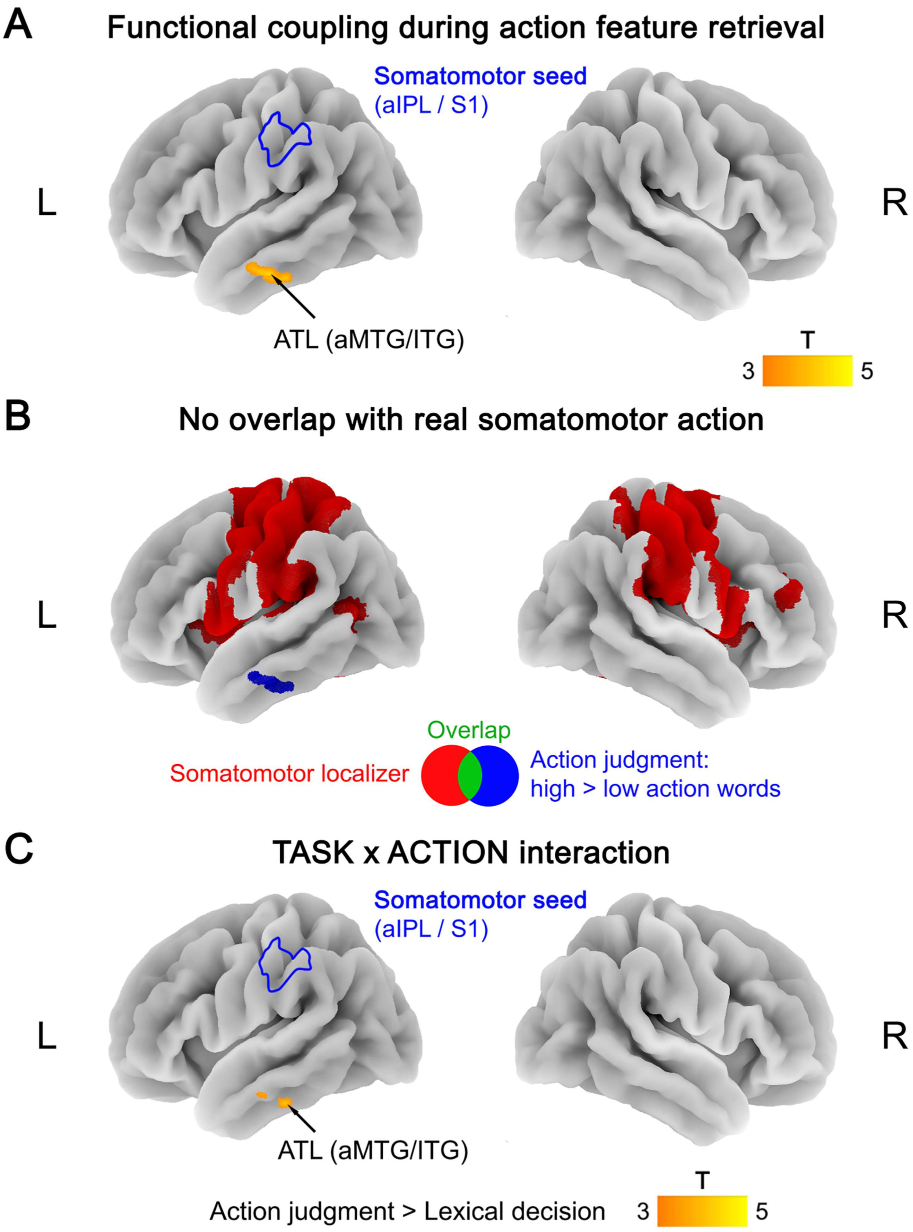

Figure 2. (A) Functional coupling with the somatomotor seed (left aIPL/S1) during action feature retrieval (action judgments: high > low action words). (B) No overlap between functional coupling with the somatomotor seed during action feature retrieval (blue) and activation for the somatomotor localizer (red; hand movements > rest). (C) TASK × ACTION interaction in functional coupling with the somatomotor seed, reflecting a stronger coupling increase for action features (high vs. low action words) during action judgments than lexical decisions. All statistical maps were thresholded at a voxel-wise $P < 0.001$ and a cluster-wise $P < 0.05$ FWE-corrected.

in left PPC functionally coupled with left AAC selectively during sound feature retrieval, and with left M1/S1 selectively during action feature retrieval. It remains unclear, however, whether these functional interactions are relevant for behavior. We reasoned that if the task-dependent functional coupling between multimodal left PPC and somatomotor or auditory cortex is behaviorally relevant, a participant's individual coupling strength should be related to their personal action and sound associations with concepts. Crucially, this relationship should be modality-specific: Coupling between left PPC and M1/S1 (during action feature retrieval) should correlate with action, but not sound associations, whereas coupling between left PPC and AAC (during sound feature retrieval) should correlate with sound, but not action associations.

Indeed, we found that participants' functional coupling strength between left PPC and M1/S1 for action-related (vs. unrelated) words during action judgments positively correlated with their personal action ratings for these words (Fig. 6A), but not with their sound ratings (Fig. 6B). For action ratings, the data were ~6 times more likely under the hypothesis that participants with stronger functional coupling between left PPC and M1/S1 during action feature retrieval had stronger action associations than under the null hypothesis of no correlation ($BF_{10} = 5.96$). For sound ratings, the data were ~5 times more

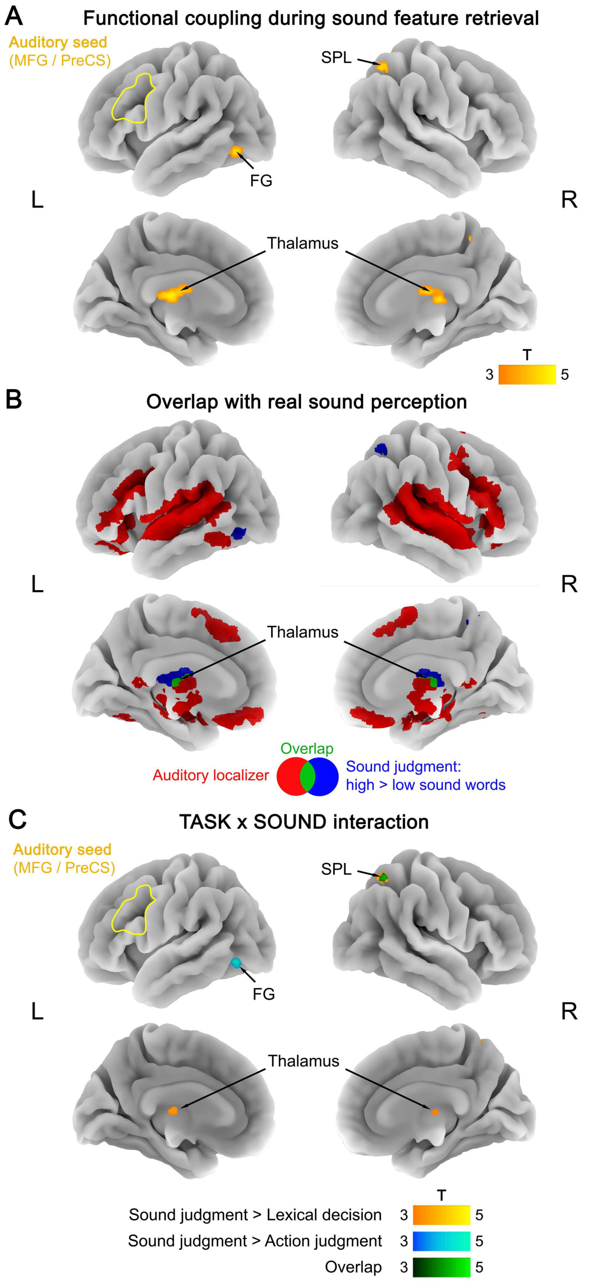

Figure 3. (A) Functional coupling with the auditory seed (left MFG/PreCS) during sound feature retrieval (sound judgments: high > low sound words). (B) Overlap (green) between functional coupling with the auditory seed during sound feature retrieval (blue) and activation for the auditory localizer (red; real sounds > silence). (C) TASK × SOUND interaction in functional coupling with the auditory seed, reflecting a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during lexical decisions (yellow), action judgments (blue), or both (green). All statistical maps were thresholded at a voxel-wise $P < 0.001$ and a cluster-wise $P < 0.05$ FWE-corrected.

likely under the null hypothesis ($BF_{10} = 0.20$ or equivalently $BF_{01} = 4.91$).

Conversely, the individual functional connectivity between left PPC and AAC for sound-related (vs. unrelated) words during sound judgments was associated with participants' sound ratings (Fig. 6D; $BF_{10} = 2.13$), but not with their action ratings (Fig. 6C; $BF_{10} = 0.43$ or $BF_{01} = 2.34$). Thus, participants with stronger functional connectivity between left PPC and AAC had stronger sound associations for sound-related concepts. These results support the hypothesized modality-specific association between task-dependent functional coupling of multimodal with perceptual-motor brain areas and conceptual associations on the behavioral level.

A control analysis showed that action and sound ratings did not correlate with response times for action or sound judgments on the same words (Supplementary Fig. 3). Moreover, our PPI analyses included participant-specific response time regressors. This indicates that interindividual differences in action and sound conceptual associations, and their association with functional coupling between multimodal and modality-specific areas, cannot be explained by differences in action and sound judgment performance. Stronger functional coupling between multimodal PPC and somatomotor or auditory cortices predicts stronger action and sound conceptual associations, above and beyond task performance differences.

Dynamic Causal Modeling

Although PPI can reveal task-dependent changes in functional coupling between a seed region and the rest of the brain, it cannot assess the direction of information flow between brain regions. To provide insight into the information flow between multimodal PPC and modality-specific areas, we leveraged the PPI results to inform a complementary DCM analysis (Friston et al. 2003). The DCM model included left PPC (the multimodal PPI seed), auditory cortex (AAC; PPI cluster for sound feature retrieval), and somatomotor cortex (M1/S1; PPI cluster for action feature retrieval). This analysis allowed us to determine whether information flow between multimodal and modality-specific areas is top-down, bottom-up, or bidirectional; and how it is modulated during sound and action knowledge retrieval.

We performed a DCM group analysis using BMR (Friston et al. 2016; Zeidman et al. 2019b). To this end, a "full" DCM model was defined for each participant (Fig. 7A): In this model, left PPC, AAC, and M1/S1 were bidirectionally connected with each other. Sound and action judgment tasks could serve as driving inputs to every region. Each between-region connection could receive modulatory input from high- and low-sound words, as well as high- and low-action words.

BMR then compared this model with numerous reduced models that had certain parameters (e.g., connections, modulatory inputs) removed. Finally, we computed the Bayesian model average (BMA), the average of parameter values across models weighted by each model's probability, and thresholded the BMA at 95% parameter probability. The results are shown in Fig. 7B and Table 1.

Intrinsic Connectivity

We found strong evidence for all possible intrinsic (i.e., task-independent) connections between the three regions ($Pp > 0.999$), except for the connection from PPC to M1/S1 ($Pp < 0.001$). PPC had an excitatory connection to AAC; AAC weakly excited M1/S1 and inhibited PPC; and M1/S1 positively drove both PPC and AAC (Table 1).

Driving Inputs

Sound and action judgment tasks drove activity in PPC (sound: 0.144 Hz; action: 0.149 Hz) and AAC (sound: 0.175 Hz; action:

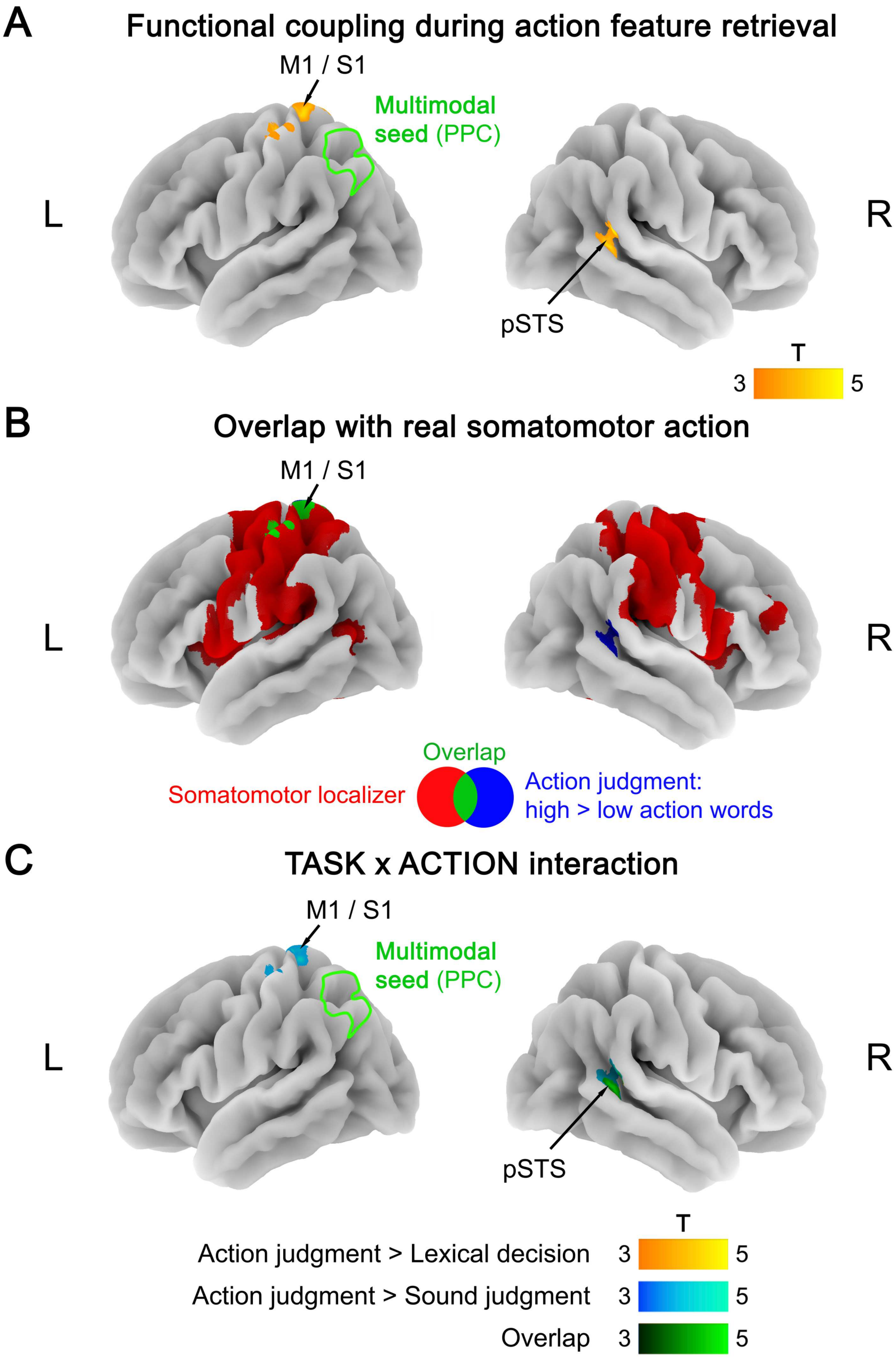

Figure 4. (*A*) Functional coupling with the multimodal seed (left PPC) during action feature retrieval (action judgments: high > low action words). (*B*) Overlap (green) between functional coupling with the multimodal seed during action feature retrieval (blue) and activation for the somatomotor localizer (red; hand movements > rest). (*C*) TASK × ACTION interaction in functional coupling with the multimodal seed, reflecting a stronger coupling increase for action features (high vs. low action words) during action judgments than during lexical decisions (yellow), sound judgments (blue), or both (green). All statistical maps were thresholded at a voxel-wise $P < 0.001$ and a cluster-wise $P < 0.05$ FWE-corrected.

0.157 Hz), but not M1/S1. Importantly, Bayesian contrasts revealed that AAC was more strongly driven by sound than action judgments ($Pp = 0.95$), whereas left PPC was similarly driven by sound and action judgments ($Pp = 0.79$).

Modulatory Inputs

High-sound words selectively modulated reciprocal connectivity between PPC and AAC, further increasing the positive PPC-to-AAC connection (modulation: 0.653; result: 0.768 Hz), and

Table 1 Parameter estimates of the BMA

Connection	Intrinsic connectivity	*Pp*	high sound	*Pp*	low sound	*Pp*	high action	*Pp*	low action	*Pp*
PPC ➔ M1/S1	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
PPC ➔ AAC	**0.166 (0.001)**	**1.0**	**0.653 (0.020)**	**1.0**	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
M1/S1 ➔ PPC	**0.248 (0.001)**	**1.0**	0.0 (0)	0.0	0.470 (0.053)	0.92	**−0.815 (0.024)**	**1.0**	0.0 (0)	0.0
M1/S1 ➔ AAC	**0.258 (0.001)**	**1.0**	0.0 (0)	0.0	0.0 (0)	0.0	−0.200 (0.030)	0.67	0.0 (0)	0.0
AAC ➔ PPC	**−0.129 (0)**	**1.0**	**0.437 (0.014)**	**0.997**	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0
AAC ➔ M1/S1	**0.049 (0)**	**0.999**	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0	0.0 (0)	0.0

Note: Parameter covariance is given in parentheses. Bold font highlights parameters with a $Pp > 95\%$.

even turning the negative AAC-to-PPC connection positive (modulation: 0.437; result: 0.275 Hz). Bayesian contrasts provided strong evidence that high-sound words modulated both connections more strongly than all other word types (vs. low-sound: $Pp > 0.999$; vs. high-action: $Pp > 0.999$; vs. low-action: $Pp > 0.999$), which showed a very low probability of modulating either connection (low-sound: $Pp < 0.001$; high-action: $Pp < 0.001$; high-sound: $Pp < 0.001$).

In contrast, high-action words selectively modulated the M1/S1-to-PPC connection, rendering the positive connection negative (modulation: −0.815; result: −0.539 Hz). High-action words modulated this connection more strongly than all other word types (vs. low-action: $Pp > 0.999$; vs. high-sound: $Pp > 0.999$; vs. low-sound: $Pp > 0.999$), which had a very low probability of modulation (low-action: $Pp < 0.001$; high-sound: $Pp < 0.001$; low-sound: $Pp < 0.001$). Low-action and low-sound words did not modulate any connection with a high probability.

Discussion

This study investigated task-dependent functional and effective connectivity during conceptual processing. Specifically, we asked 1) whether modality-specific and multimodal areas interact during sound and action knowledge retrieval, 2) whether their coupling depends on the task, 3) whether information flows bottom-up, top-down, or bidirectionally, and 4) whether their coupling is relevant for behavior. Combining a whole-brain connectivity approach with directional effective connectivity analysis, we found that functional coupling between modality-specific and multimodal areas strongly depended on the task, involved both bottom-up and top-down information flow, and was behaviorally relevant: The multimodal region in the left posterior parietal cortex (PPC) showed increased coupling with left primary motor and somatosensory cortices (M1/S1) selectively when action knowledge was task-relevant. Conversely, multimodal PPC increased its functional interaction with left auditory association cortex (AAC) selectively when sound knowledge was task-relevant. DCM analyses further revealed that multimodal PPC was bidirectionally connected with AAC, and sound knowledge modulated both the top-down and bottom-up connections. In contrast, M1/S1 was unidirectionally connected to PPC, and action knowledge specifically modulated this bottom-up connection. Finally, coupling between multimodal PPC and somatomotor or auditory cortices predicted participants' personal action and sound associations with concepts, respectively. This indicates that flexible connectivity between multimodal and modality-specific areas is crucial for conceptually guided behavior.

Multimodal PPC vs. Amodal ATL

Our findings suggest that the multimodal region in left PPC acts as a functional coupling "switchboard" (cf. Wang et al. 2017; Chiou and Lambon Ralph 2019), flexibly adapting its connectivity to task-relevant modality-specific nodes. A similar function has recently been proposed for the ATL (Chiou and Lambon Ralph 2019). In that study, left ATL functionally coupled with motor regions during the implicit processing of action knowledge, and with place-related regions during the processing of place knowledge associated with object pictures. Consequently, these authors highlighted the importance of flexible coupling between the ATL and modality-specific regions during conceptual processing (see also Jackson et al. 2016; Lambon Ralph et al. 2016; Wang et al. 2017). However, based on our findings, we propose that the ATL is not unique in its role as a key node for flexible coupling with modality-specific regions, but left PPC plays a similar role in conceptual processing. This is in line with a graph-theoretic fMRI study that showed that left PPC and ATL exhibit particularly flexible functional connectivity during language processing, coactivating with different regions at different times (Chai et al. 2016).

Crucially, however, we propose a functional distinction between left PPC and ATL. In our previous fMRI study, left PPC was recruited for both sound and action features when they were task-relevant, responding to sound features during sound judgments and to action features during action judgments (Kuhnke et al. 2020b). In contrast, the ATL responded to general conceptual information (words > pseudowords; cf. Binder et al. 2009), but not to modality-specific features. These results suggest that left PPC is "multimodal" (i.e., sensitive to modality-specific information), whereas the ATL is "amodal" (i.e., insensitive to modality-specific information). This view is supported by another fMRI study that demonstrated that functional activation for word concreteness judgments correlated with the ratings for several perceptual-motor attributes in the PPC (and in mPFC and PC/PCC), but not in the ATL (Fernandino et al. 2016). Notably, we recently found that TMS over left PPC impairs behavioral performance for action, but not sound knowledge (Kuhnke et al. 2020a). Although these findings suggest that left PPC selectively supports action knowledge retrieval, they do not preclude an additional role of this area in sound knowledge retrieval. In particular, other sound-related regions may have compensated for the disruption of left PPC. Such compensatory mechanisms could be further investigated in future studies employing combined TMS-fMRI (Hartwigsen 2018).

Importantly, not only the regional response, but also the functional coupling profile seems to differ between multimodal

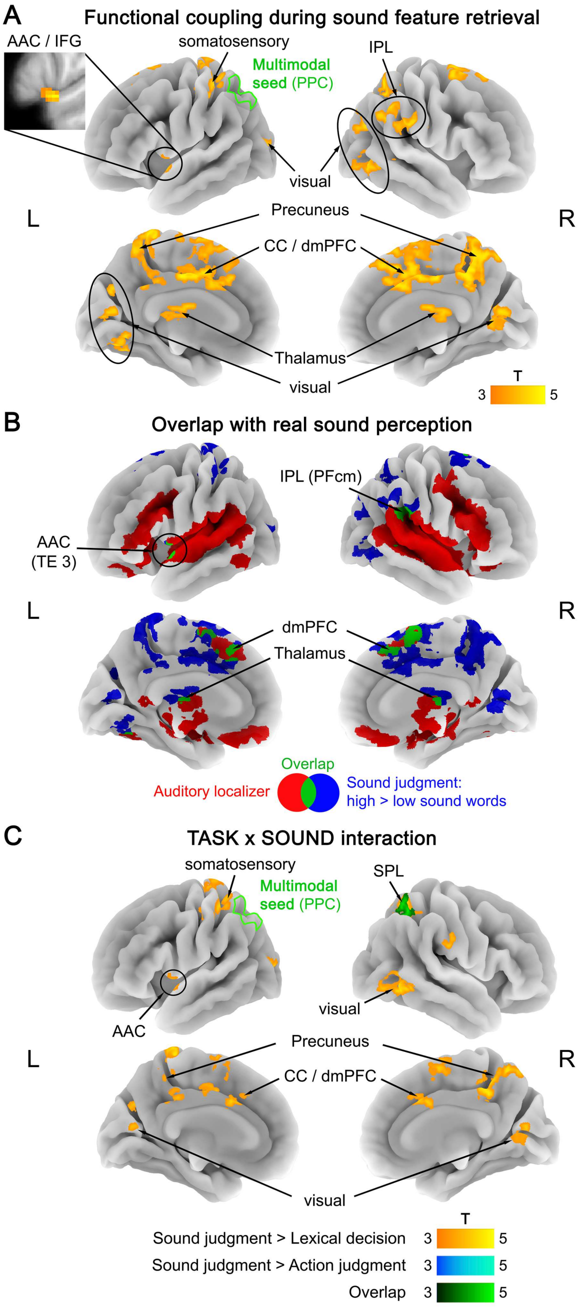

Figure 5. (*A*) Functional coupling with the multimodal seed (left PPC) during sound feature retrieval (sound judgments: high > low sound words). (*B*) Overlap (green) between functional coupling with the multimodal seed during sound feature retrieval (blue) and activation for the auditory localizer (red; real sounds > silence). (*C*) TASK × SOUND interaction in functional coupling with the multimodal seed, reflecting a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during lexical decisions (yellow), action judgments (blue), or both (green). All statistical maps were thresholded at a voxel-wise $P < 0.001$ and a cluster-wise $P < 0.05$ FWE-corrected.

PPC and amodal ATL. Indeed, a supplementary PPI analysis seeding in left ATL revealed task-dependent functional coupling with other high-level cross-modal regions, but not modality-specific cortices: Amodal ATL interacted with bilateral PC/PCC during sound feature retrieval (Supplementary Fig. 1), and with left dmPFC during action feature retrieval (Supplementary Fig. 2), neither of which overlapped with the relevant perceptual-motor localizers. Therefore, whereas multimodal PPC directly couples with modality-specific regions (e.g., left AAC and M1/S1), amodal ATL seems to mainly interact with other cross-modal convergence zones. Indeed, it might be exactly this difference in connectivity profiles that yields the difference in regional response profiles (cf. Lambon Ralph et al. 2016): Multimodal areas may be sensitive to modality-specific information by virtue of their direct interactions with modality-specific cortices. In contrast, amodal ATL might be insensitive to modality-specific features, as it exhibits little coupling with modality-specific areas.

Notably, we did observe coupling between the “somatomotor seed” in left aIPL/S1 and left lateral ATL (aMTG/ITG) during action feature retrieval (see Fig. 2). In contrast, our “amodal seed” in left ATL (defined using the contrast words > pseudowords) picked out functionally distinct voxels that selectively coupled with cross-modal, but not modality-specific nodes. This suggests that our “amodal seed” within left ATL was genuinely amodal, whereas the lateral ATL seemed to be biased toward action knowledge and connected with somatomotor areas. This dissociation is in line with the proposal of a “graded” modality-specificity within the ATL, which depends on the connectivity of different ATL subregions with modality-specific cortices (Pulvermüller et al. 2010; Lambon Ralph et al. 2016).

Functional Coupling During Conceptual Processing is Extensive

In addition to task-dependent coupling between modality-specific and multimodal areas, PPI also revealed lateral connections between different modality-specific areas and between different multimodal areas. During sound knowledge retrieval, the auditory seed in left MFG/PreCS coupled with an auditory region in the thalamus, and multimodal PPC coupled with other multimodal areas in the PC/PCC and mPFC (Fernandino et al. 2016; Kuhnke et al. 2020b). Together with our DCM results, these findings indicate that functional coupling in the conceptual system is more extensive and reciprocal than previously thought. Specifically, our results conflict with the common view that concept retrieval relies mainly on top-down information flow from cross-modal to modality-specific areas (Damasio 1989; Meyer and Damasio 2009; Fernandino et al. 2016). Sound knowledge retrieval involved bidirectional coupling between multimodal PPC and AAC, and action knowledge retrieval even selectively relied on bottom-up input from primary motor/somatosensory cortex to multimodal PPC (cf. Kiefer et al. 2011; Sim et al. 2015).

Two additional findings are noteworthy. Firstly, during sound feature retrieval, we found evidence for coupling with nonauditory modality-specific regions. Auditory seed MFG/PreCS coupled with visual (FG) and somatomotor (SPL) areas, and multimodal PPC coupled with somatosensory and visual cortices (see Fig. 5). This “cross-modality coupling” might reflect that retrieval of sound features of an object (e.g., guitar) can coactivate its visual form, action and touch information, corroborating previous findings for functional activation (Reilly et al. 2016; Lemaitre et al. 2018; Popp et al. 2019b). Secondly, we found that functional coupling during conceptual knowledge retrieval involved low-level sensory-motor areas. Selectively during sound feature retrieval, a region of the thalamus activated in the auditory localizer

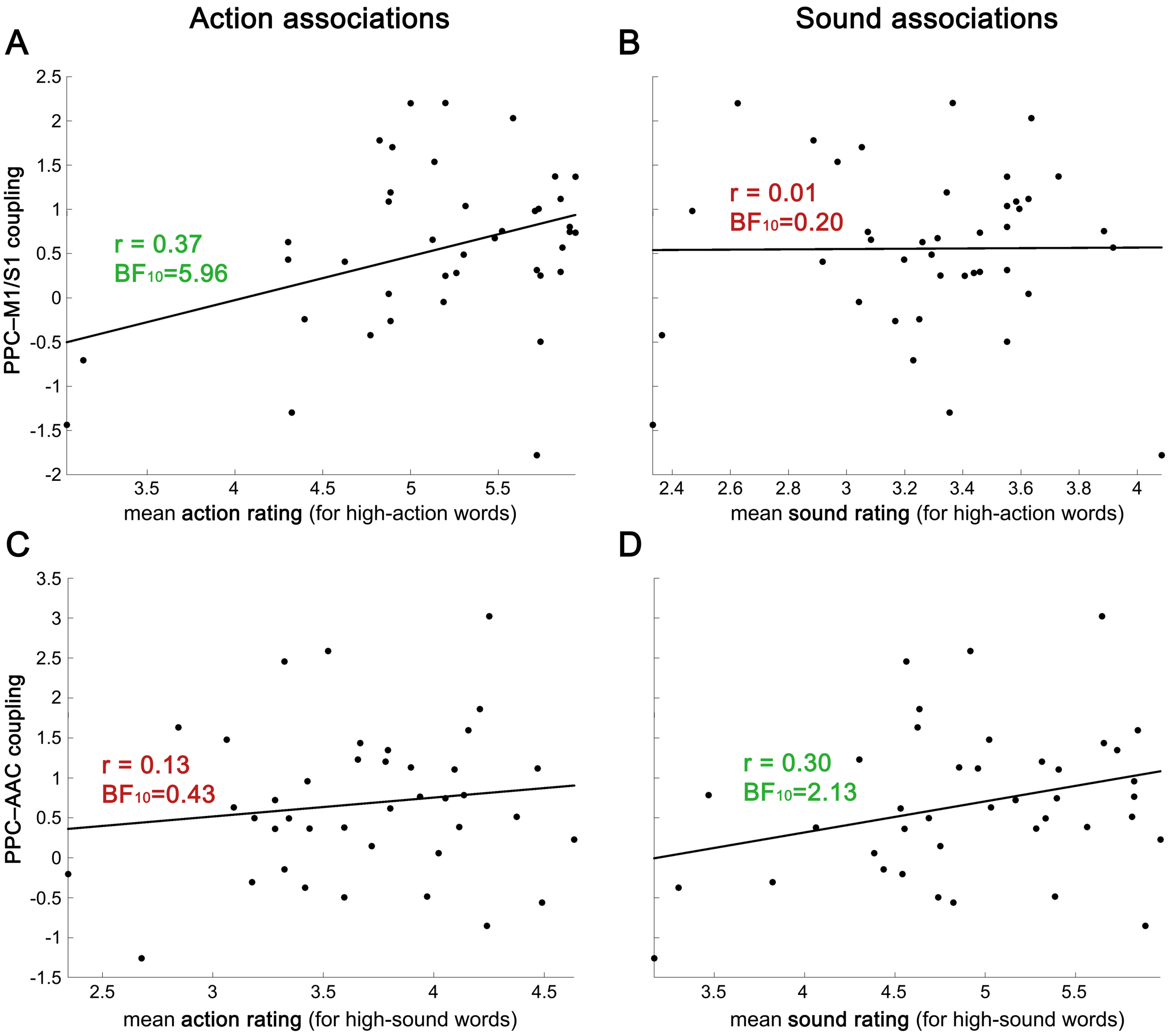

Figure 6. Individual functional coupling between multimodal left PPC and M1/S1 during action knowledge retrieval (PPI t-value for high > low action words during action judgments) predicted participants' personal action associations (A) but not sound associations (B) for action-related words. Conversely, functional coupling between PPC and AAC during sound feature retrieval (PPI t-value for high > low sound words during sound judgments) correlated with participants' individual sound associations (D) but not action associations (C) for sound-related words.

showed increased coupling with both auditory MFG/PreCS and multimodal PPC. Although a precise anatomical localization is limited by our fMRI protocol, this thalamic area might reflect the medial geniculate nucleus, a low-level auditory region that even precedes primary auditory cortex in the auditory processing hierarchy (Henkel 2018). Moreover, during action feature retrieval, primary motor/somatosensory cortex interacted with multimodal PPC. Critically, low-level sensory-motor areas rarely show functional activation in conceptual tasks (Thompson-Schill 2003; Fernandino et al. 2016; but see Hauk et al. 2004; Harpaintner et al. 2020). Indeed, our activation analyses of the same data did not identify low-level sensory-motor activity (Kuhnke et al. 2020b). Such results led some authors to conclude that low-level sensory-motor areas are not involved in conceptual processing (Martin 2016). The present results question this view, suggesting that low-level areas can be involved, at least by influencing the activity of higher-level cortical areas. As a potential explanation for the discrepancy between functional activation and coupling, local activation is generally assumed to reflect intracortical synaptic processing of inputs, whereas connectivity changes reflect cortical outputs to functionally connected areas (Ward et al. 2010; Fiori et al. 2018).

Involvement of Modality-Specific Perceptual-Motor Regions

To determine modality-specific perceptual-motor regions, we tested for overlap with activation during somatomotor and auditory localizers in the same participants. In the somatomotor localizer, participants performed different types of hand movements (finger tapping, pinching, fist making; cf. Bonner et al. 2013). Notably, the localizer itself was not modality-specific, involving both motor and somatosensory activity (due to somatosensory feedback during movement). However,

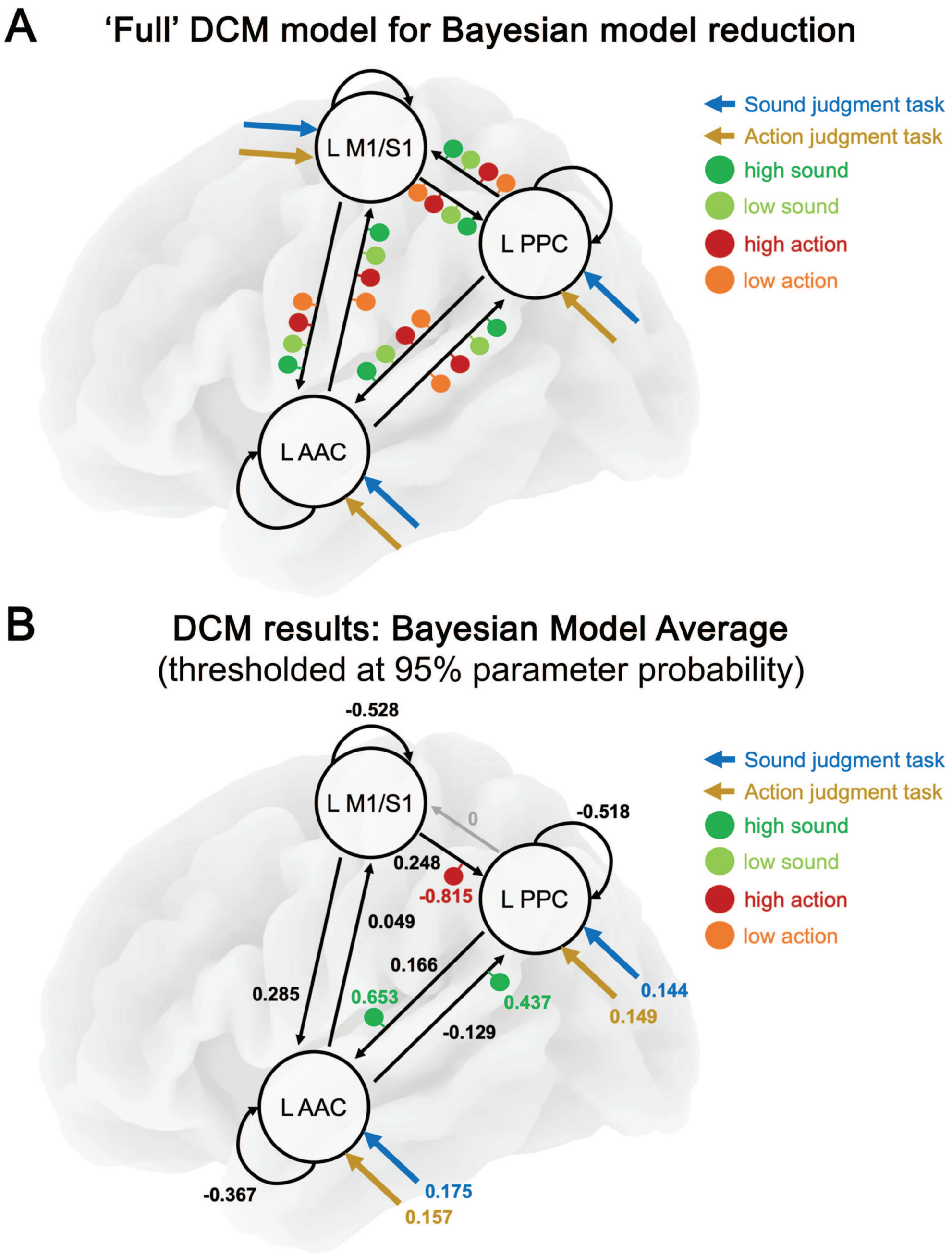

Figure 7. (A) The "full" DCM model that served as starting point for Bayesian model reduction. Black arrows represent intrinsic (i.e., task-independent) connections, colored arrows denote driving inputs (tasks), and colored dots represent modulatory inputs (word types). (B) The resulting BMA thresholded at 95% parameter probability. Driving and between-region parameters are in units of Hz. Modulatory parameters in- or decrease between-region parameters in an additive manner.

it engaged modality-specific brain regions, such as primary motor cortex (M1) and primary somatosensory cortex (S1). Crucially, both motor and somatosensory areas are involved in object-directed actions (van Elk et al. 2014; Hardwick et al. 2018) as well as action-related conceptual processing (Desai et al. 2010; Fernandino et al. 2016; Kuhnke et al. 2020b). In our study, action feature retrieval involved coupling with both left M1 and S1. Importantly, left M1 and S1 were specifically involved in action, but not sound knowledge retrieval. Note that motor and somatosensory areas may play distinct roles within action knowledge processing, representing the movement versus touch-related components of object-directed actions, respectively. Future studies should aim to disentangle these motor and somatosensory components.

In the auditory localizer, participants listened to real object sounds. We presented meaningful object sounds, and not meaningless tones, as sound features of concepts should comprise high-level auditory information (e.g., barking; Bizley and Cohen 2013), rather than low-level acoustic information (e.g., loudness, pitch) (see also Kiefer et al. 2008; Hoenig et al. 2011). The use of real object sounds risks the concomitant engagement of (possibly amodal) conceptual representations (Simanova et al. 2014). Indeed, some regions engaged by the auditory localizer may be involved in abstract conceptual processing, rather than sound perception (e.g., bilateral dmPFC; Binder and Desai 2011; Binder and Fernandino 2015). However, our main conclusions regarding left AAC and thalamus are not compromised by this issue. Left AAC was determined cytoarchitectonically as region TE 3, which is part of high-level auditory cortex (Morosan et al. 2005; Bola et al. 2017). The thalamus is a low-level sensory region (Henkel 2018), unlikely to house amodal conceptual representations. Moreover, both regions were selectively involved in sound, but not action knowledge retrieval.

Overall, the localizers served to constrain our analyses and interpretations by identifying brain regions involved in somatomotor action and sound perception with a high sensitivity but low specificity. They were not designed to define modality-specific regions on their own. Rather, the combined evidence from connectivity profiles, perceptual-motor localizer overlap, and anatomical information suggests that action and sound feature retrieval involved functional coupling with modality-specific perceptual-motor regions.

In general, we observed a task-dependent dissociation between functional coupling during sound versus action knowledge retrieval. Sound features (high > low sound words) increased functional coupling selectively during sound judgments, whereas action features (high > low action words) increased coupling specifically during action judgments. These findings support the view that conceptual processing relies on a flexible, task-dependent architecture (Hoenig et al. 2008; Binder and Desai 2011; Kemmerer 2015; Popp et al. 2019a). Different features of a concept are selectively retrieved when they are task-relevant (Lebois et al. 2015; Yee and Thompson-Schill 2016). Note that differences between the lexical decision task and other tasks could be influenced by differences in session order or responses as lexical decisions were always performed first, and participants responded “yes” to all words. Importantly, however, the dissociation between sound and action judgments cannot be explained by order or response effects as these tasks were counterbalanced within and across participants, and the comparison of high versus low sound/action words corresponded to “yes” versus “no” responses in both cases.

Future Directions to Study Functional and Effective Connectivity during Conceptual Processing

In our two-step analysis approach, we informed DCM with the results of a whole-brain PPI analysis on fMRI data. Crucially, DCM has been validated for face validity (i.e., confirming appropriate responses using simulated data; Friston et al. 2003; Stephan et al. 2009), construct validity (i.e., testing whether DCM is consistent with other approaches; Penny et al. 2004; Lee et al. 2006), predictive validity (i.e., testing whether DCM predicts a known or expected effect; David et al. 2008; Reyt et al. 2010), test–retest reliability (Schuyler et al. 2010) and reproducibility (Bernal-Casas et al. 2013). Notably, DCM will only find a difference in evidence for different models if they predict sufficiently distinct patterns of BOLD responses (Friston et al. 2003; Daunizeau et al. 2011). Temporal information to distinguish different models is limited in fMRI. Instead, fMRI-DCM mainly relies on condition-specific differences in the amplitudes of BOLD responses across regions (Stephan et al. 2010).

However, timing information is required to elucidate the precise time course of functional interactions between modality-specific and cross-modal areas (Hauk 2016). Therefore, future studies should employ methods with a high temporal resolution, such as electro- and magnetoencephalography to further investigate task-dependent functional and effective connectivity during conceptual processing. In particular, a high temporal resolution is necessary to determine whether modality-specific areas are engaged before, after, or simultaneously as cross-modal convergence zones (Kiefer et al. 2011). This question relates to the issue of bottom-up versus top-down information flow: A first engagement of modality-specific cortices would suggest bottom-up information flow, whereas an initial activation of cross-modal zones would indicate top-down processing (Fernandino et al. 2016). Timing information is also key to further refine theories of task dependency in conceptual processing. Specifically, it is currently unclear at which processing stage(s) conceptual processing is modulated by the task (Hauk 2016; but see Hoenig et al. 2008).

A Refined Model of the Neural Architecture Underlying Conceptual Processing

Overall, our findings support theories that assume conceptual processing to rely on a flexible multilevel architecture grounded in the perceptual-motor systems (Binder and Desai 2011; Kemmerer 2015; Fernandino et al. 2016). For instance, we recently proposed that conceptual knowledge is supported by a representational hierarchy from modality-specific perceptual-motor regions via multimodal convergence zones (e.g., left PPC) to an amodal hub in the ATL (Kiefer and Harpaintner 2020; Kuhnke et al. 2020b). Moreover, we argued that this system is dynamic, with different regions being engaged depending on the task (Hoenig et al. 2008; Yee and Thompson-Schill 2016; Popp et al. 2019a).

Our model is related to two other prominent theories, the “hub-and-spokes” (Patterson et al. 2007; Lambon Ralph et al. 2016) and “embodied abstraction” (Binder and Desai 2011; Fernandino et al. 2016) models. Whereas the hub-and-spokes model posits that modality-specific “spoke” regions converge onto a single cross-modal “hub” in the ATL, the embodied abstraction model proposes a hierarchy of cross-modal convergence zones in the inferior parietal, temporal, and medial prefrontal cortices. In line with embodied abstraction, our model proposes multiple levels of cross-modal areas. Consistent with the hub-and-spokes model, it considers the ATL as the top-level, most abstract cross-modal hub. However, our model differs from both approaches in that it distinguishes among cross-modal convergence zones between “multimodal” regions (e.g., left PPC) that retain modality-specific information and the “amodal” ATL that does not.

We now refine this model in two ways: First, we subdivide modality-specific areas into multiple levels (Fig. 8A). As we found that not only high-level, but also low-level sensory-motor areas contribute to conceptual processing, we propose to subdivide modality-specific areas into low-level areas and “unimodal convergence zones” that contain more abstract, but still modality-specific representations (Damasio 1989; Mesulam 1998; Simmons and Barsalou 2003). Second, we add information about task-dependent functional coupling to the model (Fig. 8B). This picture illustrates that functional coupling in the conceptual system is extensive, involving interactions

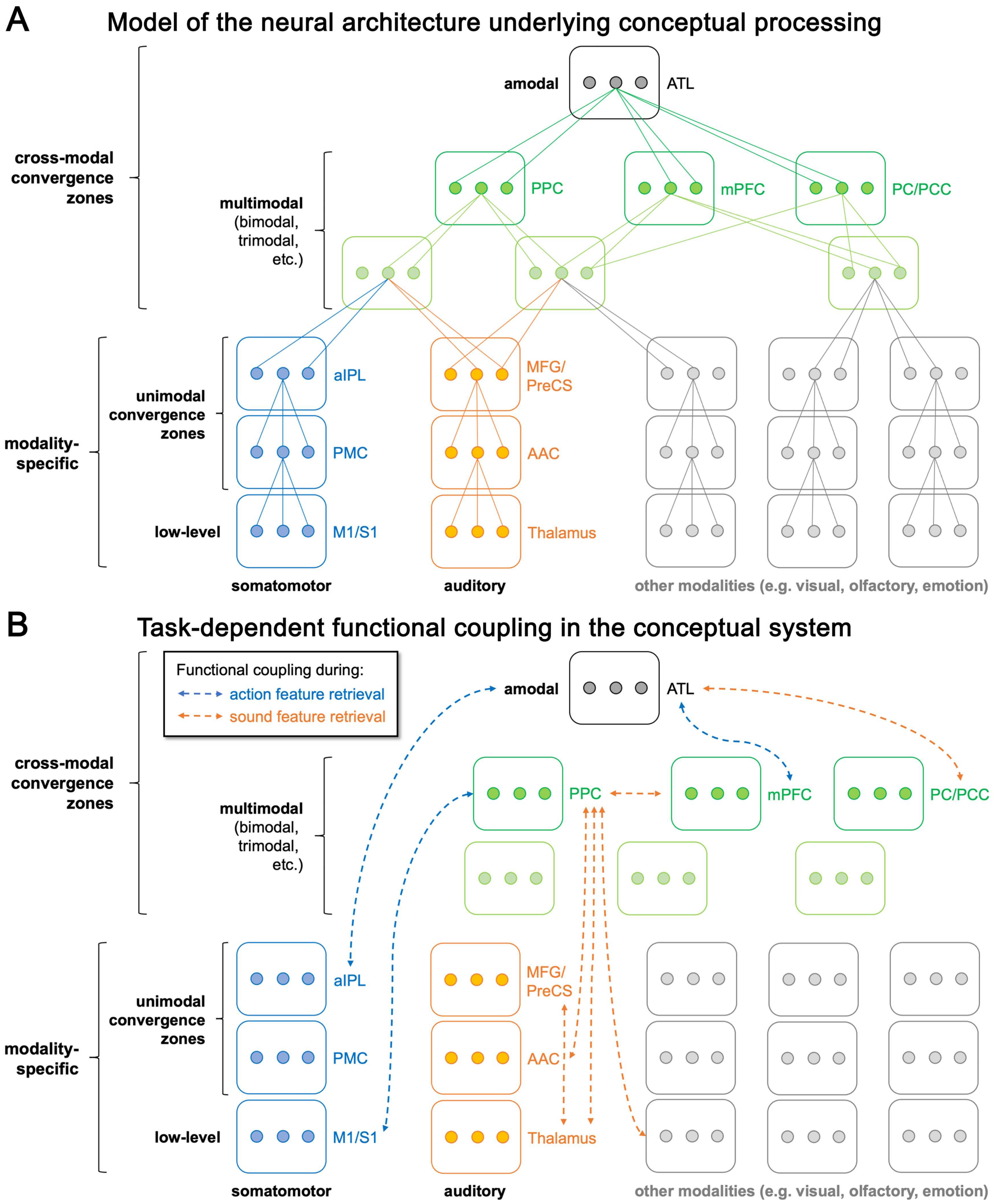

Figure 8. (*A*) A novel model of the neural architecture underlying conceptual processing. Low-level modality-specific representations converge onto more abstract modality-specific representations in unimodal convergence zones. Multimodal convergence zones integrate information across modalities, while retaining modality-specific information. Finally, amodal areas completely abstract away from modality-specific content. Boxes represent brain regions and connected dots represent individual representational units that converge onto a more abstract representation at a higher level. (*B*) Task-dependent functional coupling during action and sound feature retrieval. Functional coupling in the conceptual system is extensive and flexible. Modality-specific regions selectively come into play when the knowledge they represent is task-relevant. Multimodal PPC dynamically adapts its connectivity profile to task-relevant modality-specific nodes. Amodal ATL mainly interacts with other high-level cross-modal convergence zones in a task-dependent fashion.

between various hierarchy levels. We found functional coupling between modality-specific and amodal regions (e.g., aIPL/S1 and ATL), modality-specific and multimodal regions (e.g., M1/S1 and PPC), multimodal and amodal regions (e.g., mPFC and ATL), different modality-specific regions (e.g., MFG/PreCS and auditory thalamus), and different multimodal regions (e.g., PPC and mPFC). We even found some evidence for coupling across modalities (e.g., PPC and visual cortex coupled during sound feature retrieval). Importantly, functional coupling is flexible and systematically depends on the task, similar to functional activation. Modality-specific regions selectively come into play when the knowledge they represent is task-relevant: Somatomotor regions show increased coupling selectively during action knowledge retrieval, and auditory regions during sound knowledge retrieval. The multimodal PPC acts as a functional coupling switchboard, flexibly adapting its connectivity profile to task-relevant modality-specific nodes. In contrast, the amodal ATL mainly shows task-dependent interactions with other high-level cross-modal hubs, with few connections to modality-specific cortices.

Our model is supported by a recent computational modeling study (Jackson et al. 2021), which revealed that the core functions of the conceptual system—conceptual abstraction and task dependency—are best achieved by a hierarchical multilevel architecture composed of a modality-specific layer, an intermediate layer (∼multimodal regions), and a single top-level hub (∼amodal ATL). In line with our findings, the optimal model exhibited connectivity between modality-specific and intermediate nodes, between intermediate nodes and the top-level hub, as well as sparse "shortcut" connections between the hub and modality-specific nodes.

Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

Notes

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References

Barsalou LW. 2008. Grounded cognition. *Annu Rev Psychol*. 59:617–645.

Basilakos A, Smith KG, Fillmore P, Fridriksson J, Fedorenko E. 2018. Functional characterization of the human speech articulation network. *Cereb Cortex*. 28:1816–1830.

Bernal-Casas D, Balaguer-Ballester E, Gerchen MF, Iglesias S, Walter H, Heinz A, Meyer-Lindenberg A, Stephan KE, Kirsch P. 2013. Multi-site reproducibility of prefrontal-hippocampal connectivity estimates by stochastic DCM. *Neuroimage*. 82:555–563.

Binder JR. 2016. In defense of abstract conceptual representations. *Psychon Bull Rev*. 23:1096–1108.

Binder JR, Desai RH. 2011. The neurobiology of semantic memory. *Trends Cogn Sci*. 15:527–536.

Binder JR, Desai RH, Graves WW, Conant LL. 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*. 19:2767–2796.

Binder JR, Fernandino L. 2015. Semantic processing. In: *Brain mapping*. Amsterdam: Elsevier, pp. 445–454.

Bizley JK, Cohen YE. 2013. The what, where and how of auditory-object perception. *Nat Rev Neurosci*. 14:693–707.

Bola Ł, Zimmermann M, Mostowski P, Jednoróg K, Marchewka A, Rutkowski P, Szwed M. 2017. Task-specific reorganization of the auditory cortex in deaf humans. *Proc Natl Acad Sci*. 114:E600–E609.

Bonner MF, Grossman M. 2012. Gray matter density of auditory association cortex relates to knowledge of sound concepts in primary progressive aphasia. *J Neurosci*. 32:7986–7991.

Bonner MF, Peelle JE, Cook PA, Grossman M. 2013. Heteromodal conceptual processing in the angular gyrus. *Neuroimage*. 71:175–186.

Borghesani V, Piazza M. 2017. The neuro-cognitive representations of symbols: the case of concrete words. *Neuropsychologia*. 105:4–17.

Chai LR, Mattar MG, Blank IA, Fedorenko E, Bassett DS. 2016. Functional network dynamics of the language system. *Cereb Cortex*. 26:4148–4159.

Chen L, Lambon Ralph MA, Rogers TT. 2017. A unified model of human semantic knowledge and its disorders. *Nat Hum Behav*. 1:0039.

Chiou R, Lambon Ralph MA. 2019. Unveiling the dynamic interplay between the hub- and spoke-components of the brain's semantic system and its impact on human behaviour. *Neuroimage*. 199:114–126.

Damasio AR. 1989. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition*. 33:25–62.

Daunizeau J, David O, Stephan KE. 2011. Dynamic causal modelling: a critical review of the biophysical and statistical foundations. *Neuroimage*. 58:312–322.

David O, Guillemain I, Saillet S, Reyt S, Deransart C, Segebarth C, Depaulis A. 2008. Identifying neural drivers with functional MRI: an electrophysiological validation. *PLoS Biol*. 6: e315.

Desai RH, Binder JR, Conant LL, Seidenberg MS. 2010. Activation of sensory-motor areas in sentence comprehension. *Cereb Cortex*. 20:468–478.

Devlin JT, Russell RP, Davis MH, Price CJ, Wilson J, Moss HE, Matthews PM, Tyler LK. 2000. Susceptibility-induced loss of signal: comparing PET and fMRI on a semantic task. *Neuroimage*. 11:589–600.

Dijkstra N, Zeidman P, Ondobaka S, van Gerven MAJ, Friston K. 2017. Distinct top-down and bottom-up brain connectivity during visual perception and imagery. *Sci Rep*. 7:5677.

Fedorenko E, Hsieh P-J, Nieto-Castañón A, Whitfield-Gabrieli S, Kanwisher N. 2010. New method for fMRI investigations of language: defining ROIs functionally in individual subjects. *J Neurophysiol*. 104:1177–1194.

Fedorenko E, Kanwisher N. 2009. Neuroimaging of language: Why hasn't a clearer picture emerged? *Lang Linguist Compass*. 3:839–865.

Fedorenko E, Kanwisher N. 2011. Functionally localizing language-sensitive regions in individual subjects with fMRI: a reply to Grodzinsky's critique of Fedorenko and Kanwisher (2009). *Lang Linguist Compass*. 5:78–94.

Fedorenko E, McDermott JH, Norman-Haignere S, Kanwisher N. 2012. Sensitivity to musical structure in the human brain. *J Neurophysiol*. 108:3289–3300.

Feinberg DA, Moeller S, Smith SM, Auerbach E, Ramanna S, Glasser MF, Miller KL, Ugurbil K, Yacoub E. 2010. Multiplexed

Echo planar imaging for sub-second whole brain FMRI and fast diffusion imaging. *PLoS One*. 5:e15710.

Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex*. 1:1–47.

Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS. 2016. Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb Cortex*. 26:2018–2034.

Fiori V, Kunz L, Kuhnke P, Marangolo P, Hartwigsen G. 2018. Transcranial direct current stimulation (tDCS) facilitates verb learning by altering effective connectivity in the healthy brain. *Neuroimage*. 181:550–559.

Friston K, Buechel C, Fink G, Morris J, Rolls E, Dolan R. 1997. Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage*. 6:218–229.

Friston KJ, Harrison L, Penny W. 2003. Dynamic causal modelling. *Neuroimage*. 19:1273–1302.

Friston KJ, Litvak V, Oswal A, Razi A, Stephan KE, Van Wijk BCM, Ziegler G, Zeidman P. 2016. Bayesian model reduction and empirical Bayes for group (DCM) studies. *Neuroimage*. 128:413–431.

Gitelman DR, Penny WD, Ashburner J, Friston KJ. 2003. Modeling regional and psychophysiologic interactions in fMRI: the importance of hemodynamic deconvolution. *Neuroimage*. 19:200–207.

Goldberg RF. 2006. Perceptual knowledge retrieval activates sensory brain regions. *J Neurosci*. 26:4917–4921.

Grinband J, Wager TD, Lindquist M, Ferrera VP, Hirsch J. 2008. Detection of time-varying signals in event-related fMRI designs. *Neuroimage*. 43:509–520.

Halai AD, Welbourne SR, Embleton K, Parkes LM. 2014. A comparison of dual gradient-echo and spin-echo fMRI of the inferior temporal lobe. *Hum Brain Mapp*. 35:4118–4128.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP. 2018. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosci Biobehav Rev*. 94: 31–44.

Harpaintner M, Sim E, Trumpp NM, Ulrich M, Kiefer M. 2020. The grounding of abstract concepts in the motor and visual system: an fMRI study. *Cortex*. 124:1–22.

Hartwigsen G. 2018. Flexible redistribution in cognitive networks. *Trends Cogn Sci*. 22:687–698.

Hauk O. 2016. Only time will tell – why temporal information is essential for our neuroscientific understanding of semantics. *Psychon Bull Rev*. 23:1072–1079.

Hauk O, Johnsrude I, Pulvermüller F. 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron*. 41:301–307.

Henkel CK. 2018. The auditory system. In: *Fundamental neuroscience for basic and clinical applications*. 5th ed. Amsterdam: Elsevier, pp. 306–319.

Hoenig K, Müller C, Herrnberger B, Sim E-J, Spitzer M, Ehret G, Kiefer M. 2011. Neuroplasticity of semantic representations for musical instruments in professional musicians. *Neuroimage*. 56:1714–1725.

Hoenig K, Sim E-J, Bochev V, Herrnberger B, Kiefer M. 2008. Conceptual flexibility in the human brain: dynamic recruitment of semantic maps from visual, motor, and motion-related areas. *J Cogn Neurosci*. 20:1799–1814.

Hsu NS, Kraemer DJM, Oliver RT, Schlichting ML, Thompson-Schill SL. 2011. Color, context, and cognitive style: variations in color knowledge retrieval as a function of task and subject variables. *J Cogn Neurosci*. 23:2544–2557.

Jackson RL, Hoffman P, Pobric G, Lambon Ralph MA. 2016. The semantic network at work and rest: differential connectivity of anterior temporal lobe subregions. *J Neurosci*. 36: 1490–1501.

Jackson RL, Rogers TT, Lambon Ralph MA. 2021. Reverse-engineering the cortical architecture for controlled semantic cognition. *Nat Hum Behav*. 5:860528.

Jefferies E. 2013. The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex*. 49:611–625.

Julian JB, Fedorenko E, Webster J, Kanwisher N. 2012. An algorithmic method for functionally defining regions of interest in the ventral visual pathway. *Neuroimage*. 60:2357–2364.

Kahan J, Foltynie T. 2013. Understanding DCM: ten simple rules for the clinician. *Neuroimage*. 83:542–549.

Kemmerer D. 2015. Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible, multilevel architecture for conceptual knowledge. *Psychon Bull Rev*. 22:1068–1075.

Keuleers E, Brysbaert M. 2010. Wuggy: a multilingual pseudoword generator. *Behav Res Methods*. 42:627–633.

Kiefer M, Barsalou LW. 2013. Grounding the human conceptual system in perception, action, and internal states. In: Prinz W, Beisert M, Herwig A, editors. *Tutorials in action science*. Cambridge: The MIT Press, pp. 381–407.

Kiefer M, Harpaintner M. 2020. Varieties of abstract concepts and their grounding in perception or action. *Open Psychol*. 2:119–137.

Kiefer M, Pulvermüller F. 2012. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*. 48:805–825.

Kiefer M, Sim E-J, Helbig H, Graf M. 2011. Tracking the time course of action priming on object recognition: evidence for fast and slow influences of action on perception. *J Cogn Neurosci*. 23:1864–1874.

Kiefer M, Sim E-J, Herrnberger B, Grothe J, Hoenig K. 2008. The sound of concepts: four markers for a link between auditory and conceptual brain systems. *J Neurosci*. 28:12224–12230.

Kuhnke P, Beaupain MC, Cheung VKM, Weise K, Kiefer M, Hartwigsen G. 2020a. Left posterior inferior parietal cortex causally supports the retrieval of action knowledge. *Neuroimage*. 219:117041.

Kuhnke P, Kiefer M, Hartwigsen G. 2020b. Task-dependent recruitment of modality-specific and multimodal regions during conceptual processing. *Cereb Cortex*. 30:3938–3959.

Lakens D, McLatchie N, Isager PM, Scheel AM, Dienes Z. 2020. Improving inferences about null effects with Bayes factors and equivalence tests. *Journals Gerontol Ser B*. 75:45–57.

Lambon Ralph MA. 2014. Neurocognitive insights on conceptual knowledge and its breakdown. *Philos Trans R Soc B Biol Sci*. 369:20120392.

Lambon Ralph MA, Jefferies E, Patterson K, Rogers TT. 2016. The neural and computational bases of semantic cognition. *Nat Rev Neurosci*. 18:42–55.

Lambon Ralph MA, Sage K, Jones RW, Mayberry EJ. 2010. Coherent concepts are computed in the anterior temporal lobes. *Proc Natl Acad Sci*. 107:2717–2722.

Lebois LAM, Wilson-Mendenhall CD, Barsalou LW. 2015. Are automatic conceptual cores the gold standard of semantic processing? The context-dependence of spatial meaning in grounded congruency effects. *Cognit Sci*. 39:1764–1801.

Lee L, Friston K, Horwitz B. 2006. Large-scale neural models and dynamic causal modelling. *Neuroimage*. 30:1243–1254.

Lemaitre G, Pyles JA, Halpern AR, Navolio N, Lehet M, Heller LM. 2018. Who's that knocking at my door? Neural bases of sound source identification. *Cereb Cortex*. 28:805–818.

Margulies DS, Ghosh SS, Goulas A, Falkiewicz M, Huntenburg JM, Langs G, Bezgin G, Eickhoff SB, Castellanos FX, Petrides M *et al*. 2016. Situating the default-mode network along a principal gradient of macroscale cortical organization. *Proc Natl Acad Sci*. 113:12574–12579.

Martin A. 2016. GRAPES—grounding representations in action, perception, and emotion systems: how object properties and categories are represented in the human brain. *Psychon Bull Rev*. 23:979–990.

McLaren DG, Ries ML, Xu G, Johnson SC. 2012. A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. *Neuroimage*. 61:1277–1286.

Mesulam MM. 1998. From sensation to cognition. *Brain*. 121:1013–1052.

Meteyard L, Cuadrado SR, Bahrami B, Vigliocco G. 2012. Coming of age: a review of embodiment and the neuroscience of semantics. *Cortex*. 48:788–804.

Meyer F. 1991. Un algorithme optimal de ligne de partage des eaux. In: *Paper presented at the Dans 8me congrès de reconnaissance des formes et intelligence artificielle*. Lyon, France.

Meyer K, Damasio A. 2009. Convergence and divergence in a neural architecture for recognition and memory. *Trends Neurosci*. 32:376–382.

Morosan P, Schleicher A, Amunts K, Zilles K. 2005. Multimodal architectonic mapping of human superior temporal gyrus. *Anat Embryol*. 210:401–406.

Nichols T, Brett M, Andersson J, Wager T, Poline J-B. 2005. Valid conjunction inference with the minimum statistic. *Neuroimage*. 25:653–660.

Nieto-Castañón A, Fedorenko E. 2012. Subject-specific functional localizers increase sensitivity and functional resolution of multi-subject analyses. *Neuroimage*. 63:1646–1669.

Noppeney U, Price CJ, Penny WD, Friston KJ. 2006. Two distinct neural mechanisms for category-selective responses. *Cereb Cortex*. 16:437–445.

O'Reilly JX, Woolrich MW, Behrens TEJ, Smith SM, Johansen-Berg H. 2012. Tools of the trade: psychophysiological interactions and functional connectivity. *Soc Cogn Affect Neurosci*. 7:604–609.

Oldfield RC. 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*. 9:97–113.

Patterson K, Lambon Ralph MA. 2016. The hub-and-spoke hypothesis of semantic memory. In: *Neurobiology of language*. Amsterdam: Elsevier, pp. 765–775.

Patterson K, Nestor PJ, Rogers TT. 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci*. 8:976–987.

Penny WD, Mattout J, Trujillo-Barreto N. 2007. Bayesian model selection and averaging. In: *Statistical Parametric Mapping*. Amsterdam: Elsevier, pp. 454–467.

Penny WD, Stephan KE, Mechelli A, Friston KJ. 2004. Modelling functional integration: a comparison of structural equation and dynamic causal models. *Neuroimage*. 23:S264–S274.

Pobric G, Jefferies E, Lambon Ralph MA. 2010a. Category-specific versus category-general semantic impairment induced by transcranial magnetic stimulation. *Curr Biol*. 20: 964–968.

Pobric G, Jefferies E, Lambon Ralph MA. 2010b. Amodal semantic representations depend on both anterior temporal lobes: evidence from repetitive transcranial magnetic stimulation. *Neuropsychologia*. 48:1336–1342.

Popp M, Trumpp NM, Kiefer M. 2019a. Processing of action and sound verbs in context: an fMRI study. *Transl Neurosci*. 10:200–222.

Popp M, Trumpp NM, Sim E, Kiefer M. 2019b. Brain activation during conceptual processing of action and sound verbs. *Adv Cogn Psychol*. 15:236–255.

Poser BA, Versluis MJ, Hoogduin JM, Norris DG. 2006. BOLD contrast sensitivity enhancement and artifact reduction with multiecho EPI: parallel-acquired inhomogeneity-desensitized fMRI. *Magn Reson Med*. 55:1227–1235.

Pulvermüller F, Cooper-Pye E, Dine C, Hauk O, Nestor PJ, Patterson K. 2010. The word processing deficit in semantic dementia: all categories are equal, but some categories are more equal than others. *J Cogn Neurosci*. 22:2027–2041.

Reilly J, Garcia A, Binney RJ. 2016. Does the sound of a barking dog activate its corresponding visual form? An fMRI investigation of modality-specific semantic access. *Brain Lang*. 159:45–59.

Reyt S, Picq C, Sinniger V, Clarençon D, Bonaz B, David O. 2010. Dynamic causal modelling and physiological confounds: a functional MRI study of vagus nerve stimulation. *Neuroimage*. 52:1456–1464.

Rice GE, Lambon Ralph MA, Hoffman P. 2015. The roles of left versus right anterior temporal lobes in conceptual knowledge: an ALE meta-analysis of 97 functional neuroimaging studies. *Cereb Cortex*. 25:4374–4391.

Rogers TT, Lambon Ralph MA, Garrard P, Bozeat S, McClelland JL, Hodges JR, Patterson K. 2004. Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol Rev*. 111:205–235.

Schuyler B, Ollinger JM, Oakes TR, Johnstone T, Davidson RJ. 2010. Dynamic causal modeling applied to fMRI data shows high reliability. *Neuroimage*. 49:603–611.

Siegel JS, Power JD, Dubis JW, Vogel AC, Church JA, Schlaggar BL, Petersen SE. 2014. Statistical improvements in functional magnetic resonance imaging analyses produced by censoring high-motion data points. *Hum Brain Mapp*. 35:1981–1996.

Sim E-J, Helbig HB, Graf M, Kiefer M. 2015. When action observation facilitates visual perception: activation in Visuomotor areas contributes to object recognition. *Cereb Cortex*. 25:2907–2918.

Simanova I, Hagoort P, Oostenveld R, Van Gerven MAJ. 2014. Modality-independent decoding of semantic information from the human brain. *Cereb Cortex*. 24:426–434.

Simmons WK, Barsalou LW. 2003. The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cogn Neuropsychol*. 20:451–486.

Stephan KE, Penny WD, Daunizeau J, Moran RJ, Friston KJ. 2009. Bayesian model selection for group studies. *Neuroimage*. 46:1004–1017.

Stephan KE, Penny WD, Moran RJ, den Ouden HEM, Daunizeau J, Friston KJ. 2010. Ten simple rules for dynamic causal modeling. *Neuroimage*. 49:3099–3109.

Thompson-Schill SL. 2003. Neuroimaging studies of semantic memory: inferring "how" from "where". *Neuropsychologia*. 41:280–292.

Todd N, Moeller S, Auerbach EJ, Yacoub E, Flandin G, Weiskopf N. 2016. Evaluation of 2D multiband EPI imaging for high-resolution, whole-brain, task-based fMRI studies at 3T: sensitivity and slice leakage artifacts. *Neuroimage*. 124: 32–42.

Trumpp NM, Traub F, Pulvermüller F, Kiefer M. 2014. Unconscious automatic brain activation of acoustic and action-related conceptual features during masked repetition priming. *J Cogn Neurosci*. 26:352–364.

van Elk M, van Schie H, Bekkering H. 2014. Action semantics: a unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. *Phys Life Rev*. 11:220–250.

Van Essen DC, Maunsell JHR. 1983. Hierarchical organization and functional streams in the visual cortex. *Trends Neurosci*. 6:370–375.

Visser M, Jefferies E, Lambon Ralph MA. 2010. Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *J Cogn Neurosci*. 22:1083–1094.

Vukovic N, Feurra M, Shpektor A, Myachykov A, Shtyrov Y. 2017. Primary motor cortex functionally contributes to language comprehension: an online rTMS study. *Neuropsychologia*. 96:222–229.

Wagenmakers EJ, Love J, Marsman M, Jamil T, Ly A, Verhagen J, Selker R, Gronau QF, Dropmann D, Boutin B *et al*. 2018. Bayesian inference for psychology. Part II: example applications with JASP. *Psychon Bull Rev*. 25:58–76.

Wang Y, Collins JA, Koski J, Nugiel T, Metoki A, Olson IR. 2017. Dynamic neural architecture for social knowledge retrieval. *Proc Natl Acad Sci*. 114:E3305–E3314.

Ward NS, Bestmann S, Hartwigsen G, Weiss MM, Christensen LOD, Frackowiak RSJ, Rothwell JC, Siebner HR. 2010. Low-frequency Transcranial magnetic stimulation over left dorsal premotor cortex improves the dynamic control of visuospatially cued actions. *J Neurosci*. 30: 9216–9223.

Weiskopf N, Hutton C, Josephs O, Deichmann R. 2006. Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: a whole-brain analysis at 3 T and 1.5 T. *Neuroimage*. 33:493–504.

Yee E, Thompson-Schill SL. 2016. Putting concepts into context. *Psychon Bull Rev*. 23:1015–1027.

Zeidman P, Jafarian A, Corbin N, Seghier ML, Razi A, Price CJ, Friston KJ. 2019a. A guide to group effective connectivity analysis, part 1: first level analysis with DCM for fMRI. *Neuroimage*. 200:174–190.

Zeidman P, Jafarian A, Seghier ML, Litvak V, Cagnan H, Price CJ, Friston KJ. 2019b. A guide to group effective connectivity analysis, part 2: second level analysis with PEB. *Neuroimage*. 200:12–25.

4. TMS STUDY

The study presented in this chapter has been published as:

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Neuroimaging studies 1 and 2 suggested a key role of the left posterior parietal cortex (PPC)—particularly the posterior inferior parietal lobe (pIPL)—as a multimodal convergence zone for conceptual knowledge. However, as neuroimaging is correlational, it is unclear whether left pIPL plays a *causal* role as a multimodal conceptual hub. This chapter presents a transcranial magnetic stimulation (TMS) study that tests the causal relevance of left pIPL for action and sound knowledge retrieval.

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Left posterior inferior parietal cortex causally supports the retrieval of action knowledge

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ABSTRACT

Conceptual knowledge is central to human cognition. The left posterior inferior parietal lobe (pIPL) is implicated by neuroimaging studies as a multimodal hub representing conceptual knowledge related to various perceptual–motor modalities. However, the causal role of left pIPL in conceptual processing remains unclear. Here, we transiently disrupted left pIPL function with transcranial magnetic stimulation (TMS) to probe its causal relevance for the retrieval of action and sound knowledge. We compared effective TMS over left pIPL with sham TMS, while healthy participants performed three different tasks—lexical decision, action judgment, and sound judgment—on words with a high or low association to actions and sounds. We found that pIPL-TMS selectively impaired action judgments on low sound–low action words. For the first time, we directly related computational simulations of the TMS-induced electrical field to behavioral performance, which revealed that stronger stimulation of left pIPL is associated with worse performance for action but not sound judgments. These results indicate that left pIPL causally supports conceptual processing when action knowledge is task-relevant and cannot be compensated by sound knowledge. Our findings suggest that left pIPL is specialized for the retrieval of action knowledge, challenging the view of left pIPL as a multimodal conceptual hub.

1. Introduction

Conceptual knowledge is central to numerous cognitive abilities, including object use and word comprehension (Kiefer and Pulvermüller, 2012; Lambon Ralph, 2014; van Elk et al., 2014). The left posterior inferior parietal lobe (pIPL) is the most consistently activated region in functional neuroimaging studies on conceptual processing (Binder et al., 2009). Together with the fact that it is located between and connected with many modality-specific cortices (Margulies et al., 2016; Seghier, 2013), this suggests that left pIPL constitutes a "convergence zone" for conceptual knowledge which integrates information from multiple perceptual-motor modalities (Binder and Desai, 2011; Damasio, 1989; Mesulam, 1998; Price et al., 2015). Importantly, recent neuroimaging evidence suggests that left pIPL is not amodal but multimodal, that is, it remains sensitive to the individual modalities (Fernandino et al., 2016; Kuhnke et al., 2020). For instance, in a recent fMRI study (Kuhnke et al., 2020), we found that left pIPL (particularly areas PFm/PGa) responds to both action and sound features of word meaning. Notably, pIPL activation strongly depended on the task: Left pIPL selectively responded to action features (high vs. low action words) during action judgments, and to sound features (high vs. low sound words) during sound judgments.

However, as neuroimaging is correlational, it remains unknown whether left pIPL plays a *causal* role as a multimodal conceptual region, or instead shows activation that is incidental to behavioral performance (Price and Friston, 2002). While some studies have provided evidence that left pIPL is functionally relevant for conceptual processing in general (Hartwigsen et al., 2016; Sliwinska et al., 2015; Stoeckel et al., 2009), no study has tested the functional relevance of left pIPL for processing multiple different conceptual features. Crucially, the neuroimaging literature seems to conflict with patient studies which predominantly associate left IPL lesions with deficits in object-directed motor actions (Buxbaum et al., 2005a, 2005b; Culham and Valyear, 2006), suggesting a potential specialization for action knowledge.

The causal relevance of a brain region for a cognitive function can be

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determined in healthy human subjects using repetitive transcranial magnetic stimulation (rTMS) applied during the task-of-interest ("online") (Pascual-Leone et al., 2000; Walsh and Cowey, 2000). Compared to structural brain lesions and rTMS protocols applied before the task ("offline"), online rTMS has the advantage that its effects are transient and thus unconfounded by reorganization processes (Devlin and Watkins, 2008; Hartwigsen et al., 2015).

Here, we used online rTMS to investigate whether left pIPL is functionally relevant for the processing of sound and action features of concepts, and to what extent its involvement depends on the task. We compared effective rTMS over the left pIPL with (ineffective) sham rTMS over the vertex, while healthy participants performed three tasks—lexical decision, sound judgment, and action judgment—on words with a high or low association to sounds and actions (e.g. 'telephone' is a high sound–high action word).

Based on our fMRI results (Kuhnke et al., 2020), we hypothesized that left pIPL is multimodal and causally relevant for the processing of both sound and action features of concepts, where its contribution depends on the relevance of a conceptual feature for the concept and the task. Compared to sham stimulation, rTMS over left pIPL should impair behavioral performance (accuracy and/or response times) on both sound judgments and action judgments (which require sound and action features respectively) but not lexical decisions (which do not require access to conceptual knowledge). Action judgments should be modulated differentially for high vs. low action words, and sound judgments should be modulated differentially for high vs. low sound words.

2. Materials and methods

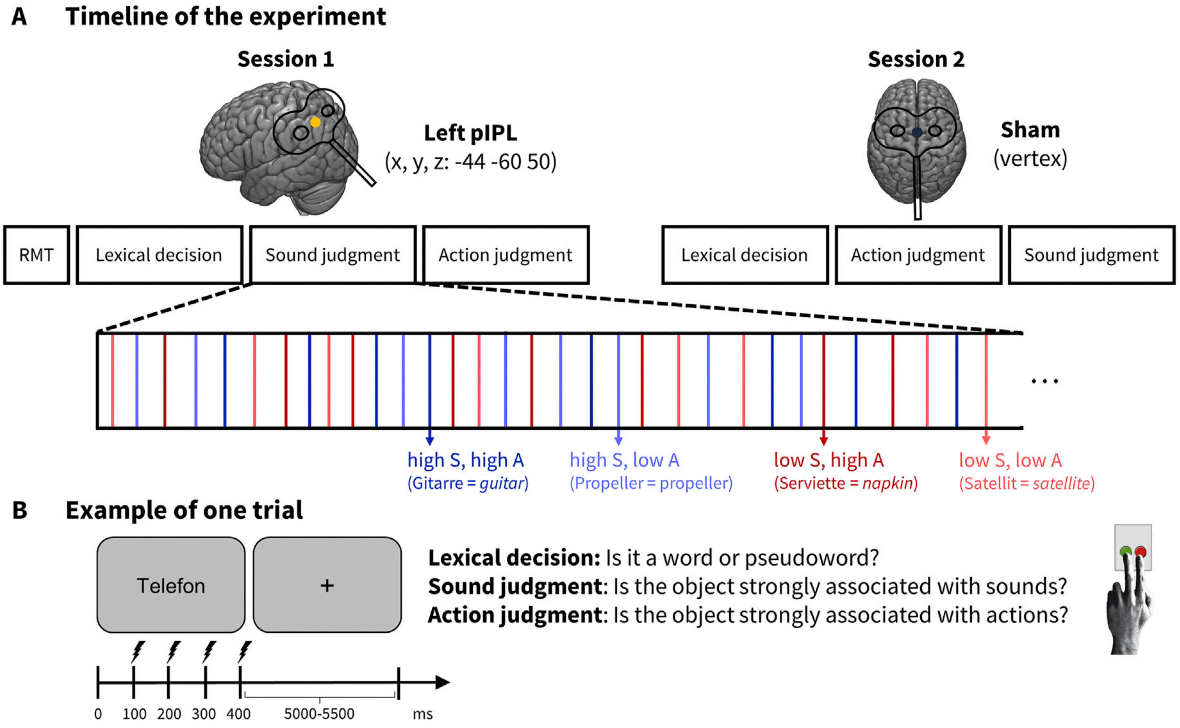
2.1. Participants

Data from 26 native German speakers (14 female; mean age: 27.7 years, SD: 4.0, range: 20–35) entered the final analysis. 29 participants were initially recruited, but 3 were excluded due to technical failure during the experiment. The sample size was determined based on comparable previous TMS studies (e.g. Klaus and Hartwigsen, 2019; Kuhnke et al., 2017; Vukovic et al., 2017) and counterbalancing requirements (see subsections 2.2 and 2.3). All participants were right-handed (mean laterality quotient: 86.8, SD: 9.99; according to Oldfield, 1971) and had no history of psychiatric, neurological, or hearing disorders. They were recruited via the subject database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. Written informed consent was obtained from each subject prior to the experiment. The study was performed according to the guidelines of the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

2.2. Experimental procedures

Fig. 1 depicts the experimental procedure. The study employed a 2 x 3 x 2 x 2 within-subject design with the factors TMS (left pIPL, sham), TASK (lexical decision, sound judgment, action judgment), SOUND (high, low association), and ACTION (high, low association). The experiment consisted of two sessions (one for each TMS condition) separated by at least 7 days (mean inter-session interval: 7.38 days, SD: 1.08) to prevent carry-over effects of TMS. Session order was counterbalanced across participants.

In each session, participants performed three tasks on 104 words denoting concrete objects with a low or high association to sounds and (human) actions. In the lexical decision task, participants decided whether the presented stimulus was a real word or pseudoword. In the sound judgment task, participants judged whether the object denoted by the word was strongly associated with sounds. Finally, in the action judgment task, participants judged whether the object was strongly associated with actions. The lexical decision task acted as a control task which did not require sound or action features of word meaning, and was always performed first so that the participants' attention was not



Lexical decision: Is it a word or pseudoword?
Sound judgment: Is the object strongly associated with sounds?
Action judgment: Is the object strongly associated with actions?

Fig. 1. Experimental procedure. (A) Each subject participated in two TMS sessions. In one session, they received effective rTMS over left pIPL, and in the other session, sham rTMS over the vertex (order counterbalanced across subjects). At the beginning of session 1, the individual resting motor threshold (RMT) was determined. Participants performed three different tasks—lexical decision, sound judgment, and action judgment—on words from the categories 1) high sound–high action (dark blue), 2) high sound–low action (light blue), 3) low sound–high action (dark red), and 4) low sound–low action (light red). (B) During each trial, a word was presented for 400 ms and 4 pulses of 10 Hz rTMS were applied at 100% RMT. Participants responded via button press.

explicitly directed towards sound or action features (cf. Kuhnke et al., 2020). The sound and action judgment tasks explicitly required retrieval of sound or action features, respectively; their order was counterbalanced within and across subjects. Within each task, trials for the four word types were pseudo-randomized (maximally 3 successive trials of a type).

The trial structure was identical in all tasks. A word was shown for 400 ms, followed by an inter-trial interval (fixation cross) of 5–5.5 s (to avoid inter-trial interference by TMS; Kiers et al., 1993). 4 pulses of 10 Hz rTMS were applied starting 100 ms after word onset to interfere with the earliest (~150 ms; Hauk and Tschentscher, 2013; Kiefer and Pulvermüller, 2012) until latest (~400 ms; Lau et al., 2008) conceptual processing stages, while sparing stimulus encoding and response execution processes (cf. Devlin et al., 2003; Hartwigsen et al., 2016). Participants responded via button press using the index and middle fingers of their left hand. They were instructed to respond as fast and as accurately as possible. Before each task, participants practiced with 8 trials (4 without and 4 with TMS) excluded from the actual experiment. Stimuli were presented using the *Presentation* software (Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com) on an EIZO 19" LCD monitor positioned ~1–1.5 m in front of the participant.

2.3. Stimuli

We used an extended stimulus set of our previous fMRI study (Kuhnke et al., 2020). 208 written German nouns denoting concrete objects, which exhibited a high or low association with sounds and actions, yielded four categories of 52 words each: 1) high sound–high action, 2) high sound–low action, 3) low sound–high action, and 4) low sound–low action (see Fig. 1 for examples). To prevent learning effects, different words were used in the two TMS sessions. Thus, the stimulus set was split into two lists of 104 words; list-to-session assignment was counterbalanced across subjects.

163 volunteers who did not participate in the TMS study rated an initial set of 891 words for their association with sounds, actions, and visual features, as well as their familiarity on a 1-to-6 scale (for a similar procedure, see Fernandino et al., 2016a; Kiefer et al., 2008). We selected 52 words for each category such that within and across lists, high and low sound words differed selectively in their sound ratings ($p < 0.001$), whereas high and low action words differed only in their action ratings ($p < 0.001$). Categories were matched on all other rating criteria, as well as on number of letters and syllables, word frequency, bi- and trigram frequencies, and number of orthographic neighbors (see Tables S3-S6). Stimuli for all word categories were selected from the same superordinate categories of animals, inanimate natural entities, and man-made objects (Goldberg et al., 2006; Kiefer et al., 2008). For the lexical decision task, a pseudoword was generated for each word matched in length, syllable structure, and transition frequencies between subsyllabic elements using the *Wuggy* software (http://crr.ugent.be/Wuggy; Keuleers and Brysbaert, 2010).

2.4. Transcranial magnetic stimulation

To investigate the causal role of left pIPL in conceptual processing, we applied short trains of 10 Hz rTMS *during* different tasks ("online"). The main advantage of online rTMS over the application before a task ("offline") is the more precise timing of the interference that allows for measuring its acute and transient consequences (Siebner et al., 2009). Whereas common offline rTMS protocols can induce adaptive changes in brain activity and connectivity that may outlast the stimulation period for up to 30–50 min depending on the particular protocol (Siebner and Rothwell, 2003; Wischnewski and Schutter, 2015), the effects of brief online rTMS bursts are too short-lasting to elicit adaptive reorganization (Bergmann et al., 2016; Hartwigsen et al., 2015; Rotenberg et al., 2014). Therefore, we are confident that online rTMS allows us to assess the functional relevance of left pIPL in conceptual tasks, unconfounded by reorganization processes.

We used stereotactic neuronavigation (TMS Navigator, Localite GmbH, Sankt Augustin, Germany) to precisely navigate the coil over the target area and maintain its location and orientation throughout the experiment. To this end, the participant's head was co-registered onto their T1-weighted MR image at the beginning of each session. T1 scans were obtained beforehand with a 3T MRI scanner (Siemens, Erlangen, Germany) using an MPRAGE sequence (176 slices in sagittal orientation; repetition time: 2.3 s; echo time: 2.98 ms; field of view: 256 mm; voxel size: 1 x 1 × 1 mm; no slice gap; flip angle: 9°; phase encoding direction: A/P).

MNI coordinates for the left pIPL target (44 –60 50 mm) corresponded to the group activation peak for both action and sound feature retrieval (conjunction of [action judgment: high > low action words] ∩ [sound judgment: high > low sound words]) in our previous fMRI study which employed the same paradigm (Kuhnke et al., 2020). To precisely target these coordinates in each individual participant, they were transformed from MNI to subject space using the *SPM12* software (Wellcome Trust Center for Neuroimaging, University College London, UK) (cf. Hartwigsen et al., 2016; Kuhnke et al., 2017). The vertex was determined manually as the midpoint between the lines connecting nasion to inion and the tragi of left to right ear (Klaus and Hartwigsen, 2019). Vertex was used for sham stimulation to increase participant blinding, that is, participants were told that any differences in sensations between TMS sessions were due to a different location of the TMS coil on the head.

Biphasic rTMS bursts were applied via a MagPro X100 stimulator (MagVenture, Farum, Denmark) equipped with a passively cooled MCF-B65 figure-of-eight coil. For sham stimulation, we employed the corresponding placebo coil (MCF-P-B65), which features the same mechanical outline and acoustic noise as the effective coil, but reduces the magnetic field strength by ~80%.

For effective rTMS over left pIPL, the coil was oriented perpendicular to the target gyrus (using the brain segmentation and rendering tools of the neuronavigation software) to maximize the strength of the induced electrical field (Opitz et al., 2011; Thielscher et al., 2011). Stimulation intensity was set to 100% of individual resting motor threshold (RMT), which corresponded to 49.5 ± 9.3% (mean ± SD) of maximum stimulator output (where 100% = 144 A/μs). RMT was determined before the first experimental session as the lowest stimulation intensity producing at least 5 motor evoked potentials of ≥50 μV in the relaxed first dorsal interosseus muscle of the right hand when single-pulse TMS was applied over the hand region of left primary motor cortex 10 times.

2.5. Analysis

Response times (RTs) for correct trials and response accuracies (% correct responses) were analyzed. To factor out any differences between conditions unrelated to effective rTMS, the data for pIPL-rTMS were normalized to sham stimulation. That is, differences in response accuracy or RT were calculated between each condition under pIPL-rTMS and their sham equivalents (cf. Devlin et al., 2003; Kuhnke et al., 2017; Vukovic et al., 2017).

Statistical inference was then performed using 3-way repeated-measures ANOVAs on sham-normalized accuracies and RTs with the factors TASK (lexical decision, sound judgment, action judgment), SOUND (high, low association), and ACTION (high, low association). We report p-values corrected for non-sphericity using the Huynh-Feldt method. Significant interactions were resolved using step-down analyses and Bonferroni-Holm corrected post-hoc comparisons on estimated marginal means.

We ran several control analyses to ensure that our results were not confounded by TMS-unrelated variables. To test for potential session order effects, we performed a mixed ANOVA (Huynh-Feldt corrected) with the same within-subject factors and an additional between-subject factor ORDER (sham first, pIPL-rTMS first). Moreover, Shapiro-Wilk tests indicated for some conditions that sham-normalized accuracies were not normally distributed ($p < 0.05$). Importantly, however, repeated-measures ANOVAs are known to be robust against violations of the normality assumption (Blanca et al., 2017; Salkind, 2010; Schmider et al., 2010). Nevertheless, to ensure that our results were not driven by violations of distributional assumptions, we also conducted non-parametric Wilcoxon signed rank tests.

Since null hypothesis significance testing cannot provide evidence for null effects, we performed a complementary Bayesian analysis using the *JASP* program (https://jasp-stats.org/; Wagenmakers et al., 2018). For each experimental condition, Bayesian comparisons tested whether the data were better predicted by the null hypothesis (i.e. performance does not differ between pIPL-rTMS and sham stimulation) or alternative hypothesis (i.e. performance differs between pIPL-rTMS and sham). We used the default prior distribution in JASP, a two-sided Cauchy$(0, \frac{1}{2}\sqrt{2})$ distribution. BF_{10} denotes the Bayes Factor in favor of the alternative hypothesis, whereas BF_{01} refers to the Bayes Factor in favor of the null hypothesis ($BF_{01} = 1/BF_{10}$). For example, $BF_{10} = 3$ means that the data were 3 times more likely under the alternative hypothesis than under the null hypothesis (Lakens et al., 2020).

2.6. *Electrical field simulations*

To characterize the location, extent and strength of the electrical field induced by rTMS over left pIPL in each individual subject, we performed electrical field simulations using SimNIBS v3.1 with high-resolution isotropic finite element models (FEMs; Saturnino et al., 2019; Thielscher et al., 2015). Individual head models were generated from T1-weighted MR images using the mri2mesh pipeline described in Nielsen et al. (2018), employing FreeSurfer (http://surfer.nmr.mgh.harvard.edu/; Dale et al., 1999; Fischl et al., 1999) and FSL (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL; Jenkinson et al., 2012; Smith et al., 2004). The head models were composed of $\sim 2.3 \times 10^6$ nodes and $\sim 13 \times 10^6$ tetrahedra. T1 images were used for segmenting the main tissues of the head: scalp, skull, grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF). Instrument markers recorded by the neuronavigation software during the experiment were used to define the individual position and orientation of the coil (Weise et al., 2020). The electrical field was calculated for 1 A/μs and scaled with the respective stimulator intensity. We used the following isotropic conductivity values: $\sigma_{Scalp} = 0.465$ S/m, $\sigma_{Skull} = 0.01$ S/m, $\sigma_{GM} = 0.275$ S/m, $\sigma_{WM} = 0.126$ S/m, $\sigma_{CSF} = 1.654$ S/m (Thielscher et al., 2011; Wagner et al., 2004). The quality of the head reconstructions and electrical field simulations was checked visually (see Figures S3 and S4). Each subject's electrical field was mapped to the fsaverage and MNI spaces for group analyses.

We extracted the average electrical field strengths from maximum probability maps of anatomical regions-of-interest in the SPM Anatomy toolbox version 2.2c (Eickhoff et al., 2005, 2006) to provide descriptive statistics of the electrical field distribution (Table 2). For visualization on the group-average electrical field image, these regions were transformed from MNI to fsaverage space (Wu et al., 2018).

To test for a potential relationship between behavioral impairments and stimulation intensity in left pIPL, we correlated the individual behavioral effect of pIPL-rTMS (accuracy change for action judgments on low sound–low action words; see Results section) with the individual mean electrical field strength in the left pIPL region engaged for action feature retrieval (Action judgment: high > low action words) in our previous fMRI study (Kuhnke et al., 2020). To determine whether this relationship was specific to action knowledge retrieval, we also correlated the electrical field strength in the same region with the accuracy change for sound judgments on the same words. Finally, to test whether the relationship between electrical field strength and action judgment performance was anatomically specific to left pIPL, we performed the same correlation in left SPL 7PC—the region outside left pIPL that received the strongest stimulation (see Table 2). Bayesian statistics again tested for evidence in favor of the null or alternative hypothesis. We used a completely uninformed prior distribution.

3. Results

3.1. *rTMS over left pIPL selectively increased errors on action judgments*

A repeated-measures ANOVA on sham-normalized response accuracies revealed a significant TASK x SOUND x ACTION interaction ($F_{2,50} = 3.877$, $p = 0.038$, partial-$\eta^2 = 0.134$). Step-down analyses by TASK revealed that this effect was driven by a SOUND x ACTION interaction in the action judgment task ($F_{1,25} = 5.768$, $p = 0.024$, partial-$\eta^2 = 0.187$), whereas no significant effects were present in the lexical decision task (SOUND: $F_{1,25} = 1.435$, $p = 0.24$; ACTION: $F_{1,25} < 0.01$, $p = 1$; SOUND x ACTION: $F_{1,25} = 0.103$, $p = 0.75$), or in the sound judgment task (SOUND: $F_{1,25} = 0.358$, $p = 0.56$; ACTION: $F_{1,25} = 0.624$, $p = 0.44$; SOUND x ACTION: $F_{1,25} = 1.5$, $p = 0.23$).

Post-hoc comparisons showed that rTMS over left pIPL selectively impaired response accuracies for action judgments on low sound–low action words, as compared to sham stimulation (Fig. 2; $t_{287} = -3.582$, $p = 0.002$, Cohen's-*d* = 0.625). pIPL-rTMS did not significantly affect action judgments on the other word types (high sound–high action: $t_{287} = -0.39$, $p = 0.7$; high sound–low action: $t_{287} = -0.231$, $p = 0.82$), albeit low sound–high action words showed a trend towards facilitation ($t_{287} = 1.862$, $p = 0.064$, Cohen's-*d* = 0.366). The impairment of low sound–low action words was greater than that of low sound–high action words ($t_{141} = -3.582$, $p < 0.001$, Cohen's-*d* = 0.991) and high sound–low action words ($t_{140} = -2.242$, $p = 0.027$, Cohen's-*d* = 0.579, does not survive correction). Crucially, low sound–low action words were selectively disrupted during action judgments: pIPL-rTMS did not significantly alter lexical decisions ($t_{287} = 0.155$, $p = 0.88$) or sound judgments ($t_{287} = 0.621$, $p = 0.54$) on the same words, and the performance decline (pIPL vs. sham) was significantly greater during action judgments than during lexical decisions ($t_{196} = 2.366$, $p = 0.019$, Cohen's-*d* = 0.656) and sound judgments ($t_{196} = 2.697$, $p = 0.008$, Cohen's-*d* = 0.747).

A control analysis showed that our results were not confounded by session order effects (Table S1). Importantly, this analysis corroborated our previous results: The TASK x SOUND x ACTION interaction remained significant ($F_{2,48} = 3.811$, $p = 0.04$, partial-$\eta^2 = 0.137$) with no other significant effects. Furthermore, to exclude that our results were driven by violations of distributional assumptions (e.g. normality), we conducted non-parametric Wilcoxon signed rank tests. These tests confirmed that pIPL-rTMS significantly disrupted action judgments on low sound–low action words ($p = 0.018$) and no other conditions ($p > 0.2$).

As null hypothesis significance testing cannot provide evidence for the absence of an effect, we performed a complementary Bayesian analysis. This analysis confirmed that pIPL-rTMS impaired action judgments on low sound–low action words, and crucially provided evidence for a null effect of pIPL-rTMS on all other conditions. For action judgments on low sound–low action words, the data were ~3 times more likely under the alternative hypothesis that pIPL-rTMS affected performance than under the null hypothesis of no TMS effect ($BF_{10} = 3.054$). In contrast, for all other conditions, the data were ~3–4 times more likely under the null hypothesis (Table 1).

3.2. *pIPL-rTMS did not alter response times (RTs)*

A repeated-measures ANOVA on sham-normalized RTs revealed no significant effects (Figure S2; TASK: $F_{2,50} = 0.98$, $p = 0.37$; SOUND: $F_{1,25} = 1.66$, $p = 0.21$; ACTION: $F_{1,25} = 3.312$, $p = 0.08$; TASK x SOUND: $F_{2,50} = 2.355$, $p = 0.12$; TASK x ACTION: $F_{2,50} = 0.284$, $p = 0.68$; SOUND x ACTION: $F_{1,25} = 0.408$, $p = 0.53$; TASK x SOUND x ACTION: $F_{2,50} = 1.882$, $p = 0.17$). Corroborating this result, Bayesian statistics provided evidence in favor of a null effect of pIPL-rTMS for all experimental conditions (Table S2).

3.3. *Localizing the TMS effect using electrical field simulations*

To better characterize the relationship between the behavioral effects

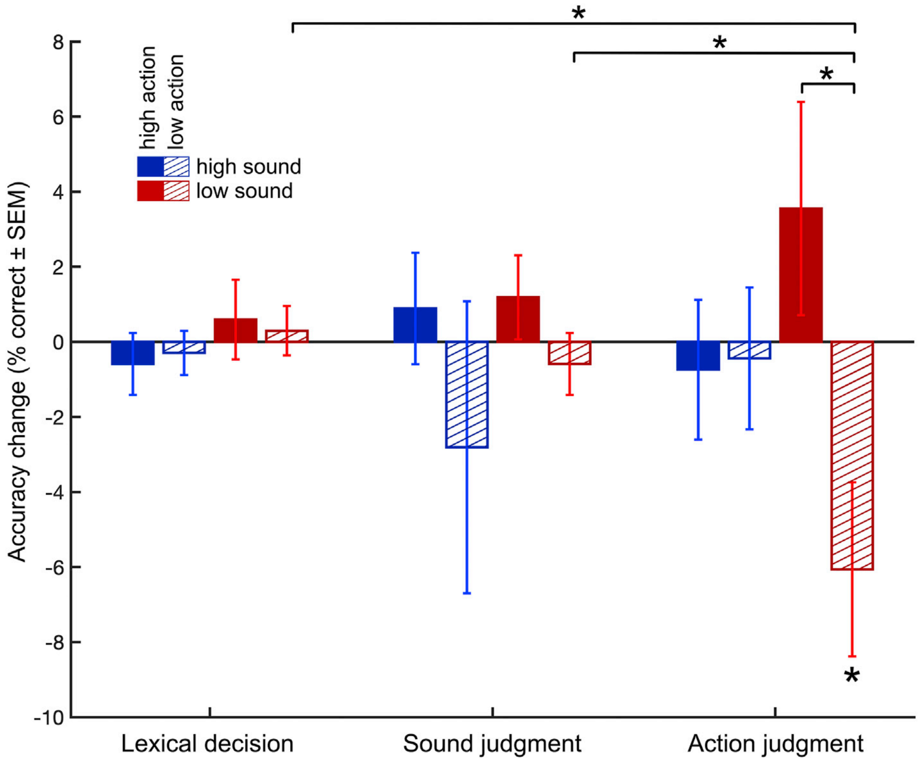


Fig. 2. rTMS over left pIPL selectively impaired response accuracy for action judgments on low sound–low action words. Change in response accuracy for pIPL-rTMS vs. sham stimulation. Error bars represent standard error of the mean (SEM). *: $p < 0.05$ (Bonferroni-Holm corrected).

Table 1
Results of the Bayesian analysis on sham-normalized accuracies.

	Mean	95% credible interval	BF_{10}	BF_{01}
L: high SF, high AF	−0.592	[–2.332, 1.149]	0.259	**3.859**
L: high SF, low AF	−0.296	[–1.533, 0.941]	0.232	**4.318**
L: low SF, high AF	0.592	[–1.635, 2.819]	0.238	**4.208**
L: low SF, low AF	0.296	[–1.088, 1.680]	0.226	**4.416**
S: high SF, high AF	0.888	[–2.229, 4.004]	0.243	**4.123**
S: high SF, low AF	−2.811	[–10.979, 5.357]	0.261	**3.838**
S: low SF, high AF	0.148	[–0.971, 1.267]	0.214	**4.664**
S: low SF, low AF	1.183	[–1.173, 3.540]	0.336	**2.979**
A: high SF, high AF	−0.740	[–4.646, 3.166]	0.222	**4.501**
A: high SF, low AF	−0.444	[–4.406, 3.519]	0.212	**4.709**
A: low SF, high AF	3.550	[–2.425, 9.525]	0.405	**2.470**
A: low SF, low AF	−6.065	[–10.942, –1.189]	**3.054**	0.327

L: lexical decision; S: sound judgment; A: action judgment; SF: sound feature; AF: action feature; BF_{10}: Bayes Factor for the alternative hypothesis; BF_{01}: Bayes Factor for the null hypothesis (where $BF_{01} = 1/BF_{10}$). Bold font highlights evidence in favor of one hypothesis over the other.

and the effectively stimulated region in left pIPL, we performed computational simulations of the electrical field induced by pIPL-rTMS in each individual subject. Importantly, we used the actual position and orientation of the coil recorded during the experiment for these simulations to maintain individual specificity.

Fig. 3 shows the average (A) and standard deviation (B) of the electrical field magnitude across subjects, and Table 2 lists the average electrical field strengths in anatomical regions-of-interest. As expected, the left posterior IPL (anatomical regions PFm and PGa) was stimulated with the highest intensity (~50 V/m at peak). However, surrounding areas were also stimulated with relatively high intensities (20–40 V/m). These regions included parts of left anterior IPL (e.g. region PFt) and intraparietal sulcus (IPS; areas hIP1-3), somatosensory cortex (especially area 1), and the superior parietal lobe (SPL; particularly areas 7PC, 7A).

3.4. *Stronger stimulation of left pIPL specifically predicted worse action judgment performance*

We reasoned that if left pIPL is indeed causally relevant for action knowledge retrieval, subjects whose action-related pIPL region was stimulated more strongly should show worse performance on action judgments. To test this, we correlated the individual behavioral effect of pIPL-rTMS (i.e. the accuracy change for action judgments on low sound–low action words, as compared to sham stimulation) with the electrical field strength in the left pIPL region that was activated for action knowledge retrieval in our previous fMRI study (Fig. 3C). Indeed, the electrical field strength in the action-related pIPL area was negatively correlated with the individual accuracy change (Fig. 3D; $r = -0.46$, $p = 0.018$, $BF_{10} = 3.461$), supporting the hypothesized association between higher electrical field strengths and larger individual impairments of action judgments. In contrast, the electrical field strength was not associated with behavioral performance for sound judgments on the same words (Figure S5; $r = 0.08$, $p = 0.71$, $BF_{10} = 0.260$), indicating that left pIPL is specialized for action knowledge retrieval. Moreover, left SPL 7PC—the region outside left pIPL that received the strongest stimulation—did not show a significant relationship between electrical field strength and action judgment performance (Figure S6; $r = -0.15$, $p = 0.46$, $BF_{10} = 0.344$). This suggests that the behavior–electrical field relationship was anatomically specific to left pIPL. Note that the region-of-interest in left pIPL was selected based on the results of our fMRI study with a completely different group of subjects, and was thus unbiased with respect to the current data.

3.5. *Errors caused by pIPL-rTMS were associated with a typical RT*

To further elucidate the nature of the behavioral impairment caused by rTMS over left pIPL, we analyzed the response times (RTs) for errors during action judgments on low sound–low action words. As compared to sham stimulation, pIPL-rTMS predominantly increased errors with a “typical” RT, close to the individual mean ($t_{25} = 2.628$, $p = 0.01$,

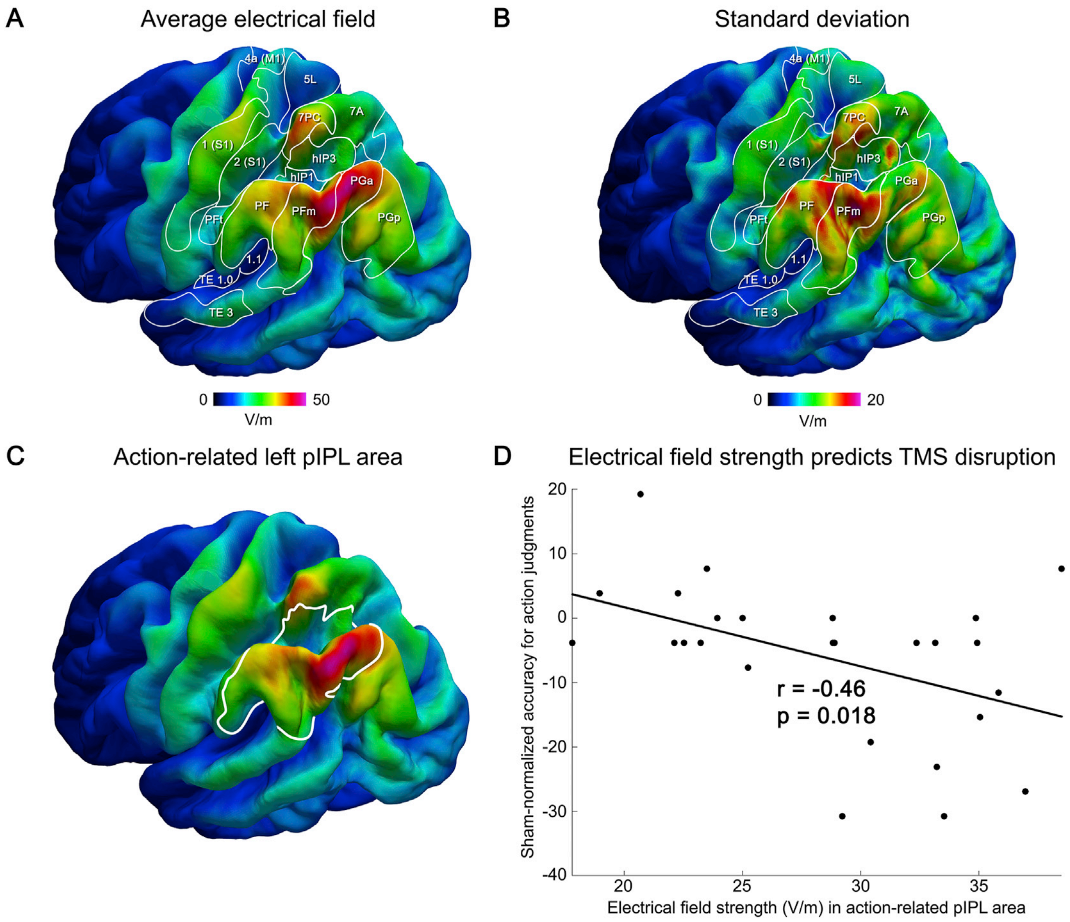


Fig. 3. Results of electrical field simulations. (A) The average strength of the induced electrical field across subjects is displayed on the normalized cortical surface (fsaverage). Anatomical regions from the SPM Anatomy toolbox (Eickhoff et al., 2005, 2006) are outlined in white. (B) The standard deviation of the electrical field strength across subjects. (C) The action-related region-of-interest in left pIPL is outlined on the average electrical field image. (D) Correlation between the electrical field strength in action-related left pIPL and individual behavioral impairment of action judgments for low sound–low action words (i.e. accuracy change in % for pIPL-rTMS vs. sham stimulation).

Cohen's-$d = 0.515$; Fig. 4; Table 3). This indicates that subjects erroneously decided that a low sound–low action word was action-related in a normal period of time, and renders it highly unlikely that the TMS effect reflects a speed-accuracy tradeoff.

4. Discussion

This study tested the causal role of left pIPL as a multimodal convergence zone in conceptual processing. Specifically, we investigated the functional relevance of left pIPL for processing action and sound features of concepts. We found that rTMS over the left pIPL selectively increased errors for action judgments on low sound–low action words, as compared to sham stimulation. Electrical field simulations provided the first evidence that stronger stimulation of left pIPL is associated with worse performance on action but not sound judgments. These findings strongly suggest that left pIPL is causally relevant for processing action but not sound knowledge. Therefore, our results question the view that left pIPL acts as a multimodal conceptual hub.

Our data indicate that the causal involvement of left pIPL in conceptual processing strongly depends on the task. Low sound–low action words were selectively disrupted during action judgments, whereas the *same* words were not affected during lexical decisions or sound judgments. This suggests that left pIPL selectively supports conceptual processing when action knowledge is task-relevant. This result supports theories that assume conceptual processing to rely on a flexible, task-dependent architecture (Binder and Desai, 2011; Hoenig et al., 2008; Kemmerer, 2015; Popp et al., 2019). The neural representation of a concept is not a static, task-independent entity, but it is flexibly shaped to the requirements of the current context (Lebois et al., 2015; Yee and Thompson-Schill, 2016).

In addition to the task, the critical involvement of left pIPL also depends on the relevance of action and sound knowledge for word meaning. Considering action feature relevance, pIPL-TMS impaired low sound–*low* action words, but tended to facilitate the corresponding *high* action words. As a potential mechanism for these effects, we propose that rTMS increased action-related activity in left pIPL (Miniussi et al., 2013). In case of both word types, rTMS increased the likelihood to judge an object as action-related. In addition, errors caused by pIPL-rTMS were associated with a "typical" response time close to the individual mean. This indicates that participants made the intentional decision that a low-action word was action-related. These facts suggest that rTMS increased action-related activity in left pIPL, leading to a higher likelihood to judge an object as action-related, even if it was not.

Regarding sound feature relevance, pIPL-rTMS selectively affected low-sound, but not high-sound words, during action judgments. This finding might be explained via "action–sound coupling" mechanisms (Lemaitre et al., 2018). Actions often elicit typical sounds (e.g. hammering, guitar playing). Thus, in the case of high-sound words, participants might leverage the sound feature to support action judgments. Such action–sound coupling could provide some functional "degeneracy" (Price and Friston, 2002) to the neural representations of sound and action features, and robustness against disruption (e.g. by TMS

Table 2
Average electrical field strength (in V/m) in anatomical regions-of-interest.

Region	Mean e-field (SD)	Region	Mean e-field (SD)	Region	Mean e-field (SD)
Left IPL		**Left SPL**		**Left motor**	
PFt	21.73 (6.69)	7A	23.12 (7.37)	4a	11.79 (3.47)
PF	27.88 (8.16)	7PC	30.82 (8.34)	4p	13.17 (3.24)
PFm	31.84 (7.77)	7P	13.97 (4.50)		
PGa	31.52 (6.64)	7M	6.76 (2.74)	**Left auditory**	
PGp	29.38 (7.20)	5L	15.92 (6.69)	TE 1.0	7.08 (2.56)
PFop	18.18 (5.42)	5M	6.47 (2.52)	TE 1.1	4.87 (2.17)
PFcm	11.52 (4.41)	5Ci	7.39 (1.37)	TE 1.2	8.07 (2.09)
				TE 3	14.47 (3.76)
Left IPS		**Left somatosensory**			
hIP1	21.80 (5.30)				
hIP2	27.56 (7.10)	1	26.31 (5.75)		
hIP3	24.14 (5.31)	2	20.30 (4.80)		
		3a	12.82 (2.69)		
		3b	20.66 (4.79)		

To facilitate readability, the table is colored according to average field strength: <15 (dark blue), 15-20 (light blue), 20-25 (green), 25-30 (orange), >30 V/m (red). IPL = inferior parietal lobe; IPS = intraparietal sulcus; SPL = superior parietal lobe. Anatomical regions were derived from the SPM Anatomy toolbox v2.2c (Eickhoff et al., 2005, 2006).

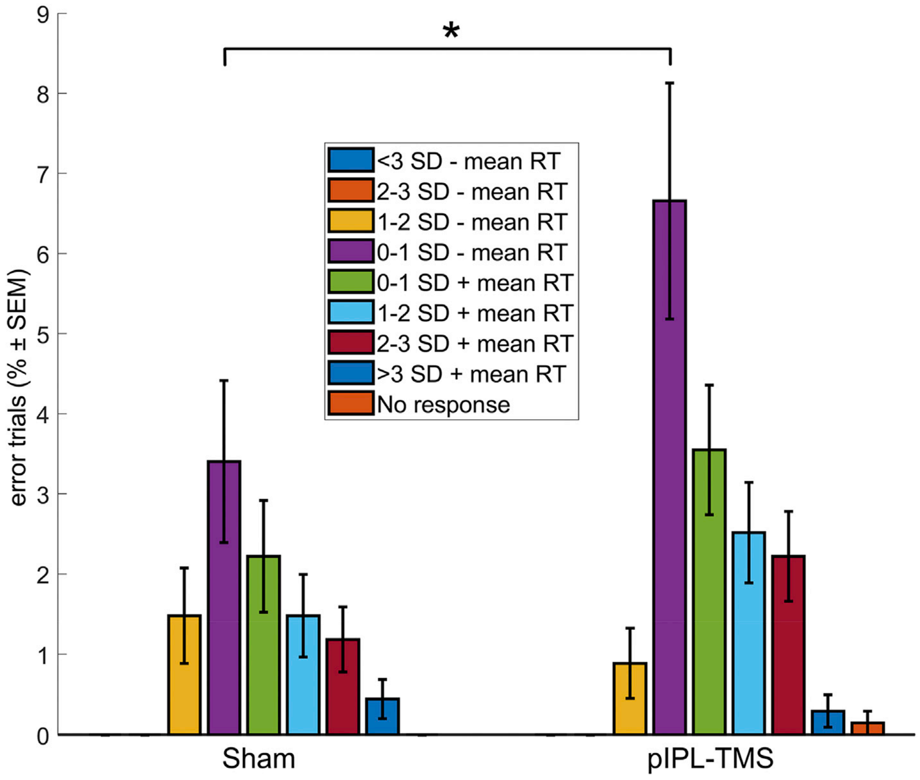


Fig. 4. Response times (RT) for errors during action judgments on low sound–low action words. Errors caused by pIPL-rTMS had a “typical” RT close to the individual mean (mean RT – 0–1 SD). Bars display mean percentage of trials with an error in a given RT bin. Error bars represent standard error of the mean (SEM). *: $p < 0.05$.

Table 3
Response times (RTs) for errors during action judgments on low sound–low action words.

RT bin	Sham (SEM)	pIPL-rTMS (SEM)	Difference (SEM)	t	p
Typical RT					
mean RT – 0–1 SD	3.40 (1.01)	6.66 (1.47)	3.26 (1.21)	2.628	**0.01**
mean RT + 0–1 SD	2.22 (0.70)	3.55 (0.81)	1.33 (0.69)	1.887	0.07
Fast RT					
< mean RT – 3 SD	0 (0)	0 (0)	0 (0)	0	1
mean RT – 2–3 SD	0 (0)	0 (0)	0 (0)	0	1
mean RT – 1–2 SD	1.48 (0.59)	0.89 (0.43)	−0.59 (0.54)	−1.072	0.29
Slow RT					
mean RT + 1–2 SD	1.48 (0.52)	2.51 (0.63)	1.03 (0.68)	1.494	0.15
mean RT + 2–3 SD	1.18 (0.41)	2.22 (0.56)	1.04 (0.71)	1.428	0.17
> mean RT + 3 SD	0.44 (0.24)	0.30 (0.20)	−0.14 (0.25)	−0.570	0.57
No response	0 (0)	0.15 (0.15)	0.15 (0.15)	1.0	0.33

or brain lesions). In contrast, low-sound words cannot employ action–sound coupling and are therefore vulnerable to disruptions of action feature representations.

In contrast to our hypotheses, pIPL-rTMS did not affect sound judgments. Note that this inference is based not merely on a non-significant result, but Bayesian statistics provided evidence for a null effect of pIPL-rTMS. This finding conflicts with our previous fMRI study that found task-dependent activation of left pIPL for both action and sound knowledge (Kuhnke et al., 2020). It also challenges the view that left pIPL represents a multimodal conceptual region (Binder and Desai, 2011; Fernandino et al., 2016). Indeed, one possible reason for the lacking disruption of sound judgments is that left pIPL is not causally relevant for processing sound knowledge. Sound-related activation in fMRI might be incidental to behavioral performance (Price and Friston, 2002). Alternatively, it is possible that left pIPL *is* functionally relevant for sound feature retrieval, but rTMS did not disrupt sound feature processing strongly enough to cause an observable behavioral impairment as it was stabilized by other sound-related regions. In line with this view, electrical field simulations indicated that pIPL-rTMS did not strongly affect other sound-related regions: Auditory areas (TE 1.0, 1.1, 1.2, 3), as well as prefrontal areas associated with sound-related conceptual processing (Fernandino et al., 2016; Kuhnke et al., 2020) were all stimulated at relatively low intensities (see Fig. 3; Table 2). Intact functioning of these regions may have compensated for the disruption of a single critical node. Such compensatory mechanisms could be further investigated in future studies employing combined TMS-fMRI (Hartwigsen, 2018).

In contrast, pIPL-rTMS might have affected nearby action-related regions, leading to a strong disruption of the action network as a whole. Electrical field simulations showed that pIPL-rTMS induced relatively high stimulation intensities not only in left pIPL itself, but also in surrounding areas such as left aIPL/IPS, SPL, and somatosensory cortex. All of these regions have previously been associated with action-related conceptual processing (Fernandino et al., 2016; Kuhnke et al., 2020). Thus, stimulation of surrounding action-related areas may have contributed to the observed behavioral impairment of action judgments. However, the electrical field strength within left pIPL (Fig. 3D), but not left SPL (Figure S6), correlated with the individual behavioral impairment on action judgments. This strongly suggests that left pIPL itself is crucial for action knowledge retrieval, and not only surrounding areas.

Note that we used a state-of-the-art computational pipeline for head reconstruction (Nielsen et al., 2018) and electrical field modeling (Saturnino et al., 2019; Thielscher et al., 2015). While electrical field modeling may include inaccuracies, it seems highly unlikely that they drove the correlation between electrical field strength and behavioral performance. Modeling errors are random and not systematically related to behavior. Moreover, the correlation was both task-specific to action (but not sound) judgments, and anatomically specific to left pIPL (and not SPL). Finally, we averaged electrical field strength over a large cortical area, which greatly reduces the influence of small errors. Therefore, we are confident that our results indicate that stronger stimulation of left pIPL is associated with worse performance for action knowledge.

Left IPL has previously been implicated in action knowledge retrieval. Meta-analyses of functional neuroimaging studies show consistent engagement of left IPL during action-related conceptual processing on words or pictures (Binder et al., 2009; Watson et al., 2013). However, as neuroimaging is correlational, these studies do not provide evidence for a behavioral relevance of left IPL for processing action knowledge. Two previous TMS studies provided evidence for a causal role of left IPL in action knowledge retrieval (Ishibashi et al., 2011; Pobric et al., 2010). In these studies, offline rTMS over left IPL impaired picture naming of manipulable but not non-manipulable objects (Pobric et al., 2010), and slowed matching of tool names by manipulation but not by function (Ishibashi et al., 2011). However, Pobric et al. exclusively varied the relevance of action knowledge for the concept, but not for the task, and vice versa in the study by Ishibashi et al. Therefore, neither study could assess potential interactions between task and feature relevance. Moreover, both studies only manipulated the relevance of action knowledge and no other modalities (e.g. sound). Thus, it remained unclear whether left IPL was indeed action-specific, or rather multimodal (i.e. sensitive to the relevance of multiple different conceptual features). Finally, in contrast to online rTMS, offline rTMS can lead to large-scale functional reorganization (Hartwigsen, 2018; Hartwigsen et al., 2017; Jung and Lambon Ralph, 2016). This renders it ambiguous whether the behavioral effects were indeed related to the stimulated area or other, distant nodes. To avoid these limitations, we applied online rTMS over left pIPL, while participants performed three different tasks on words that systematically varied in their association with both actions and sounds. We substantially extend the previous findings by showing that pIPL-rTMS interacts with task, action and sound knowledge: Left pIPL is necessary for conceptual processing selectively when action knowledge is task-relevant and cannot be compensated by sound knowledge via action–sound coupling.

Left IPL is not only implicated in action knowledge retrieval, but also in real motor action. Neuroimaging studies consistently find left IPL activation during action execution, imitation, observation, and imagery (Hardwick et al., 2018; Papitto et al., 2019). Neurons in the homologue region of the macaque monkey (area PF/PFG) code the behavioral intention of an action. For instance, Fogassi et al. (2005) found monkey IPL neurons to respond specifically when the monkey grasps a piece of food to eat it, but not to place it somewhere else, or vice versa. Ideomotor apraxia, a deficit in producing skilled object-directed movements (Culham and Valyear, 2006), is specifically associated with damage in and near left IPL (Buxbaum et al., 2005a, 2005b; Haaland et al., 2000). Ideomotor apraxics are impaired at performing and pantomiming the appropriate movements for object use, while retaining the ability to grasp objects based on their physical properties (Buxbaum et al., 2003). These facts suggest that left IPL represents the motor skills for object-directed actions (Culham and Valyear, 2006; Johnson-Frey, 2004; van Elk et al., 2014).

The common role of left IPL in both real motor action and action-related conceptual processing supports grounded theories of cognition, and conflicts with amodal theories. Amodal theories posit that concepts consist of abstract symbols represented outside perceptual-motor systems (Fodor, 1975; Pylyshyn, 1984). In contrast, grounded theories propose concept retrieval to involve a "simulation"—a partial reinstatement of activity in perceptual-motor brain areas during actual experience

(Barsalou, 2008; Kiefer and Pulvermüller, 2012; Pulvermüller, 1999). For instance, to retrieve action knowledge about guitars, neural activity in motor-related regions during guitar playing is partially reinstated (Sim et al., 2015). Together with previous evidence, our findings suggest that action knowledge retrieval involves a simulation of object-use motor skills in left IPL.

It is important to consider whether the behavioral effects of pIPL-rTMS were confounded by stimulation-unrelated factors. Unlike sham stimulation, effective TMS produces a somatosensory stimulus on the scalp that can be unpleasant, and the level of discomfort correlates with behavioral impairments (Holmes and Meteyard, 2018). This raises the concern that any effects of effective TMS could be related to unpleasantness and/or task difficulty. However, this is highly unlikely in the present study. Firstly, rTMS over left pIPL produces little to no discomfort (Meteyard and Holmes, 2018). Secondly, pIPL-rTMS was highly condition-specific and selectively disrupted action judgments on low sound–low action words. Crucially, this condition was not the most difficult (see Figures S1 and S2). In contrast, the most difficult condition (sound judgments on high sound–low action words) was not affected by pIPL-rTMS. Finally, pIPL-rTMS even tended to *improve* performance for action judgments on low sound–high action words. These facts render it highly unlikely that the behavioral effects of pIPL-rTMS were related to unpleasantness or task difficulty. Moreover, control analyses showed that our results were not confounded by session order effects or violations of distributional assumptions. Therefore, we are confident that the impairment of action judgments on low sound–low action words was caused by left pIPL stimulation, indicating a causal role of left pIPL in action knowledge retrieval.

As our study exclusively compared effective rTMS over left pIPL with ineffective sham stimulation, it remains unclear whether stimulation of other brain regions leads to similar, different, or no effects. In particular, future TMS studies should target potential sound-specific areas such as left posterior superior/middle temporal gyrus (Kiefer et al., 2008; Trumpp et al., 2013), and other potential multimodal convergence zones like medial prefrontal cortex (Binder, 2016; Fernandino et al., 2016; Kuhnke et al., 2020) to test for selective effects on sound knowledge retrieval or both sound and action knowledge retrieval, respectively. Moreover, “chronometric” TMS studies could systematically manipulate the stimulation timing to determine the precise timepoint(s) when a certain region causally contributes to conceptual tasks (Schuhmann et al., 2012; Stoeckel et al., 2009). For example, a recent chronometric TMS study showed that primary motor cortex is crucially involved in processing literal and metaphoric action sentences after 300 ms (Reilly et al., 2019).

5. Conclusions

In conclusion, our data strongly support a selective causal role of left pIPL in the processing of action knowledge. rTMS over left pIPL interfered with conceptual processing specifically when action knowledge was task-relevant and could not be compensated by sound knowledge. Electrical field simulations revealed that stronger stimulation of left pIPL led to worse performance on action judgments. To our knowledge, this study is the first that directly relates the electrical field induced by TMS to behavior in a cognitive task. We believe our novel approach could benefit future TMS studies of cognition since it provides much stronger evidence for a behavioral relevance of the stimulated cortical area than the classical testing for a group effect of TMS alone.

Declaration of competing interest

The authors declare no competing interests.

CRediT authorship contribution statement

Philipp Kuhnke: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Marie C. Beaupain:** Data curation, Investigation. **Vincent K.M. Cheung:** Data curation, Investigation, Formal analysis, Methodology, Writing - review & editing. **Konstantin Weise:** Formal analysis, Methodology, Writing - review & editing. **Markus Kiefer:** Conceptualization, Writing - review & editing. **Gesa Hartwigsen:** Conceptualization, Funding acquisition, Supervision, Project administration, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.117041.

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Data and code availability

Analysis code, raw and derived data are available via the Open Access Framework: https://osf.io/63vbr/?view_only=778ed65cdd4040f7a15bfb9829bd5517.

References

Barsalou, L.W., 2008. Grounded cognition. Annu. Rev. Psychol. 59, 617–645. https://doi.org/10.1146/annurev.psych.59.103006.093639.

Bergmann, T.O., Karabanov, A., Hartwigsen, G., Thielscher, A., Siebner, H.R., 2016. Combining non-invasive transcranial brain stimulation with neuroimaging and electrophysiology: current approaches and future perspectives. Neuroimage 140, 4–19. https://doi.org/10.1016/j.neuroimage.2016.02.012.

Binder, J.R., 2016. In defense of abstract conceptual representations. Psychon. Bull. Rev. 23, 1096–1108. https://doi.org/10.3758/s13423-015-0909-1.

Binder, J.R., Desai, R.H., 2011. The neurobiology of semantic memory. Trends Cognit. Sci. 15, 527–536. https://doi.org/10.1016/j.tics.2011.10.001.

Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.L., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cerebr. Cortex 19, 2767–2796. https://doi.org/10.1093/cercor/bhp055.

Blanca, M.J., Alarcón, R., Arnau, J., Bono, R., Bendayan, R., 2017. Non-normal data: is ANOVA still a valid option? Psicothema 29, 552–557. https://doi.org/10.7334/psicothema2016.383.

Buxbaum, L.J., Johnson-Frey, S.H., Bartlett-Williams, M., 2005a. Deficient internal models for planning hand-object interactions in apraxia. Neuropsychologia 43, 917–929. https://doi.org/10.1016/j.neuropsychologia.2004.09.006.

Buxbaum, L.J., Kyle, K.M., Menon, R., 2005b. On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. Cognit. Brain Res. 25, 226–239. https://doi.org/10.1016/j.cogbrainres.2005.05.014.

Buxbaum, L.J., Sirigu, A., Schwartz, M.F., Klatzky, R., 2003. Cognitive representations of hand posture in ideomotor apraxia. Neuropsychologia 41, 1091–1113. https://doi.org/10.1016/S0028-3932(02)00314-7.

Culham, J.C., Valyear, K.F., 2006. Human parietal cortex in action. Curr. Opin. Neurobiol. 16, 205–212. https://doi.org/10.1016/j.conb.2006.03.005.

Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis. Neuroimage 9, 179–194. https://doi.org/10.1006/nimg.1998.0395.

Damasio, A.R., 1989. The brain binds entities and events by multiregional activation from convergence zones. Neural Comput. 1, 123–132. https://doi.org/10.1162/neco.1989.1.1.123.

Devlin, J., Watkins, K., 2008. Investigating language organization with TMS. In: Wassermann, E.M., Epstein, C.M., Ziemann, U., Lisanby, S., Paus, T., Walsh, V. (Eds.), Oxford Handbook of Transcranial Stimulation. Oxford University Press, Oxford, pp. 479–499.

Devlin, J.T., Matthews, P.M., Rushworth, M.F.S., 2003. Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. J. Cognit. Neurosci. 15, 71–84. https://doi.org/10.1162/089892903321107837.

Eickhoff, S.B., Heim, S., Zilles, K., Amunts, K., 2006. Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. Neuroimage 32, 570–582. https://doi.org/10.1016/j.neuroimage.2006.04.204.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25, 1325–1335. https://doi.org/10.1016/j.neuroimage.2004.12.034.

Fernandino, L., Binder, J.R., Desai, R.H., Pendl, S.L., Humphries, C.J., Gross, W.L., Conant, L.L., Seidenberg, M.S., 2016. Concept representation reflects multimodal abstraction: a framework for embodied semantics. Cerebr. Cortex 26, 2018–2034. https://doi.org/10.1093/cercor/bhv020.

Fischl, B., Sereno, M.I., Dale, A.M., 1999. Cortical surface-based analysis. Neuroimage 9, 195–207. https://doi.org/10.1006/nimg.1998.0396.

Fodor, J.A., 1975. The Language of Thought. Harvard University Press, Cambridge, MA.

Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolotti, G., 2005. Parietal lobe: from action organization to intention understanding. Science 308, 662–667. https://doi.org/10.1126/science.1106138.

Goldberg, R.F., Perfetti, C.A., Schneider, W., 2006. Perceptual knowledge retrieval activates sensory brain regions. J. Neurosci. 26, 4917–4921. https://doi.org/10.1523/JNEUROSCI.5389-05.2006.

Haaland, K.Y., Harrington, D.L., Knight, R.T., 2000. Neural representations of skilled movement. Brain 123, 2306–2313. https://doi.org/10.1093/brain/123.11.2306.

Hardwick, R.M., Caspers, S., Eickhoff, S.B., Swinnen, S.P., 2018. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. Neurosci. Biobehav. Rev. 94, 31–44. https://doi.org/10.1016/j.neubiorev.2018.08.003.

Hartwigsen, G., 2018. Flexible redistribution in cognitive networks. Trends Cognit. Sci. 22, 687–698. https://doi.org/10.1016/j.tics.2018.05.008.

Hartwigsen, G., Bergmann, T.O., Herz, D.M., Angstmann, S., Karabanov, A., Raffin, E., Thielscher, A., Siebner, H.R., 2015. Modeling the effects of noninvasive transcranial brain stimulation at the biophysical, network, and cognitive Level. Prog. Brain Res. 222, 261–287. https://doi.org/10.1016/bs.pbr.2015.06.014.

Hartwigsen, G., Bzdok, D., Klein, M., Wawrzyniak, M., Stockert, A., Wrede, K., Classen, J., Saur, D., 2017. Rapid short-term reorganization in the language network. Elife 6, e25964. https://doi.org/10.7554/eLife.25964.001.

Hartwigsen, G., Weigel, A., Schuschan, P., Siebner, H.R., Weise, D., Classen, J., Saur, D., 2016. Dissociating parieto-frontal networks for phonological and semantic word decisions: a condition-and-perturb TMS study. Cerebr. Cortex 26, 2590–2601. https://doi.org/10.1093/cercor/bhv092.

Hauk, O., Tschentscher, N., 2013. The body of evidence: what can neuroscience tell us about embodied semantics? Front. Psychol. 4, 1–14. https://doi.org/10.3389/fpsyg.2013.00050.

Hoenig, K., Sim, E.-J., Bochev, V., Herrnberger, B., Kiefer, M., 2008. Conceptual flexibility in the human brain: dynamic recruitment of semantic maps from visual, motor, and motion-related areas. J. Cognit. Neurosci. 20, 1799–1814. https://doi.org/10.1162/jocn.2008.20123.

Holmes, N.P., Meteyard, L., 2018. Subjective discomfort of TMS predicts reaction times differences in published studies. Front. Psychol. 9, 1–4. https://doi.org/10.3389/fpsyg.2018.01989.

Ishibashi, R., Lambon Ralph, M.A., Saito, S., Pobric, G., 2011. Different roles of lateral anterior temporal lobe and inferior parietal lobule in coding function and manipulation tool knowledge: evidence from an rTMS study. Neuropsychologia 49, 1128–1135. https://doi.org/10.1016/j.neuropsychologia.2011.01.004.

Jenkinson, M., Beckmann, C.F., Behrens, T.E.J., Woolrich, M.W., Smith, S.M., 2012. FSL. Neuroimage 62, 782–790. https://doi.org/10.1016/j.neuroimage.2011.09.015.

Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. Trends Cognit. Sci. 8, 71–78. https://doi.org/10.1016/j.tics.2003.12.002.

Jung, J., Lambon Ralph, M.A., 2016. Mapping the dynamic network interactions underpinning cognition: a cTBS-fMRI study of the flexible adaptive neural system for semantics. Cerebr. Cortex 26, 3580–3590. https://doi.org/10.1093/cercor/bhw149.

Kemmerer, D., 2015. Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible, multilevel architecture for conceptual knowledge. Psychon. Bull. Rev. 22, 1068–1075. https://doi.org/10.3758/s13423-014-0784-1.

Keuleers, E., Brysbaert, M., 2010. Wuggy: a multilingual pseudoword generator. Behav. Res. Methods 42, 627–633. https://doi.org/10.3758/BRM.42.3.627.

Kiefer, M., Pulvermüller, F., 2012. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. Cortex 48, 805–825. https://doi.org/10.1016/j.cortex.2011.04.006.

Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., Hoenig, K., 2008. The sound of concepts: four markers for a link between auditory and conceptual brain systems. J. Neurosci. 28, 12224–12230. https://doi.org/10.1523/JNEUROSCI.3579-08.2008.

Kiers, L., Cros, D., Chiappa, K.H., Fang, J., 1993. Variability of motor potentials evoked by transcranial magnetic stimulation. Electroencephalogr. Clin. Neurophysiol. Potentials Sect. 89, 415–423. https://doi.org/10.1016/0168-5597(93)90115-6.

Klaus, J., Hartwigsen, G., 2019. Dissociating semantic and phonological contributions of the left inferior frontal gyrus to language production. Hum. Brain Mapp. 40, 3279–3287. https://doi.org/10.1002/hbm.24597.

Kuhnke, P., Kiefer, M., Hartwigsen, G., 2020. Task-dependent recruitment of modality-specific and multimodal regions during conceptual processing. Cereb. Cortex 30, 3938–3959. https://doi.org/10.1093/cercor/bhaa010.

Kuhnke, P., Meyer, L., Friederici, A.D., Hartwigsen, G., 2017. Left posterior inferior frontal gyrus is causally involved in reordering during sentence processing. Neuroimage 148, 254–263. https://doi.org/10.1016/j.neuroimage.2017.01.013.

Lakens, D., McLatchie, N., Isager, P.M., Scheel, A.M., Dienes, Z., 2020. Improving inferences about null effects with Bayes factors and equivalence tests. J. Gerontol. Ser. B 75, 45–57. https://doi.org/10.1093/geronb/gby065.

Lambon Ralph, M.A., 2014. Neurocognitive insights on conceptual knowledge and its breakdown. Philos. Trans. R. Soc. B Biol. Sci. 369, 20120392. https://doi.org/10.1098/rstb.2012.0392.

Lau, E.F., Phillips, C., Poeppel, D., 2008. A cortical network for semantics: (de)constructing the N400. Nat. Rev. Neurosci. 9, 920–933. https://doi.org/10.1038/nrn2532.

Lebois, L.A.M., Wilson-Mendenhall, C.D., Barsalou, L.W., 2015. Are automatic conceptual cores the gold standard of semantic processing? The context-dependence of spatial meaning in grounded congruency effects. Cognit. Sci. 39, 1764–1801. https://doi.org/10.1111/cogs.12174.

Lemaitre, G., Pyles, J.A., Halpern, A.R., Navolio, N., Lehet, M., Heller, L.M., 2018. Who's that knocking at my door? Neural bases of sound source identification. Cerebr. Cortex 28, 805–818. https://doi.org/10.1093/cercor/bhw397.

Margulies, D.S., Ghosh, S.S., Goulas, A., Falkiewicz, M., Huntenburg, J.M., Langs, G., Bezgin, G., Eickhoff, S.B., Castellanos, F.X., Petrides, M., Jefferies, E., Smallwood, J., 2016. Situating the default-mode network along a principal gradient of macroscale cortical organization. Proc. Natl. Acad. Sci. Unit. States Am. 113, 12574–12579. https://doi.org/10.1073/pnas.1608282113.

Mesulam, M.M., 1998. From sensation to cognition. Brain 121, 1013–1052. https://doi.org/10.1093/brain/121.6.1013.

Meteyard, L., Holmes, N.P., 2018. TMS SMART – scalp mapping of annoyance ratings and twitches caused by Transcranial Magnetic Stimulation. J. Neurosci. Methods 299, 34–44. https://doi.org/10.1016/j.jneumeth.2018.02.008.

Miniussi, C., Harris, J.A., Ruzzoli, M., 2013. Modelling non-invasive brain stimulation in cognitive neuroscience. Neurosci. Biobehav. Rev. 37, 1702–1712. https://doi.org/10.1016/j.neubiorev.2013.06.014.

Nielsen, J.D., Madsen, K.H., Puonti, O., Siebner, H.R., Bauer, C., Madsen, C.G., Saturnino, G.B., Thielscher, A., 2018. Automatic skull segmentation from MR images for realistic volume conductor models of the head: assessment of the state-of-the-art. Neuroimage 174, 587–598. https://doi.org/10.1016/j.neuroimage.2018.03.001.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.

Opitz, A., Windhoff, M., Heidemann, R.M., Turner, R., Thielscher, A., 2011. How the brain tissue shapes the electric field induced by transcranial magnetic stimulation. Neuroimage 58, 849–859. https://doi.org/10.1016/j.neuroimage.2011.06.069.

Papitto, G., Friederici, A.D., Zaccarella, E., 2019. The topographical organization of motor processing: an ALE meta-analysis on six action domains and the relevance of Broca's region. Neuroimage 116321. https://doi.org/10.1016/j.neuroimage.2019.116321.

Pascual-Leone, A., Walsh, V., Rothwell, J., 2000. Transcranial magnetic stimulation in cognitive neuroscience – virtual lesion, chronometry, and functional connectivity. Curr. Opin. Neurobiol. 10, 232–237. https://doi.org/10.1016/S0959-4388(00)00081-7.

Pobric, G., Jefferies, E., Lambon Ralph, M.A., 2010. Category-specific versus category-general semantic impairment induced by transcranial magnetic stimulation. Curr. Biol. 20, 964–968. https://doi.org/10.1016/j.cub.2010.03.070.

Popp, M., Trumpp, N.M., Kiefer, M., 2019. Processing of action and sound verbs in context: an FMRI study. Transl. Neurosci. 10, 200–222. https://doi.org/10.1515/tnsci-2019-0035.

Price, A.R., Bonner, M.F., Grossman, M., 2015. Semantic memory: cognitive and neuroanatomical perspectives. In: Brain Mapping. Elsevier, Amsterdam, pp. 529–536. https://doi.org/10.1016/B978-0-12-397025-1.00280-3.

Price, C.J., Friston, K.J., 2002. Degeneracy and cognitive anatomy. Trends Cognit. Sci. 6, 416–421. https://doi.org/10.1016/S1364-6613(02)01976-9.

Pulvermüller, F., 1999. Words in the brain's language. Behav. Brain Sci. 22, 253–279. https://doi.org/10.1017/S0140525X9900182X.

Pylyshyn, Z.W., 1984. Computation and Cognition: toward a Foundation for Cognitive Science, Psychological Review. The MIT Press. https://doi.org/10.1016/0004-3702(89)90062-3.

Reilly, M., Howerton, O., Desai, R.H., 2019. Time-Course of motor involvement in literal and metaphoric action sentence processing: a TMS study. Front. Psychol. 10, 1–11. https://doi.org/10.3389/fpsyg.2019.00371.

Rotenberg, A., Horvath, J.C., Pascual-Leone, A. (Eds.), 2014. Neuromethods: Transcranial Magnetic Stimulation. Springer, New York, NY. https://doi.org/10.1007/978-1-4939-0879-0.

Salkind, N.J., 2010. Encyclopedia of Research Design. Sage, Los Angeles.

Saturnino, G.B., Madsen, K.H., Thielscher, A., 2019. Electric field simulations for transcranial brain stimulation using FEM: an efficient implementation and error analysis. J. Neural. Eng. 16, 066032 https://doi.org/10.1088/1741-2552/ab41ba.

Schmider, E., Ziegler, M., Danay, E., Beyer, L., Bühner, M., 2010. Is it Really Robust?: reinvestigating the robustness of ANOVA against violations of the normal distribution assumption. Methodology 6, 147–151. https://doi.org/10.1027/1614-2241/a000016.

Schuhmann, T., Schiller, N.O., Goebel, R., Sack, A.T., 2012. Speaking of which: dissecting the neurocognitive network of language production in picture naming. Cerebr. Cortex 22, 701–709. https://doi.org/10.1093/cercor/bhr155.

Seghier, M.L., 2013. The angular gyrus: multiple functions and multiple subdivisions. Neuroscientist 19, 43–61. https://doi.org/10.1177/1073858412440596.

Siebner, H., Rothwell, J., 2003. Transcranial magnetic stimulation: new insights into representational cortical plasticity. Exp. Brain Res. 148, 1–16. https://doi.org/10.1007/s00221-002-1234-2.

Siebner, H.R., Hartwigsen, G., Kassuba, T., Rothwell, J.C., 2009. How does transcranial magnetic stimulation modify neuronal activity in the brain? Implications for studies of cognition. Cortex 45, 1035–1042. https://doi.org/10.1016/j.cortex.2009.02.007.

Sim, E.-J., Helbig, H.B., Graf, M., Kiefer, M., 2015. When action observation facilitates visual perception: activation in visuo-motor areas contributes to object recognition. Cerebr. Cortex 25, 2907–2918. https://doi.org/10.1093/cercor/bhu087.

Sliwinska, M.W., James, A., Devlin, J.T., 2015. Inferior parietal lobule contributions to visual word recognition. J. Cognit. Neurosci. 27, 593–604. https://doi.org/10.1162/jocn_a_00721.

Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E.J., Johansen-Berg, H., Bannister, P.R., De Luca, M., Drobnjak, I., Flitney, D.E., Niazy, R.K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J.M., Matthews, P.M., 2004. Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage 23, S208–S219. https://doi.org/10.1016/j.neuroimage.2004.07.051.

Stoeckel, C., Gough, P.M., Watkins, K.E., Devlin, J.T., 2009. Supramarginal gyrus involvement in visual word recognition. Cortex 45, 1091–1096. https://doi.org/10.1016/j.cortex.2008.12.004.

Thielscher, A., Antunes, A., Saturnino, G.B., 2015. Field modeling for transcranial magnetic stimulation: a useful tool to understand the physiological effects of TMS?. In: 2015 37th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC), pp. 222–225. https://doi.org/10.1109/EMBC.2015.7318340. IEEE.

Thielscher, A., Opitz, A., Windhoff, M., 2011. Impact of the gyral geometry on the electric field induced by transcranial magnetic stimulation. Neuroimage 54, 234–243. https://doi.org/10.1016/j.neuroimage.2010.07.061.

Trumpp, N.M., Kliese, D., Hoenig, K., Haarmeier, T., Kiefer, M., 2013. Losing the sound of concepts: damage to auditory association cortex impairs the processing of sound-related concepts. Cortex 49, 474–486. https://doi.org/10.1016/j.cortex.2012.02.002.

van Elk, M., van Schie, H., Bekkering, H., 2014. Action semantics: a unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. Phys. Life Rev. 11, 220–250. https://doi.org/10.1016/j.plrev.2013.11.005.

Vukovic, N., Feurra, M., Shpektor, A., Myachykov, A., Shtyrov, Y., 2017. Primary motor cortex functionally contributes to language comprehension: an online rTMS study. Neuropsychologia 96, 222–229. https://doi.org/10.1016/j.neuropsychologia.2017.01.025.

Wagenmakers, E.J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Selker, R., Gronau, Q.F., Dropmann, D., Boutin, B., Meerhoff, F., Knight, P., Raj, A., van Kesteren, E.J., van Doorn, J., Šmíra, M., Epskamp, S., Etz, A., Matzke, D., de Jong, T., van den Bergh, D., Sarafoglou, A., Steingroever, H., Derks, K., Rouder, J.N., Morey, R.D., 2018. Bayesian inference for psychology. Part II: example applications with JASP. Psychon. Bull. Rev. 25, 58–76. https://doi.org/10.3758/s13423-017-1323-7.

Wagner, T.A., Zahn, M., Grodzinsky, A.J., Pascual-Leone, A., 2004. Three-dimensional head model simulation of transcranial magnetic stimulation. IEEE Trans. Biomed. Eng. 51, 1586–1598. https://doi.org/10.1109/TBME.2004.827925.

Walsh, V., Cowey, A., 2000. Transcranial magnetic stimulation and cognitive neuroscience. Nat. Rev. Neurosci. 1, 73–80. https://doi.org/10.1038/35036239.

Watson, C.E., Cardillo, E.R., Ianni, G.R., Chatterjee, A., 2013. Action concepts in the brain: an activation likelihood estimation meta-analysis. J. Cognit. Neurosci. 25, 1191–1205. https://doi.org/10.1162/jocn_a_00401.

Weise, K., Numssen, O., Thielscher, A., Hartwigsen, G., Knösche, T.R., 2020. A novel approach to localize cortical TMS effects. Neuroimage 209, 116486. https://doi.org/10.1016/j.neuroimage.2019.116486.

Wischnewski, M., Schutter, D.J.L.G., 2015. Efficacy and time course of theta burst stimulation in healthy humans. Brain Stimul 8, 685–692. https://doi.org/10.1016/j.brs.2015.03.004.

Wu, J., Ngo, G.H., Greve, D., Li, J., He, T., Fischl, B., Eickhoff, S.B., Yeo, B.T.T., 2018. Accurate nonlinear mapping between MNI volumetric and FreeSurfer surface coordinate systems. Hum. Brain Mapp. 39, 3793–3808. https://doi.org/10.1002/hbm.24213.

Yee, E., Thompson-Schill, S.L., 2016. Putting concepts into context. Psychon. Bull. Rev. 23, 1015–1027. https://doi.org/10.3758/s13423-015-0948-7.

5. GENERAL DISCUSSION

5.1 Summary of main results and implications

This thesis aimed to advance our knowledge of the neural basis of conceptual knowledge retrieval. Using functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) in the healthy human brain, we addressed the following key issues:
(1) task dependency of conceptual feature retrieval,
(2) functional interaction between modality-specific and multimodal areas, and
(3) causal relevance of the left posterior parietal cortex (PPC) as a multimodal hub.

Study 1—an fMRI activation study—tested to what extent the retrieval of sound and action features of concepts, and the resulting engagement of auditory and somatomotor brain regions depend on the concurrent task (Kuhnke et al., 2020b). 40 participants performed three different tasks—lexical decision, sound judgment, and action judgment—on words that systematically varied in their association to sounds and actions. We found that the retrieval of action and sound features, and recruitment of modality-specific brain regions strongly depended on the task: Somatomotor-related regions (also engaged during real hand movements) selectively responded to action features of concepts (high > low action words) during action judgments, i.e. when action features were task-relevant. Auditory-related regions (also activated during real sound perception) were specifically engaged for sound features (high > low sound words) during sound judgments, i.e. when sound features were task-relevant. Surprisingly, several regions (including left PPC) were recruited for both sound and action features when they were task-relevant, responding to sound features during sound judgments and to action features during action judgments. We therefore propose these regions to be "multimodal", and not "amodal", convergence zones which retain modality-specific information. In contrast, the ATL seems to be amodal (i.e. insensitive to modality-specific information) as it responded to general conceptual information (words > pseudowords; see Figure S2.2) but not to modality-specific features (high > low action / sound words).

Based on these findings, we formulated a new hybrid model of the conceptual system. According to this model (Figure 5.1), conceptual processing relies on a representational hierarchy from modality-specific perceptual-motor regions to multimodal convergence zones (e.g. left PPC) up to an amodal hub in the ATL. Initial modality-specific representations converge onto increasingly abstract representations, until they become completely amodal at the highest level. This model represents a synthesis between our empirical results and previous models (Binder and Desai, 2011; Fernandino et al., 2016a; Lambon Ralph et al., 2016). The distinction between multimodal and amodal areas within the same model constitutes a significant novel contribution of our work to the literature. Crucially, this hierarchical system is assumed to be flexible (Binder and Desai, 2011; Hoenig et al., 2008; Kemmerer, 2015): Regions representing a certain conceptual feature are selectively engaged when that feature is task-relevant. Notably, our model is largely based on data for concrete concepts (e.g. objects, actions), and future research should determine to what extent this framework can be generalized to more abstract concepts (Barsalou, 2016; Kiefer and Harpaintner, 2020).

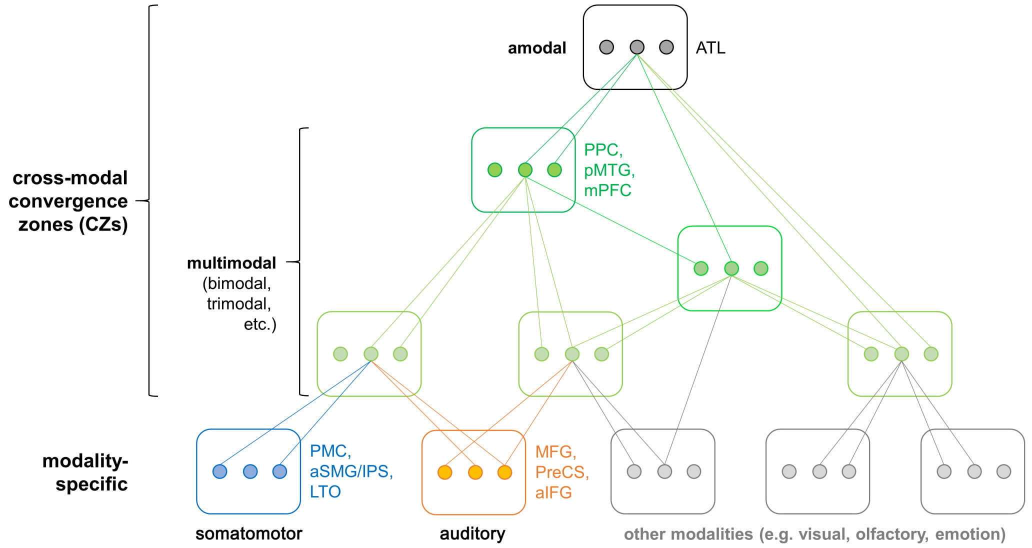

Fig. 5.1: (Adapted with permission from Kuhnke et al., 2020b.) Our model of the neural architecture underlying conceptual representation, based on the results of study 1 and previous models (Binder and Desai, 2011; Fernandino et al., 2016a; Lambon Ralph et al., 2016). *Modality-specific* representations are integrated into increasingly abstract representations via multiple levels of cross-modal convergence zones. Cross-modal convergence zones can be subdivided into *multimodal* regions that retain modality-specific information, and *amodal* regions that do not. Boxes represent brain regions and dots represent individual representational units that converge onto a more abstract representation at a higher level.

While study 1 revealed a task-dependent engagement of both modality-specific and multimodal regions in conceptual knowledge retrieval, it remained open whether and how modality-specific and multimodal areas *interact* during conceptual tasks. **Study 2**—an fMRI connectivity study—investigated the functional interaction between modality-specific and multimodal nodes during conceptual processing (Kuhnke et al., 2021). Specifically, we asked (1) whether modality-specific and multimodal regions are functionally coupled during conceptual feature retrieval, (2) whether their coupling depends on the task, (3) whether information flows bottom-up, top-down, or both, and (4) whether their coupling is relevant for behavior. In a two-stage analysis approach, we combined whole-brain psychophysiological interaction (PPI) analyses with dynamic causal modeling (DCM). We found that functional coupling between modality-specific and multimodal areas strongly depended on the task: Selectively during action judgments, action feature retrieval (high > low action words) increased coupling between the multimodal region in left PPC and left primary motor/somatosensory cortex (M1/S1). Conversely, selectively during sound judgments, sound feature retrieval (high > low sound words) involved increased coupling between multimodal PPC and left auditory association cortex (AAC). DCM analyses revealed both top-down and bottom-up information flow between multimodal and modality-specific nodes: Multimodal PPC was bidirectionally coupled with left AAC and sound knowledge modulated both the top-down and bottom-up connections. In contrast, left M1/S1 was unidirectionally connected to multimodal PPC and action knowledge specifically modulated this bottom-up connection.

These results are striking as they contradict the common view that conceptual processing exclusively involves top-down information flow from cross-modal convergence zones to modality-specific areas (Damasio, 1989a; Fernandino et al., 2016a; Meyer and Damasio, 2009). Crucially, functional coupling between multimodal and modality-specific cortices predicted behavior in a modality-specific fashion: Individual coupling strength between multimodal PPC and M1/S1 was associated with participants' individual action, but not sound associations. In contrast, coupling between multimodal PPC and AAC predicted participants' sound, but not action associations. These results indicate that flexible coupling between multimodal and modality-specific areas is relevant for conceptually-guided behavior. Notably, in addition to coupling between modality-specific and multimodal nodes, PPI also revealed task-dependent interactions between modality-specific and amodal regions (e.g. aIPL/S1 and ATL), amodal and multimodal regions (e.g. ATL and mPFC), different modality-specific areas (e.g. MFG/PreCS and auditory thalamus) and different multimodal areas (e.g. PPC and mPFC).

The results of study 2 allowed us to refine our model of the conceptual system (Figure 5.2A). As we found that functional coupling involved not only high-level (e.g. MFG/PreCS), but also low-level perceptual-motor areas (e.g. M1/S1), we subdivided modality-specific regions into low-level areas and "unimodal convergence zones". Moreover, we extended our model with information on functional interactions (Figure 5.2B). This new model illustrates that functional coupling during conceptual processing is extensive, reciprocal, and task-dependent: Somatomotor regions selectively come into play when action knowledge is task-relevant, and auditory regions when sound knowledge is task-relevant. Crucially, the multimodal region in left PPC seems to act as a functional coupling "switchboard" which dynamically adapts its connectivity profile to task-relevant modality-specific nodes.

Hence, fMRI studies 1 and 2 suggested a key role of the left PPC as a multimodal convergence zone (or "hub") for conceptual knowledge. However, as fMRI is correlational, it remained unknown whether left PPC plays a *causal* role as a multimodal conceptual hub. Therefore, in **study 3**—a TMS study—we tested whether left PPC is causally relevant for the retrieval of both sound and action features of concepts, and to what extent this causal contribution depends on the task (Kuhnke et al., 2020a). We compared effective TMS over left PPC with sham TMS, while 26 new participants performed the three tasks (lexical decision, sound judgment, and action judgment) on words with a high or low association to sounds and actions. We found that PPC-TMS selectively impaired action judgments on low sound–low action words, as compared to sham stimulation. Bayesian analyses confirmed that PPC-TMS affected action judgments, but not sound judgments or lexical decisions. For the first time, we directly related computational simulations of the TMS-induced electrical field to behavioral performance, which revealed that stronger stimulation of left PPC was associated with worse performance on action, but not sound, judgments. These results indicate that left PPC causally supports conceptual processing when action knowledge is task-relevant and cannot be compensated by sound knowledge. Our findings suggest that left PPC is specialized for processing action knowledge, which challenges the view of left PPC as a multimodal conceptual hub.

Overall, our studies provided novel insights into the task dependency of conceptual knowledge retrieval and its neural bases. Our results suggest that perceptual-motor features of concepts are selectively retrieved when they are task-relevant. This flexibility can manifest itself in a task-dependent modulation of neural activity (study 1), functional coupling (study 2), and causal relevance of brain structures (study 3) within a dynamic multi-level architecture comprising modality-specific, multimodal and amodal areas.

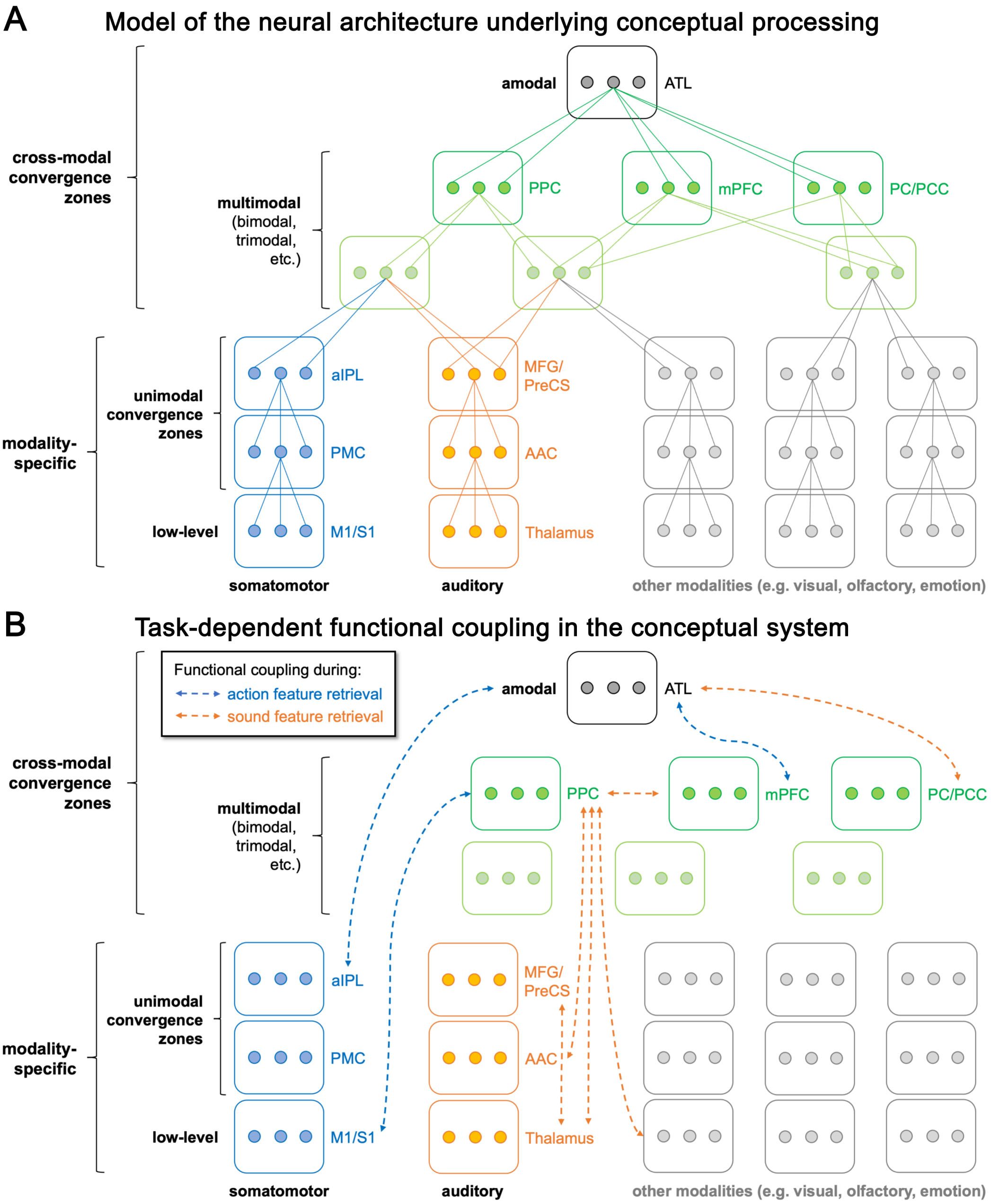

Fig. 5.2: (Reproduced with permission from Kuhnke et al., 2021.) (A) Our new model of the neural architecture underlying conceptual processing, refined using the results of study 2. Low-level modality-specific representations converge onto more abstract modality-specific representations in unimodal convergence zones. Multimodal convergence zones integrate information across modalities, while retaining modality-specific information. Finally, amodal areas completely abstract away from modality-specific content. (B) Task-dependent functional coupling during action and sound feature retrieval. Functional coupling in the conceptual system is extensive and flexible. Modality-specific regions selectively come into play when the knowledge they represent is task-relevant. Multimodal PPC dynamically adapts its connectivity profile to task-relevant modality-specific nodes. Amodal ATL mainly interacts with other high-level cross-modal convergence zones in a task-dependent fashion.

5.2 Open questions for future research

While our studies addressed several key questions on the neural basis of conceptual knowledge retrieval, they also opened up new questions that should be tackled in future research.

Adaptive plasticity in the conceptual system (combined TMS-fMRI)

Our fMRI and TMS results seem to conflict with each other: Whereas the fMRI studies suggest that left PPC represents a key multimodal hub, the TMS study seems to indicate that left PPC selectively supports the retrieval of action (but not sound) knowledge. Importantly, however, the TMS results are consistent with the alternative interpretation that left PPC is also relevant for processing sound knowledge, and other sound-related regions compensated for the TMS-induced disruption. In line with this view, the electrical field simulations indicated that PPC-TMS did not strongly affect auditory cortices (cytoarchitectonic areas TE 1.0, 1.1, 1.2, 3) or prefrontal areas implicated in sound-related conceptual processing (e.g. MFG/PreCS; Fernandino et al., 2016a; Kuhnke et al., 2020b). Thus, these other sound-related regions may have compensated for the perturbation of left PPC by adapting their task-related functional activation and/or connectivity (Hartwigsen, 2018).

Such mechanisms of short-term reorganization or “adaptive plasticity” could be investigated in future studies that combine TMS with a neuroimaging read-out like fMRI (Bergmann et al., 2016; Hartwigsen, 2016, 2018). Previous studies using combined TMS-fMRI have revealed adaptive changes in functional activation (Binney and Lambon Ralph, 2015; Hallam et al., 2016; Hartwigsen et al., 2017; Jung and Lambon Ralph, 2016) and/or effective connectivity (Hallam et al., 2016; Hartwigsen et al., 2017; Jung and Lambon Ralph, 2016) after TMS was applied before a “general” conceptual task (e.g. synonym judgments, or natural/man-made decisions). However, no previous study has investigated adaptive plasticity during the retrieval of a specific conceptual feature (e.g. sound, or action). Thus, a combined TMS-fMRI study could not only help resolve the apparent conflict between our fMRI and TMS results, but also substantially advance our understanding of the neural architecture underlying conceptual processing and its potential for adaptive plasticity. Please note that combined TMS-fMRI studies would also be of clinical relevance as they could indicate how the conceptual system might compensate for actual brain damage, e.g. following a stroke (Hartwigsen, 2016, 2018).

Representational content of modality-specific and cross-modal areas (MVPA / RSA)

While our studies revealed that conceptual processing involves both modality-specific perceptual-motor and multimodal brain regions in a task-dependent fashion, the *representational content* of these regions remains unknown. Previous research suggests that mental contents are represented as “population codes”—patterns of activity distributed across multiple representational units (e.g. neurons or neural populations) (Connolly et al., 2012; Haxby et al., 2014; Ritchie et al., 2019). Population codes can be studied using multivariate pattern analyses (MVPA) of functional neuroimaging data, which look for information in the activity pattern across multiple voxels (Haxby et al., 2014; Mur et al., 2009; Norman et al., 2006). Two main types of MVPA approaches can be distinguished: (1) decoding, and (2) representational similarity analysis (RSA).

Decoding aims to predict a mental content given a particular activity pattern within a brain region (Haxby, 2012; Haynes and Rees, 2006; Tong and Pratte, 2012). In practice, a machine learning classifier is trained to optimally distinguish the activity patterns associated with different stimulus classes, and tested on new data (Haxby et al., 2014; Haynes, 2015; Norman et al., 2006). Notably, decoding enables testing the generalizability of mental representations (Skerry and Saxe, 2014; Wurm and Lingnau, 2015). For instance, a classifier could be trained on high vs. low sound words in one task (e.g. sound judgment) and tested on high vs. low sound words in another task (e.g. lexical decision). Successful decoding would indicate the presence of task-*independent* feature representations, which would substantially extend our findings of task-dependent activations (study 1) and coupling (study 2).

Representational Similarity Analysis (RSA) allows to test explicit hypotheses about the representational structure within a brain region, relying on the assumption that similar mental contents are represented using similar activity patterns (Haxby et al., 2014; Kriegeskorte et al., 2008). The representational space of a brain region is represented as a "representational dissimilarity matrix" (RDM) which encodes the pairwise distances between the activity patterns for all experimental stimuli (Dimsdale-Zucker and Ranganath, 2019; Kriegeskorte and Kievit, 2013). This "neural RDM" can then be compared to "model RDMs" which reflect different hypotheses about representational space (Kriegeskorte and Kievit, 2013; Kriegeskorte et al., 2008). For instance, a model RDM for sound features could assume that the activity patterns for all high-sound words are similar to each other and dissimilar to low-sound words, and vice versa ("categorical RDM"; Figure 5.3A). The categorical RDM could then be compared to a more fine-grained RDM based on sound ratings from the general population ("population RDM"; Figure 5.3B), as well as to a RDM based on the personal sound ratings of the respective participant ("personal RDM"; Figure 5.3C). In this way, it could be directly tested whether the representational structure of a brain region reflects common, encyclopedic knowledge or individual experience. This is a crucial question for current theories of conceptual processing as grounded theories predict that conceptual representations are formed through and depend on individual experience (Barsalou, 1999; Kiefer and Barsalou, 2013; Kiefer and Pulvermüller, 2012).

Moreover, RSA could be used to test whether representational space is task-dependent. Note that it is possible that representational space (i.e. the similarity relationships between activation patterns) stays constant, even if overall activation magnitude (study 1) and functional coupling (study 2) change between tasks (Hebart and Baker, 2018). Alternatively, also the representational space might change between tasks. This is a particularly intriguing possibility for multimodal regions, whose representational space might shift between features across tasks: During sound judgments, a multimodal region (e.g. left PPC) might encode sound feature similarity, whereas during action judgments, its representational space might adapt to reflect action feature similarity. Investigating the representational content of cross-modal convergence zones is crucial to advance theories of conceptual processing as some models propose cross-modal areas to only contain 'pointers' to distributed modality-specific representations without representing any conceptual content themselves (e.g. Damasio, 1989a,b; Meyer and Damasio, 2009), whereas other models posit that cross-modal areas do represent conceptual content (e.g. Binder, 2016; Fernandino et al., 2016a,b; Simmons and Barsalou, 2003). Overall, multivariate analyses of fMRI data are complementary to the studies presented in this thesis as they have the potential to unravel the representational content of different brain regions engaged in conceptual processing.

Time course of conceptual processing (EEG / MEG)

The time course of conceptual processing—how neural activity in the conceptual system unfolds over time—remains unclear. These temporal dynamics can only be studied using

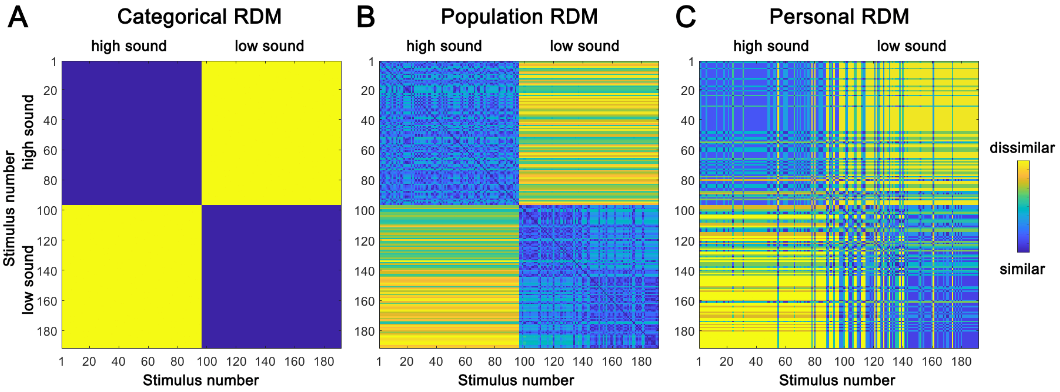

Fig. 5.3: Representational dissimilarity matrices (RDMs) reflecting different hypotheses about the representational space of a brain region encoding sound features of concepts. (A) The "categorical RDM" reflects the basic hypothesis that high-sound words have similar activity patterns to each other, and dissimilar patterns from low-sound words (and vice versa). (B) The "population RDM" reflects more fine-grained differences between sound associations based on average sound ratings from the general population. Ratings were obtained from a total of 163 subjects who did not participate in the fMRI and TMS experiments. (C) The "personal RDM" is based on the sound ratings of an individual participant, reflecting their personal experience-dependent sound associations with the different concepts. The similarity structure of fMRI participant 24 is shown as an example.

neurophysiological methods with a high temporal resolution, such as electroencephalography (EEG) and magnetoencephalography (MEG) (Baillet, 2017; Biasiucci et al., 2019; Hauk, 2016). In particular, timing information is required to resolve distinct processing stages. Functional activation for a "conceptual contrast" (e.g. meaningful > meaningless stimuli) in neuroimaging studies could reflect a combination of various different processes (e.g. retrieval from lexical and/or semantic long-term memory, working memory, mental imagery, decision- and response-related processes; Hauk, 2016; Hauk et al., 2008). Distinguishing these different processes is particularly important for modality-specific perceptual-motor activations due to the ongoing debate whether modality-specific activity reflects early conceptual retrieval (Hauk et al., 2008; Pulvermüller and Shtyrov, 2006) or late mental imagery (Mahon and Caramazza, 2008). Thus, early modality-specific effects (< 200 ms after stimulus onset) are typically taken as evidence that modality-specific perceptual-motor activity indeed reflects conceptual knowledge retrieval (e.g. Kiefer et al., 2008; Klepp et al., 2014; Popp et al., 2016; Trumpp et al., 2013b, 2014).

Moreover, a high temporal resolution is necessary to determine whether modality-specific areas are engaged before, after, or simultaneously as cross-modal convergence zones. This question relates to the issue of bottom-up vs. top-down information flow (Hauk, 2016): A first engagement of modality-specific cortices would suggest bottom-up information flow, whereas an initial activation of cross-modal zones would indicate top-down processing (Fernandino et al., 2016a). Our DCM results (study 2) suggest that conceptual processing involves both top-down and bottom-up processing: During action knowledge retrieval, left motor/somatosensory cortex provided bottom-up input to multimodal left PPC. During sound knowledge retrieval, multimodal PPC and auditory association cortex interacted reciprocally, both via bottom-up and top-down input. However, the precise time course of these interactions remains open. Crucially, previous EEG/MEG evidence indicates that functional interactions between distinct brain regions are supported by synchronized "oscillations" in specific frequency bands (Hauk, 2016; Lopes da Silva, 2013). Bottom-up information flow seems to rely on oscillatory activity in the gamma band ($\sim$30–90 Hz), whereas top-down processing seems to be supported by beta oscillations ($\sim$14–30 Hz) (Baillet, 2017; Siegel et al., 2012). Clearly, investigating these high-frequency interactions requires a temporal resolution in the millisecond range, such as that offered by EEG and MEG (Baillet, 2017; Biasiucci et al., 2019; Hauk, 2016).

Timing information is also key to further refine theories of task dependency in conceptual processing. Specifically, it is currently unknown at which processing stage(s) conceptual processing is modulated by the task (Hauk, 2016). Does the task influence early perceptual, lexical, conceptual access, or late decision-related processes, or even multiple stages? Interestingly, one EEG–MEG study provided evidence for early ($<$ 200 ms) task-dependent modulations of word frequency and imageability effects in occipito-temporal cortices, and late ($>$ 200 ms) task-independent effects in the ATL (Chen et al., 2015).

Finally, temporal information can inform "chronometric" TMS studies that assess the timing of causal contributions of different brain regions (Hauk, 2016; Hauk et al., 2008). Hence, EEG/MEG can provide correlational evidence at which time point a certain region is involved in conceptual processing; chronometric TMS can then be used to test the causal relevance of the region at this time point (and control time points). For instance, Schuhmann et al. (2012) employed chronometric TMS to demonstrate that picture naming requires left MTG at 225 ms, left IFG at 300 ms, and left pSTG at 400 ms after stimulus onset. In an analogous way, future TMS studies could potentially unravel the time course of causal engagement of modality-specific, multimodal and amodal brain regions in conceptual knowledge retrieval.

5.3 Conclusion

This thesis investigated the neural bases of conceptual knowledge retrieval using fMRI and TMS in healthy human participants. Study 1—an fMRI activation study—revealed that both modality-specific perceptual-motor and multimodal brain regions selectively respond to sound and action features of concepts when they are task-relevant. Study 2—an fMRI connectivity study—showed that functional coupling between modality-specific and multimodal regions is task-dependent, reciprocal, and behaviorally relevant. Study 3—a TMS study—provided evidence for a causal role of left PPC in the retrieval of action knowledge.

Overall, our findings support "hybrid theories" which assume that conceptual processing involves both modality-specific perceptual-motor regions and cross-modal convergence zones. In our own new model of the conceptual system, we propose conceptual processing to rely on a flexible representational hierarchy grounded in the perceptual and motor systems: Modality-specific representations converge onto more abstract conceptual representations via multiple levels of cross-modal convergence zones. Critically, we posit a novel distinction among cross-modal convergence zones between *multimodal* areas, which retain modality-specific information, and *amodal* areas, which do not. As a core feature of our model, we assume this hierarchical system to be flexible, with different regions being engaged in a task-dependent fashion: Modality-specific regions are selectively recruited when the conceptual feature they represent is task-relevant. Multimodal PPC acts as a "switchboard" that guides the retrieval of task-relevant features via dynamic coupling with different modality-specific cortices.

Our new model not only reconciles the seemingly opposing grounded cognition and amodal theories (as well as the hub-and-spokes and embodied abstraction models), it also accounts for the task dependency of conceptually-related brain activity and connectivity, thereby addressing several key contemporary issues on the neural basis of conceptual processing.

BIBLIOGRAPHY

Anderson, J. R. (1978). Arguments concerning representations for mental imagery. *Psychological review*, 85(4):249.

Baillet, S. (2017). Magnetoencephalography for brain electrophysiology and imaging. *Nature Neuroscience*, 20(3):327–339.

Bajada, C. J., Jackson, R. L., Haroon, H. A., Azadbakht, H., Parker, G. J., Lambon Ralph, M. A., and Cloutman, L. L. (2017). A graded tractographic parcellation of the temporal lobe. *NeuroImage*, 155:503–512.

Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., and Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, 124(1):103–120.

Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., and Hodges, J. R. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, 129(2):321–332.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4):577–609.

Barsalou, L. W. (2008). Grounded Cognition. *Annual Review of Psychology*, 59(1):617–645.

Barsalou, L. W. (2016). On Staying Grounded and Avoiding Quixotic Dead Ends. *Psychonomic Bulletin and Review*, 23(4):1122–1142.

Bassett, D. S. and Sporns, O. (2017). Network neuroscience. *Nature Neuroscience*, 20(3):353–364.

Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., and Saxe, R. (2008). Concepts are more than percepts: the case of action verbs. *J Neurosci*, 28(44):11347–11353.

Bergmann, T. O., Karabanov, A., Hartwigsen, G., Thielscher, A., and Siebner, H. R. (2016). Combining non-invasive transcranial brain stimulation with neuroimaging and electrophysiology: Current approaches and future perspectives. *NeuroImage*, 140:4–19.

Biasiucci, A., Franceschiello, B., and Murray, M. M. (2019). Electroencephalography. *Current Biology*, 29(3):R80–R85.

Binder, J. R. (2016). In defense of abstract conceptual representations. *Psychonomic Bulletin & Review*, 23(4):1096–1108.

Binder, J. R. and Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11):527–536.

Binder, J. R., Desai, R. H., Graves, W. W., and Conant, L. L. (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cerebral Cortex*, 19(12):2767–2796.

Binder, J. R. and Fernandino, L. (2015). Semantic Processing. In *Brain Mapping: An Encyclopedic Reference*, pages 445–454. Elsevier, Amsterdam.

Binney, R. J. and Lambon Ralph, M. A. (2015). Using a combination of fMRI and anterior temporal lobe rTMS to measure intrinsic and induced activation changes across the semantic cognition network. *Neuropsychologia*, 76:170–181.

Binney, R. J., Parker, G. J. M., and Lambon Ralph, M. A. (2012). Convergent Connectivity and Graded Specialization in the Rostral Human Temporal Lobe as Revealed by Diffusion-Weighted Imaging Probabilistic Tractography. *Journal of Cognitive Neuroscience*, 24(10):1998–2014.

Bonner, M. F. and Grossman, M. (2012). Gray matter density of auditory association cortex relates to knowledge of sound concepts in primary progressive aphasia. *Journal of Neuroscience*, 32(23):7986–7991.

Bonner, M. F., Peelle, J. E., Cook, P. A., and Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. *NeuroImage*, 71:175–186.

Borghesani, V. and Piazza, M. (2017). The neuro-cognitive representations of symbols: the case of concrete words. *Neuropsychologia*, 105:4–17.

Bright, P., Moss, H., Stamatakis, E., and Tyler, L. (2008). Longitudinal studies of semantic dementia: The relationship between structural and functional changes over time. *Neuropsychologia*, 46(8):2177–2188.

Chen, Y., Davis, M. H., Pulvermüller, F., and Hauk, O. (2015). Early Visual Word Processing Is Flexible: Evidence from Spatiotemporal Brain Dynamics. *Journal of Cognitive Neuroscience*, 27(9):1738–1751.

Connolly, A. C., Gobbini, M. I., and Haxby, J. V. (2012). Three Virtues of Similarity-based Multivariate Pattern Analysis : An example from the human object vision pathway. In Kriegeskorte, N. and Kreiman, G., editors, *Understanding visual population codes: Toward a common multivariate framework for cell recording and functional imaging*, pages 335–356. MIT Press, Cambridge.

Culham, J. C. and Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, 16(2):205–212.

Damasio, A. R. (1989a). The Brain Binds Entities and Events by Multiregional Activation from Convergence Zones. *Neural Computation*, 1(1):123–132.

Damasio, A. R. (1989b). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, 33(1-2):25–62.

Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., and Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience*, 35(46):15230–15239.

Desai, R. H., Binder, J. R., Conant, L. L., and Seidenberg, M. S. (2010). Activation of Sensory-Motor Areas in Sentence Comprehension. *Cerebral Cortex*, 20(2):468–478.

Dimsdale-Zucker, H. R. and Ranganath, C. (2019). Representational Similarity Analyses: A Practical Guide for Functional MRI Applications. In *Handbook of in Vivo Neural Plasticity Techniques*, volume 28, pages 509–525. Academic Press, Cambridge.

Ding, J., Chen, K., Liu, H., Huang, L., Chen, Y., Lv, Y., Yang, Q., Guo, Q., Han, Z., and Lambon Ralph, M. A. (2020). A unified neurocognitive model of semantics language social behaviour and face recognition in semantic dementia. *Nature Communications*, 11(1):2595.

Fernandino, L., Binder, J. R., Desai, R. H., Pendl, S. L., Humphries, C. J., Gross, W. L., Conant, L. L., and Seidenberg, M. S. (2016a). Concept Representation Reflects Multimodal Abstraction: A Framework for Embodied Semantics. *Cerebral Cortex*, 26(5):2018–2034.

Fernandino, L., Humphries, C. J., Conant, L. L., Seidenberg, M. S., and Binder, J. R. (2016b). Heteromodal Cortical Areas Encode Sensory-Motor Features of Word Meaning. *Journal of Neuroscience*, 36(38):9763–9769.

Fodor, J. A. (1975). *The Language of Thought*. Harvard University Press, Cambridge.

Galton, C. J., Patterson, K., Graham, K., Lambon-Ralph, M., Williams, G., Antoun, N., Sahakian, B., and Hodges, J. (2001). Differing patterns of temporal atrophy in Alzheimer's disease and semantic dementia. *Neurology*, 57(2):216–225.

Goldberg, R. F. (2006). Perceptual Knowledge Retrieval Activates Sensory Brain Regions. *Journal of Neuroscience*, 26(18):4917–4921.

Gorno-Tempini, M. L., Dronkers, N. F., Rankin, K. P., Ogar, J. M., Phengrasamy, L., Rosen, H. J., Johnson, J. K., Weiner, M. W., and Miller, B. L. (2004). Cognition and Amatomy in Three Variants of Primany Progressive Aphasia. *Annals of Neurology*, 55(3):335–346.

Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., and McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, 71(18):1396–1401.

Hallam, G. P., Whitney, C., Hymers, M., Gouws, A. D., and Jefferies, E. (2016). Charting the effects of TMS with fMRI: Modulation of cortical recruitment within the distributed network supporting semantic control. *Neuropsychologia*, 93:40–52.

Hardwick, R. M., Caspers, S., Eickhoff, S. B., and Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience & Biobehavioral Reviews*, 94:31–44.

Harnad, S. (1990). The symbol grounding problem. *Physica D: Nonlinear Phenomena*, 42(1-3):335–346.

Hartwigsen, G. (2016). Adaptive Plasticity in the Healthy Language Network: Implications for Language Recovery after Stroke. *Neural Plasticity*, 2016:9674790.

Hartwigsen, G. (2018). Flexible Redistribution in Cognitive Networks. *Trends in Cognitive Sciences*, 22(8):687–698.

Hartwigsen, G., Bzdok, D., Klein, M., Wawrzyniak, M., Stockert, A., Wrede, K., Classen, J., and Saur, D. (2017). Rapid short-term reorganization in the language network. *eLife*, 6:e25964.

Hartwigsen, G., Weigel, A., Schuschan, P., Siebner, H. R., Weise, D., Classen, J., and Saur, D. (2016). Dissociating Parieto-Frontal Networks for Phonological and Semantic Word Decisions: A Condition-and-Perturb TMS Study. *Cerebral Cortex*, 26(6):2590–2601.

Hauk, O. (2016). Only time will tell – why temporal information is essential for our neuroscientific understanding of semantics. *Psychonomic Bulletin & Review*, 23(4):1072 – 1079.

Hauk, O., Johnsrude, I., and Pulvermüller, F. (2004). Somatotopic Representation of Action Words in Human Motor and Premotor Cortex. *Neuron*, 41(2):301–307.

Hauk, O. and Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21(3):191–201.

Hauk, O., Shtyrov, Y., and Pulvermüller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology Paris*, 102(1-3):50–58.

Hauk, O. and Tschentscher, N. (2013). The Body of Evidence: What Can Neuroscience Tell Us about Embodied Semantics? *Frontiers in Psychology*, 4:50.

Haxby, J. V. (2012). Multivariate pattern analysis of fMRI: The early beginnings. *NeuroImage*, 62(2):852–855.

Haxby, J. V., Connolly, A. C., and Guntupalli, J. S. (2014). Decoding Neural Representational Spaces Using Multivariate Pattern Analysis. *Annual Review of Neuroscience*, 37(1):435–456.

Haynes, J.-D. (2015). A Primer on Pattern-Based Approaches to fMRI: Principles, Pitfalls, and Perspectives. *Neuron*, 87(2):257–270.

Haynes, J.-D. and Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, 7(7):523–534.

Hebart, M. N. and Baker, C. I. (2018). Deconstructing multivariate decoding for the study of brain function. *NeuroImage*, 180:4–18.

Hillis, A. E., Heidler-Gary, J., Newhart, M., Chang, S., Ken, L., and Bak, T. H. (2006). Naming and comprehension in primary progressive aphasia: The influence of grammatical word class. *Aphasiology*, 20(2-4):246–256.

Hodges, J. R. and Patterson, K. (2007). Semantic dementia: a unique clinicopathological syndrome. *The Lancet Neurology*, 6(11):1004–1014.

Hoenig, K., Müller, C., Herrnberger, B., Sim, E.-J., Spitzer, M., Ehret, G., and Kiefer, M. (2011). Neuroplasticity of semantic representations for musical instruments in professional musicians. *NeuroImage*, 56(3):1714–1725.

Hoenig, K., Sim, E.-J., Bochev, V., Herrnberger, B., and Kiefer, M. (2008). Conceptual Flexibility in the Human Brain: Dynamic Recruitment of Semantic Maps from Visual, Motor, and Motion-related Areas. *Journal of Cognitive Neuroscience*, 20(10):1799–1814.

Hoffman, P., Binney, R. J., and Lambon Ralph, M. A. (2015). Differing contributions of inferior prefrontal and anterior temporal cortex to concrete and abstract conceptual knowledge. *Cortex*, 63:250–266.

Jackson, R. L. (2021). The neural correlates of semantic control revisited. *NeuroImage*, 224:117444.

Jefferies, E. (2013). The neural basis of semantic cognition: Converging evidence from neuropsychology, neuroimaging and TMS. *Cortex*, 49(3):611–625.

Jefferies, E. and Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. *Brain*, 129(8):2132–2147.

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8(2):71–78.

Jung, J. and Lambon Ralph, M. A. (2016). Mapping the Dynamic Network Interactions Underpinning Cognition: A cTBS-fMRI Study of the Flexible Adaptive Neural System for Semantics. *Cerebral Cortex*, 26(8):3580–3590.

Kellenbach, M. L., Brett, M., and Patterson, K. (2001). Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective, & Behavioral Neuroscience*, 1(3):207–221.

Kellenbach, M. L., Brett, M., and Patterson, K. (2003). Actions Speak Louder Than Functions: The Importance of Manipulability and Action in Tool Representation. *Journal of Cognitive Neuroscience*, 15(1):30–46.

Kemmerer, D. (2014). *Cognitive neuroscience of language*. Psychology Press, New York and London.

Kemmerer, D. (2015). Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible, multilevel architecture for conceptual knowledge. *Psychonomic Bulletin & Review*, 22(4):1068–1075.

Kiefer, M. and Barsalou, L. W. (2013). Grounding the Human Conceptual System in Perception, Action, and Internal States. In Prinz, W., Beisert, M., and Herwig, A., editors, *Tutorials in action science*, pages 381–407. The MIT Press, Cambridge.

Kiefer, M. and Harpaintner, M. (2020). Varieties of abstract concepts and their grounding in perception or action. *Open Psychology*, 2(1):119–137.

Kiefer, M. and Pulvermüller, F. (2012). Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. *Cortex*, 48(7):805–825.

Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., and Hoenig, K. (2008). The Sound of Concepts: Four Markers for a Link between Auditory and Conceptual Brain Systems. *Journal of Neuroscience*, 28(47):12224–12230.

Klepp, A., Weissler, H., Niccolai, V., Terhalle, A., Geisler, H., Schnitzler, A., and Biermann-Ruben, K. (2014). Neuromagnetic hand and foot motor sources recruited during action verb processing. *Brain and Language*, 128(1):41–52.

Kriegeskorte, N. and Kievit, R. A. (2013). Representational geometry: integrating cognition, computation, and the brain. *Trends in Cognitive Sciences*, 17(8):401–412.

Kriegeskorte, N., Mur, M., and Bandettini, P. (2008). Representational similarity analysis – connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, 2:4.

Kuhnke, P., Beaupain, M. C., Cheung, V. K. M., Weise, K., Kiefer, M., and Hartwigsen, G. (2020a). Left posterior inferior parietal cortex causally supports the retrieval of action knowledge. *NeuroImage*, 219:117041.

Kuhnke, P., Kiefer, M., and Hartwigsen, G. (2020b). Task-Dependent Recruitment of Modality-Specific and Multimodal Regions during Conceptual Processing. *Cerebral Cortex*, 30(7):3938–3959.

Kuhnke, P., Kiefer, M., and Hartwigsen, G. (2021). Task-Dependent Functional and Effective Connectivity during Conceptual Processing. *Cerebral Cortex*, 31(7):3475–3493.

Lambon Ralph, M. A. (2014). Neurocognitive insights on conceptual knowledge and its breakdown. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1634):20120392.

Lambon Ralph, M. A., Jefferies, E., Patterson, K., and Rogers, T. T. (2016). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1):42–55.

Lambon Ralph, M. A., Pobric, G., and Jefferies, E. (2009). Conceptual Knowledge Is Underpinned by the Temporal Pole Bilaterally: Convergent Evidence from rTMS. *Cerebral Cortex*, 19(4):832–838.

Lambon Ralph, M. A., Sage, K., Jones, R. W., and Mayberry, E. J. (2010). Coherent concepts are computed in the anterior temporal lobes. *Proceedings of the National Academy of Sciences*, 107(6):2717–2722.

Lo Gerfo, E., Oliveri, M., Torriero, S., Salerno, S., Koch, G., and Caltagirone, C. (2008). The influence of rTMS over prefrontal and motor areas in a morphological task: Grammatical vs. semantic effects. *Neuropsychologia*, 46(2):764–770.

Lopes da Silva, F. (2013). EEG and MEG: Relevance to Neuroscience. *Neuron*, 80(5):1112–1128.

Mahon, B. Z. (2015). What is embodied about cognition? *Language, Cognition and Neuroscience*, 30(4):420–429.

Mahon, B. Z. and Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology-Paris*, 102(1-3):59–70.

Makris, N., Papadimitriou, G. M., Kaiser, J. R., Sorg, S., Kennedy, D. N., and Pandya, D. N. (2009). Delineation of the middle longitudinal fascicle in humans: A quantitative, in vivo, DT-MRI study. *Cerebral Cortex*, 19(4):777–785.

Margulies, D. S., Ghosh, S. S., Goulas, A., Falkiewicz, M., Huntenburg, J. M., Langs, G., Bezgin, G., Eickhoff, S. B., Castellanos, F. X., Petrides, M., Jefferies, E., and Smallwood, J. (2016). Situating the default-mode network along a principal gradient of macroscale cortical organization. *Proceedings of the National Academy of Sciences*, 113(44):12574–12579.

Martin, A., Haxby, J. V., Lalonde, F. o. M., Wiggs, C. L., and Ungerleider, L. G. (1995). Discrete Cortical Regions Associated with Knowledge of Color and Knowledge of Action. *Science*, 270(5233):102–105.

Martin, A., Kyle Simmons, W., Beauchamp, M. S., and Gotts, S. J. (2014). Is a single 'hub', with lots of spokes, an accurate description of the neural architecture of action semantics? Comment on "Action semantics: A unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge" by van Elk, van Schie and Bekkering. *Physics of Life Reviews*, 11(2):261–262.

Meteyard, L., Cuadrado, S. R., Bahrami, B., and Vigliocco, G. (2012). Coming of age: A review of embodiment and the neuroscience of semantics. *Cortex*, 48(7):788–804.

Meyer, K. and Damasio, A. (2009). Convergence and divergence in a neural architecture for recognition and memory. *Trends in Neurosciences*, 32(7):376–382.

Mion, M., Patterson, K., Acosta-Cabronero, J., Pengas, G., Izquierdo-Garcia, D., Hong, Y. T., Fryer, T. D., Williams, G. B., Hodges, J. R., and Nestor, P. J. (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain*, 133(11):3256–3268.

Morán, M. A., Mufson, E. J., and Mesulam, M. M. (1987). Neural inputs into the temporopolar cortex of the rhesus monkey. *Journal of Comparative Neurology*, 256(1):88–103.

Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S., and Hodges, J. R. (2000). A voxel-based morphometry study of semantic dementia: Relationship between temporal lobe atrophy and semantic memory. *Annals of Neurology*, 47(1):36–45.

Mur, M., Bandettini, P. A., and Kriegeskorte, N. (2009). Revealing representational content with pattern-information fMRI—an introductory guide. *Social Cognitive and Affective Neuroscience*, 4(1):101–109.

Niccolai, V., Klepp, A., Weissler, H., Hoogenboom, N., Schnitzler, A., and Biermann-Ruben, K. (2014). Grasping Hand Verbs: Oscillatory Beta and Alpha Correlates of Action-Word Processing. *PLoS ONE*, 9(9):e108059.

Noonan, K. A., Jefferies, E., Corbett, F., and Lambon Ralph, M. A. (2010). Elucidating the Nature of Deregulated Semantic Cognition in Semantic Aphasia: Evidence for the Roles of Prefrontal and Temporo-parietal Cortices. *Journal of Cognitive Neuroscience*, 22(7):1597–1613.

Noonan, K. A., Jefferies, E., Visser, M., and Lambon Ralph, M. A. (2013). Going beyond Inferior Prefrontal Involvement in Semantic Control: Evidence for the Additional Contribution of Dorsal Angular Gyrus and Posterior Middle Temporal Cortex. *Journal of Cognitive Neuroscience*, 25(11):1824–1850.

Norman, K. A., Polyn, S. M., Detre, G. J., and Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, 10(9):424–430.

Papeo, L., Vallesi, A., Isaja, A., and Rumiati, R. I. (2009). Effects of TMS on Different Stages of Motor and Non-Motor Verb Processing in the Primary Motor Cortex. *PLoS ONE*, 4(2):e4508.

Patterson, K. and Lambon Ralph, M. A. (2016). The hub-and-spoke hypothesis of semantic memory. In *Neurobiology of language*, pages 765–775. Elsevier, Amsterdam.

Patterson, K., Nestor, P. J., and Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12):976–987.

Pobric, G., Jefferies, E., and Lambon Ralph, M. A. (2010a). Amodal semantic representations depend on both anterior temporal lobes: Evidence from repetitive transcranial magnetic stimulation. *Neuropsychologia*, 48(5):1336–1342.

Pobric, G., Jefferies, E., and Lambon Ralph, M. A. (2010b). Category-Specific versus Category-General Semantic Impairment Induced by Transcranial Magnetic Stimulation. *Current Biology*, 20(10):964–968.

Pobric, G., Jefferies, E., and Ralph, M. A. L. (2007). Anterior temporal lobes mediate semantic representation: Mimicking semantic dementia by using rTMS in normal participants. *Proceedings of the National Academy of Sciences*, 104(50):20137–20141.

Popp, M., Trumpp, N. M., and Kiefer, M. (2016). Feature-Specific Event-Related Potential Effects to Action- and Sound-Related Verbs during Visual Word Recognition. *Frontiers in Human Neuroscience*, 10:637.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., and de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *NeuroImage*, 43(3):634–644.

Price, A., Bonner, M., and Grossman, M. (2015). Semantic Memory: Cognitive and Neuroanatomical Perspectives. In *Brain Mapping: An Encyclopedic Reference*, volume 3, pages 529–536. Elsevier, Amsterdam, Amsterdam.

Price, C. J. and Friston, K. J. (2002). Degeneracy and cognitive anatomy. *Trends in Cognitive Sciences*, 6(10):416–421.

Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences*, 22(2):253–279.

Pulvermüller, F. (2013). How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics. *Trends in Cognitive Sciences*, 17(9):458–470.

Pulvermüller, F. (2018). Neurobiological Mechanisms for Semantic Feature Extraction and Conceptual Flexibility. *Topics in Cognitive Science*, 10(3):590–620.

Pulvermüller, F., Hauk, O., Nikulin, V. V., and Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, 21(3):793–797.

Pulvermüller, F. and Shtyrov, Y. (2006). Language outside the focus of attention: The mismatch negativity as a tool for studying higher cognitive processes. *Progress in Neurobiology*, 79(1):49–71.

Pylyshyn, Z. W. (1984). *Computation and Cognition: Toward a Foundation for Cognitive Science*. The MIT Press, Cambridge.

Raposo, A., Moss, H. E., Stamatakis, E. A., and Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia*, 47(2):388–396.

Repetto, C., Colombo, B., Cipresso, P., and Riva, G. (2013). The effects of rTMS over the primary motor cortex: The link between action and language. *Neuropsychologia*, 51(1):8–13.

Rice, G. E., Lambon Ralph, M. A., and Hoffman, P. (2015). The Roles of Left Versus Right Anterior Temporal Lobes in Conceptual Knowledge: An ALE Meta-analysis of 97 Functional Neuroimaging Studies. *Cerebral Cortex*, 25(11):4374–4391.

Ritchie, J. B., Kaplan, D. M., and Klein, C. (2019). Decoding the Brain: Neural Representation and the Limits of Multivariate Pattern Analysis in Cognitive Neuroscience. *The British Journal for the Philosophy of Science*, 70(2):581–607.

Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., and Patterson, K. (2004). Structure and Deterioration of Semantic Memory: A Neuropsychological and Computational Investigation. *Psychological Review*, 111(1):205–235.

Schuhmann, T., Schiller, N. O., Goebel, R., and Sack, A. T. (2012). Speaking of Which: Dissecting the Neurocognitive Network of Language Production in Picture Naming. *Cerebral Cortex*, 22(3):701–709.

Searle, J. R. (1980). Minds, Brains, and Programs. *Behavioral and Brain Sciences*, 3(3):415–457.

Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, 19(1):43–61.

Shtyrov, Y., Hauk, O., and Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. *The European journal of neuroscience*, 19(4):1083–92.

Siegel, M., Donner, T. H., and Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. *Nature Reviews Neuroscience*, 13(2):121–134.

Simmons, W. K. and Barsalou, L. W. (2003). The Similarity-in-Topography Principle: Reconciling Theories of Conceptual Deficits. *Cognitive Neuropsychology*, 20(3-6):451–486.

Skerry, A. E. and Saxe, R. (2014). A Common Neural Code for Perceived and Inferred Emotion. *Journal of Neuroscience*, 34(48):15997–16008.

Sliwinska, M. W., James, A., and Devlin, J. T. (2015). Inferior Parietal Lobule Contributions to Visual Word Recognition. *Journal of Cognitive Neuroscience*, 27(3):593–604.

Sporns, O. (2014). Contributions and challenges for network models in cognitive neuroscience. *Nature Neuroscience*, 17(5):652–660.

Stoeckel, C., Gough, P. M., Watkins, K. E., and Devlin, J. T. (2009). Supramarginal gyrus involvement in visual word recognition. *Cortex*, 45(9):1091–1096.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., and Perani, D. (2005). Listening to Action-related Sentences Activates Fronto-parietal Motor Circuits. *Journal of Cognitive Neuroscience*, 17(2):273–281.

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: inferring “how” from “where”. *Neuropsychologia*, 41(3):280–292.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., and Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, 94(26):14792–14797.

Tong, F. and Pratte, M. S. (2012). Decoding Patterns of Human Brain Activity. *Annual Review of Psychology*, 63(1):483–509.

Trumpp, N. M., Kliese, D., Hoenig, K., Haarmeier, T., and Kiefer, M. (2013a). Losing the sound of concepts: Damage to auditory association cortex impairs the processing of sound-related concepts. *Cortex*, 49(2):474–486.

Trumpp, N. M., Traub, F., and Kiefer, M. (2013b). Masked Priming of Conceptual Features Reveals Differential Brain Activation during Unconscious Access to Conceptual Action and Sound Information. *PLoS ONE*, 8(5):e65910.

Trumpp, N. M., Traub, F., Pulvermüller, F., and Kiefer, M. (2014). Unconscious Automatic Brain Activation of Acoustic and Action-related Conceptual Features during Masked Repetition Priming. *Journal of Cognitive Neuroscience*, 26(2):352–364.

Tune, S. and Asaridou, S. S. (2016). Stimulating the Semantic Network: What Can TMS Tell Us about the Roles of the Posterior Middle Temporal Gyrus and Angular Gyrus? *Journal of Neuroscience*, 36(16):4405–4407.

van Elk, M., van Schie, H., and Bekkering, H. (2014). Action semantics: A unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. *Physics of Life Reviews*, 11(2):220–250.

Visser, M., Jefferies, E., Embleton, K. V., and Lambon Ralph, M. A. (2012). Both the Middle Temporal Gyrus and the Ventral Anterior Temporal Area Are Crucial for Multimodal Semantic Processing: Distortion-corrected fMRI Evidence for a Double Gradient of Information Convergence in the Temporal Lobes. *Journal of Cognitive Neuroscience*, 24(8):1766–1778.

Visser, M., Jefferies, E., and Lambon Ralph, M. A. (2010). Semantic Processing in the Anterior Temporal Lobes: A Meta-analysis of the Functional Neuroimaging Literature. *Journal of Cognitive Neuroscience*, 22(6):1083–1094.

Vukovic, N., Feurra, M., Shpektor, A., Myachykov, A., and Shtyrov, Y. (2017). Primary motor cortex functionally contributes to language comprehension: An online rTMS study. *Neuropsychologia*, 96:222–229.

Wagner, A. D., Paré-Blagoev, E., Clark, J., and Poldrack, R. A. (2001). Recovering Meaning: Left Prefrontal Cortex Guides Controlled Semantic Retrieval. *Neuron*, 31(2):329–338.

Walsh, V. and Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. *Nature Reviews Neuroscience*, 1(1):73–80.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., and Jefferies, E. (2011). The Neural Organization of Semantic Control: TMS Evidence for a Distributed Network in Left Inferior Frontal and Posterior Middle Temporal Gyrus. *Cerebral Cortex*, 21(5):1066–1075.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., and Jefferies, E. (2012). Executive Semantic Processing Is Underpinned by a Large-scale Neural Network: Revealing the Contribution of Left Prefrontal, Posterior Temporal, and Parietal Cortex to Controlled Retrieval and Selection Using TMS. *Journal of Cognitive Neuroscience*, 24(1):133–147.

Willems, R. M. and Casasanto, D. (2011). Flexibility in embodied language understanding. *Frontiers in Psychology*, 2:116.

Wurm, M. F. and Lingnau, A. (2015). Decoding Actions at Different Levels of Abstraction. *Journal of Neuroscience*, 35(20):7727–7735.

Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., and Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106(3):1125–1165.

Supplementary Material

Supplementary material for study 1 (fMRI activation)

Table S1. Psycholinguistic measures for the four word categories (means; SD in parentheses).

	low sound	**high sound**	**p**	**low action**	**high action**	**p**
Sound rating	1.33 (0.29)	4.92 (0.62)	**$<10^{-113}$**	2.92 (1.67)	3.34 (2.03)	0.12
Action rating	3.19 (1.64)	3.4 (1.64)	0.37	1.73 (0.49)	4.86 (0.45)	**$<10^{-103}$**
Visual rating	4.21 (0.54)	4.07 (0.81)	0.15	4.16 (0.82)	4.13 (0.52)	0.77
Familiarity rating	5.52 (0.39)	5.47 (0.41)	0.41	5.45 (0.42)	5.55 (0.37)	0.08
Letters	6.23 (1.61)	6.36 (2.0)	0.61	6.27 (1.98)	6.32 (1.63)	0.84
Syllables	2.21 (0.77)	2.29 (0.71)	0.44	2.22 (0.71)	2.28 (0.76)	0.56
Lemma freq.	5.33 (6.33)	5.56 (10.35)	0.85	4.74 (6.34)	6.14 (10.3)	0.26
Bigram freq.	254220.81 (136859.15)	231922.15 (122883.01)	0.24	254413.24 (139511.49)	231729.73 (119826.78)	0.23
Trigram freq.	145830.18 (85313.42)	132754.69 (76696.95)	0.27	146068.82 (84690.3)	132516.05 (77342.95)	0.25
Orthographic neighbors	7.41 (6.7)	6.09 (5.86)	0.15	7.05 (6.83)	6.44 (5.77)	0.5

Ratings were obtained from a total of 163 subjects who did not participate in the fMRI experiment. All other psycholinguistic measures were extracted from the *dlexDB* database (Heister et al., 2011; http://dlexdb.de/). Lemma, bigram and trigram frequencies and number of orthographic neighbors are given per one million words.

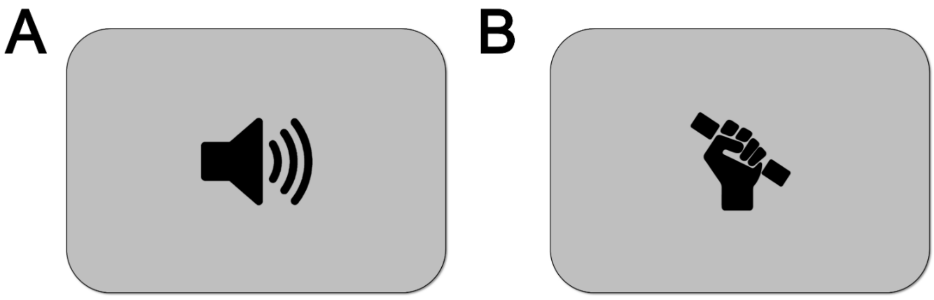

Figure S1. Cues presented at the beginning of mini-blocks for the sound judgment task (A) or action judgment task (B).

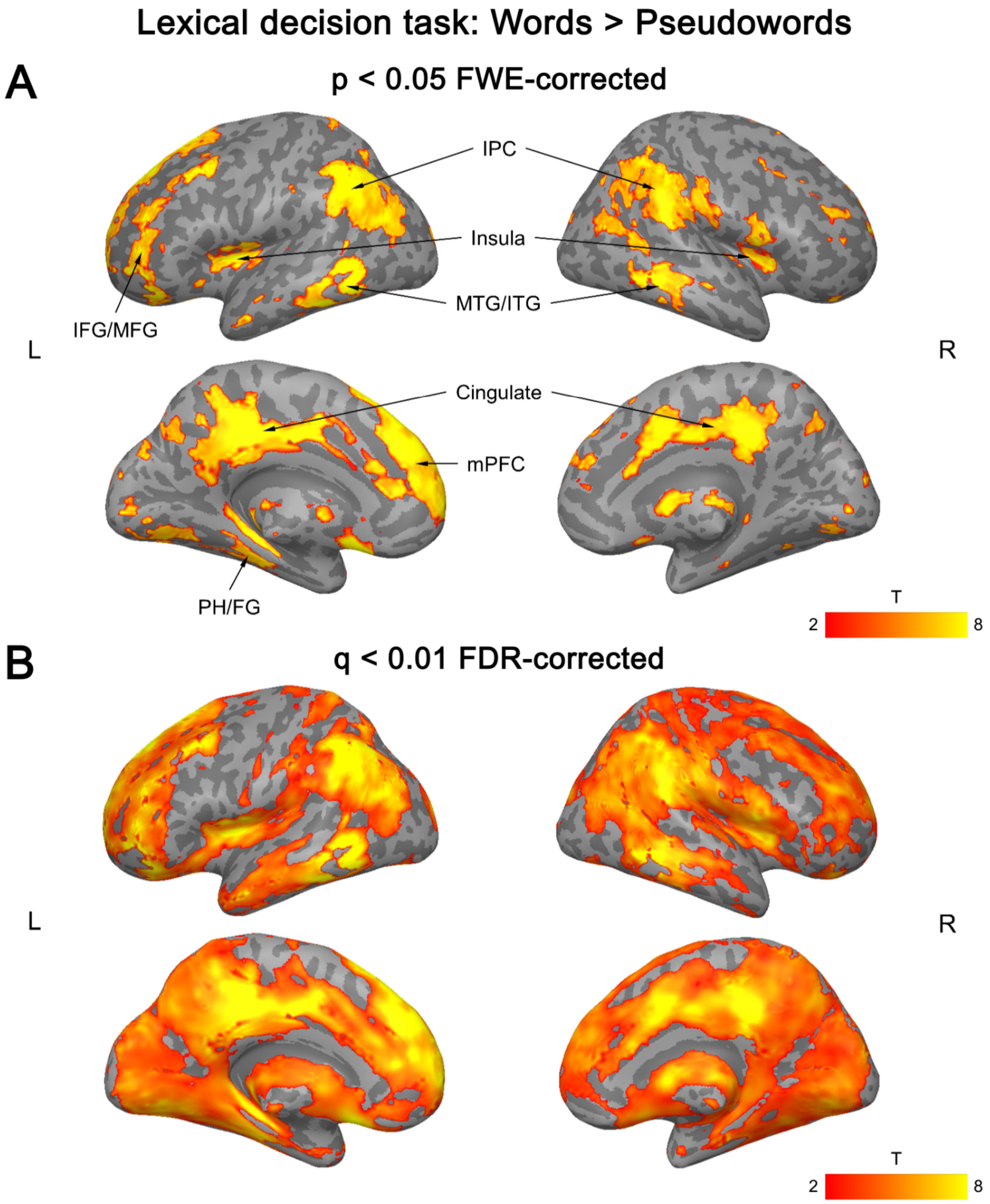

Figure S2. The "general" conceptual system (cf. Binder et al., 2009). Activation for words > pseudowords in the lexical decision task, at two different thresholds: (A) voxel-wise $p < 0.05$ family wise error (FWE) corrected; (B) voxel-wise $q < 0.01$ false discovery rate (FDR) corrected. FG = fusiform gyrus; IFG = inferior frontal gyrus; IPC = inferior parietal cortex; ITG = inferior temporal gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; mPFC = medial prefrontal cortex; PH = parahippocampal gyrus.

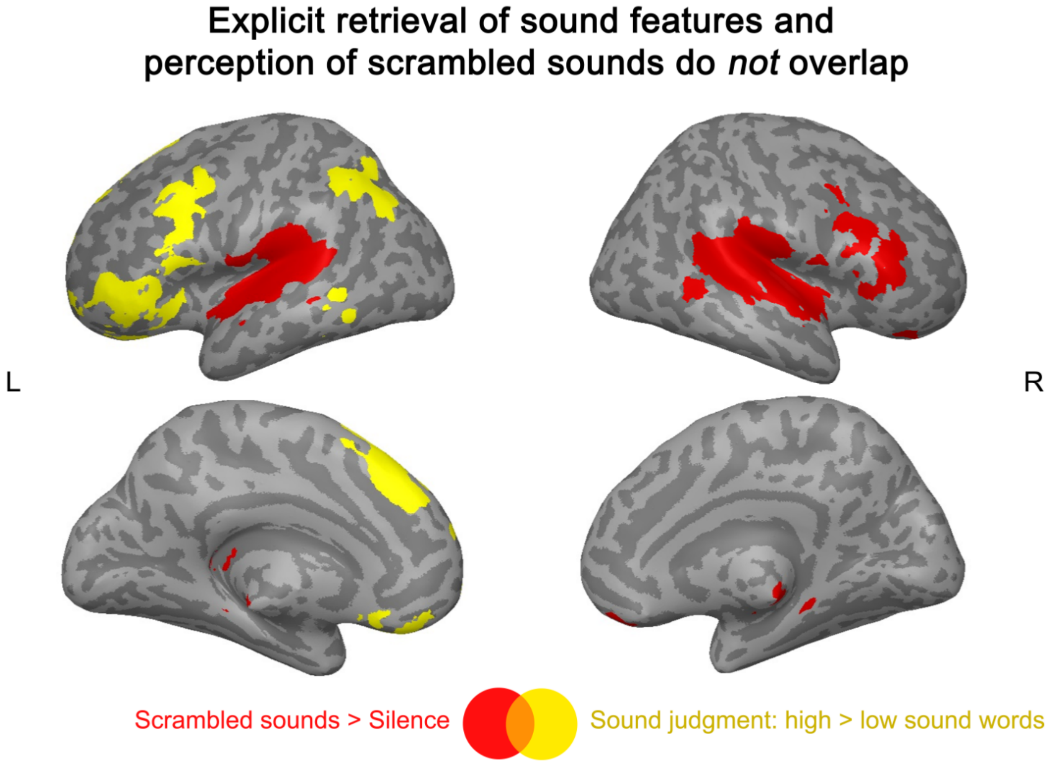

Figure S3. Activation for the explicit retrieval of sound features (yellow) does *not* overlap with activation for listening to scrambled sounds (red).

Activation Tables

The following tables show activations thresholded at q < 0.05 FDR-corrected (extent > 20 voxels). Up to 10 peaks per cluster are reported with T > 3.31 (p < 0.001 uncorrected) and more than 8 mm apart. Coordinates are in MNI space. Anatomical labels were determined using the SPM Anatomy toolbox (Version 2.2c; Eickhoff et al., 2005), the Harvard-Oxford atlas distributed with FSL (http://www.fmrib.ox.ac.uk/fsl/), and the human motor area template (http://lrnlab.org/; Mayka et al., 2006).

AG = angular gyrus; ACC = anterior cingulate cortex; MCC = middle cingulate cortex; PCC = posterior cingulate cortex; FG = fusiform gyrus; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; IPS = inferior parietal sulcus; ITG = inferior temporal gyrus; LTO = lateral temporal-occipital junction; MTG = middle temporal gyrus; MFG = middle frontal gyrus; PFC = prefrontal cortex; dmPFC = dorsomedial PFC; vmPFC = ventromedial PFC; PMC = premotor cortex; PMd = dorsal PMC; PMv = ventral PMC; S1 = primary somatosensory cortex; S2 = secondary somatosensory cortex; SFG = superior frontal gyrus; SMA = supplementary motor area; SMG = supramarginal gyrus; SPL = superior parietal lobe; STG = superior temporal gyrus; a (prefix) = anterior; p (prefix) = posterior.

Table S2. Motor localizer: Hand movements > Rest.

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L/R M1, PMC, S1/S2, aSMG/IPS	234 719				
L M1 (4p)		-34	-24	55	21.53
R M1 (4p)		36	-22	55	19.87
L M1		-37	-17	65	19.53
L M1 (4p)		-32	-32	55	17.11
L SMA		-7	-7	52	15.99
L S1		-50	-20	55	15.31
R S1		50	-20	58	13.88
L S2 (OP1)		-44	-27	20	11.63
L parietal operculum		-47	-34	22	11.53
L thalamus (prefrontal)		-14	-20	8	11.19
L/R cerebellum	98 438				
L cerebellum (VI)		-20	-50	-22	18.53
R cerebellum (VI)		20	-50	-22	17.30
R cerebellum (VI)		26	-47	-28	16.82
R cerebellum (V)		6	-60	-12	16.00
R cerebellum (VIIIb)		16	-60	-52	14.84
L cerebellum (VIIIb)		-20	-57	-50	13.17
L cerebellum (V)		-4	-62	-18	12.16
R cerebellum (VIIIa)		8	-64	-32	11.99
L cerebellum (VIIIa)		-7	-64	-35	8.19
R frontal pole / MFG	6141				

R MFG		38	40	20	4.63
R frontal pole		33	46	-2	4.52
R frontal pole		26	43	-8	3.87
R frontal pole		23	46	-10	3.58
L pMTG/LTO	2500	-47	-62	8	7.23
L MFG	1469	-32	36	30	4.04
L MFG		-30	33	25	4.00
R pMTG/LTO	547	48	-60	5	4.07
R inferior occipital gyrus (V3v)	469	28	-94	-5	3.58
L superior orbital gyrus (Fo3)	453	-17	43	-15	3.81

Table S3. Auditory localizer.

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
Real sounds > Silence					
L/R early auditory cortices, IFG	302 906				
L A1 (TE 1.0)		-50	-20	5	25.59
R A1 (TE 1.0)		56	-20	5	24.39
R STG (TE 3)		63	-30	10	21.39
R A1 (TE 1.0)		50	-10	0	19.68
R A1 (TE 1.1)		43	-22	8	19.68
R A1 (TE 1.2)		53	-2	-5	18.83
L STG (TE 3)		-67	-24	12	16.73
R STG (TE 3)		60	-10	-5	16.55
L A1 (TE 1.2)		-47	-10	-5	16.25
L STG		-54	-30	8	15.93
L/R dmPFC	5188				
R dmPFC (SFG)		6	6	62	5.67
L dmPFC (SFG)		-2	16	52	5.29
L dmPFC (SFG)		-2	28	48	4.54
L/R brainstem	1969				
R brainstem		6	-32	-38	4.88
R brainstem		18	-34	-38	3.98
L brainstem		-7	-34	-38	3.89
L IPS (hIP3)	1047	-30	-57	40	4.22
L IPS (hIP3)		-32	-64	48	3.64
L MCC	734	-2	3	25	4.95
Scrambled sounds > Silence					
R early auditory cortex	44 922				
R A1 (TE 1.1)		43	-22	10	24.32
R A1 (TE 1.0)		53	-20	5	22.67
R STG (TE 3)		63	-22	10	16.85
R STG/SMG (PF)		66	-30	12	16.67

R STG/SMG (PFcm)		46	-34	12	15.36
L early auditory cortex	31 531				
L A1 (TE 1.0)		-47	-22	8	23.73
L A1 (TE 1.1)		-40	-27	10	22.71
L STG		-47	-10	-5	13.26
L STG (TE 3)		-67	-27	12	10.32
L cerebellum	17 188				
L cerebellum (VII)		-12	-74	-40	7.86
L cerebellum (VIIb)		-24	-67	-50	6.42
L cerebellum (crus 1)		-10	-77	-30	5.65
L cerebellum (VIIb)		-32	-72	-55	4.99
L cerebellum (VI)		-22	-70	-28	4.73
L cerebellum (crus 1)		-34	-70	-28	4.31
R IFG	15 125				
R aIFG (pars triangularis)		46	36	2	5.84
R aIFG (pars triangularis)		50	33	20	5.28
R aIFG (pars triangularis)		43	26	18	5.11
R aIFG (pars triangularis)		53	26	22	4.94
R pIFG (pars opercularis)		40	8	30	4.19
L/R brainstem	5250				
R brainstem		16	-24	-10	5.85
R brainstem		3	-34	-8	5.63
L brainstem		-4	-32	-10	5.45
R cerebellum	2906				
R cerebellum (crus 2)		10	-80	-35	4.88
R cerebellum (crus 1)		16	-77	-25	4.29
R vmPFC	2703				
R vmPFC (Fo3)		28	33	-12	4.78
R vmPFC (Fp2)		8	53	-18	3.76
R brainstem	844	13	-37	-40	4.61
L brainstem	609	-10	-34	-40	4.54

Table S4. Action judgment task: high > low action words.

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L posterior temporal and inferior parietal cortices	63891				
L IPS (hIP2)		-47	-44	48	8.21
L SMG (PFm)		-44	-54	52	6.97
L pITG		-57	-42	-18	6.90
L SMG (PF)		-57	-37	45	6.51
L pMTG/LTO		-57	-54	2	6.08
L SPL (7A)		-37	-60	55	5.98
L pMTG/LTO		-64	-47	-2	5.65
L SMG (PF)		-60	-42	32	5.00
L IPS (hIP3)		-30	-64	42	4.63
L pITG		-62	-30	-20	4.52

R cerebellum	24078				
R cerebellum (crus II)		30	-77	-45	4.53
R cerebellum (crus I)		40	-62	-40	4.52
R cerebellum (crus II)		38	-70	-42	4.47
R cerebellum (lobule VI)		28	-60	-22	4.43
R cerebellum (lobule VI)		26	-70	-28	4.31
R cerebellum (lobule VIIb)		16	-72	-45	4.23
R cerebellum (crus I)		16	-80	-30	4.00
R cerebellum (crus I)		43	-60	-28	3.46
L anterior inferior frontal cortex, vmPFC	20203				
L caudate nucleus		-10	13	0	6.23
L aIFG (pars orbitalis)		-17	26	-20	6.09
L vmPFC (middle orbital gyrus)		-44	50	-2	5.56
L aIFG (pars orbitalis)		-44	43	-15	5.44
L aIFG (pars triangularis)		-47	46	8	4.37
L vmPFC (Fp1)		-17	63	-8	4.13
L vmPFC (Fp1)		-10	63	-15	4.08
L MFG		-44	46	18	4.02
L vmPFC (Fp1)		-10	66	5	3.67
L vmPFC (Fp1)		-30	60	-5	3.51
L dmPFC, SMA, ACC	17672				
L dmPFC (SFG)		-14	6	62	4.49
L dmPFC (SFG)		-4	33	32	4.30
L dmPFC (SFG)		-17	48	40	4.09
L ACC		-7	38	22	4.04
L dmPFC (SFG)		-20	13	65	4.00
L dmPFC (SFG)		-4	30	42	3.89
L ACC		-4	43	10	3.82
L dmPFC (SFG)		-17	33	55	3.81
L SMA		0	0	62	3.70
L dmPFC (SFG)		-12	3	75	3.65
L cingulate cortex	11719				
L PCC		-2	-32	32	5.34
L ACC		-4	-2	30	4.50
L premotor, somatosensory and inferior frontal cortex	11328				
L PMv		-47	3	22	4.48
L pIFG (pars opercularis)		-50	10	8	4.23
L insula		-34	18	-5	3.51
L insula		-30	16	5	3.51
L PMd		-50	6	45	3.44
L PMv		-50	6	35	3.32
L aIFG (pars triangularis)		-60	18	8	3.32
R inferior occipital cortex	5703				
R inferior occipital gyrus		23	-92	-5	3.72
R calcarine gyrus		16	-82	15	3.61

R posterior middle and inferior temporal gyri	5453				
R pMTG/LTO		66	-50	-5	4.12
R pMTG/LTO		48	-57	2	3.80
R pITG		63	-47	-12	3.56
R pITG		60	-57	-10	3.34
R SMG (PF)	4891	53	-37	52	4.36
L middle occipital gyrus	3844	-30	-90	-2	5.13
R basal ganglia	2297				
R pallidum		10	0	-5	5.53
R caudate nucleus		10	13	2	3.59
L cerebellum	2078				
L cerebellum (lobule VIII)		-12	-67	-50	3.50
L cerebellum (lobule VIIb)		-20	-77	-52	3.41
R premotor and somatosensory cortices	1125				
R PMv		63	6	22	3.52
R S1		66	-10	30	3.42
L thalamus	891	-10	-27	-10	3.96
L basal forebrain (Ch 4)	563	-12	-2	-12	3.74
R cerebellar vermis	453	6	-37	-20	3.54
R cerebellum (lobule VI)	453	33	-37	-32	3.44

Table S5. Conjunction: [Action judgment task: high > low action words] ∩ [Motor localizer: Hand movements > Rest].

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L aSMG/IPS (extending into SPL), somatosensory cortex	11234				
L S2		-42	-42	50	5.73
L SPL (7PC)		-42	-44	55	5.65
L S2		-44	-40	48	5.42
L S2		-50	-40	58	5.22
L SMG (PFt)		-54	-32	45	4.96
L SMG (PF)		-57	-37	32	4.52
L SPL (7PC)		-34	-52	62	4.10
L SMG (PFop)		-50	-22	25	3.42
L PMC	6984				
L PMv		-47	3	20	4.39
L PMv		-50	10	8	4.23
L PMd		-50	3	45	3.40
L PMv		-50	6	35	3.32
R cerebellum	3922				
R cerebellum (lobule VI)		28	-60	-22	4.43
R cerebellum (lobule VI)		26	-67	-25	4.26
R cerebellum (crus I)		40	-60	-28	3.45
R cerebellum (crus I)		46	-57	-30	3.36
R aSMG/IPS, somatosensory cortex	2922				

R S1		50	-34	52	4.14
R S2		50	-37	58	3.94
R S2		40	-34	38	3.34
L/R (pre-)SMA	2719				
L SMA		0	0	62	3.70
L pre-SMA		-10	3	72	3.63
R SMA		3	0	70	3.48
L cerebellum (lobule VI)	2469	-20	-62	-15	3.84
L cerebellum (lobule VI)		-34	-64	-22	3.55
L cerebellum (lobule VI)		-27	-62	-22	3.43
R cerebellum (lobule VIIb)	2172	16	-72	-45	4.23
L pMTG/LTO	1984	-52	-62	5	5.52
L cerebellum (lobule VIIIa)	1406	-12	-67	-50	3.50
L MCC	922	-4	3	32	3.91
L thalamus	844	-10	-27	-10	3.96
R cerebellum (lobule VI)	453	33	-37	-32	3.44
R PMv	438	63	6	22	3.52
R inferior occipital gyrus (V3v)	438	28	-92	-5	3.44
R pMTG/LTO	391	46	-57	5	3.69
L insula	391	-30	16	5	3.51

Table S6. Sound judgment task: high > low sound words.

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L aIFG, MFG / precentral sulcus, vmPFC	28281				
L frontal pole		-47	46	-12	6.07
L vmPFC (Fo2)		-12	18	-18	5.57
L vmPFC (Fo3)		-20	33	-20	5.12
L MFG		-44	16	40	5.1
L aIFG (pars orbitalis)		-37	36	-18	5.07
L insula		-30	23	-10	4.87
L MFG		-40	10	48	4.69
L aIFG (pars triangularis)		-44	48	5	4.65
L aIFG (pars orbitalis)		-50	23	-10	4.3
L aIFG (pars triangularis)		-50	26	18	4.21
L posterior IPL (AG, pSMG, pIPS)	11547				
L AG (PGa)		-44	-62	50	6.14
L AG (PGa)		-37	-72	48	5.08
L IPS (hIP2)		-47	-44	50	4.87
L AG (PGp)		-50	-70	38	4.14
L dmPFC	11094				
L dmPFC (SFG)		-7	33	38	6.93
L dmPFC (SFG)		-4	30	48	5.7
L dmPFC (SFG)		-12	46	38	4.87
L dmPFC (SFG)		-10	28	58	4.39
L pMTG	1766	-57	-42	-12	4.83

R cerebellum (crus I)	1594	38	-77	-42	3.87
L SFG	594	-12	63	22	3.69

Table S7. Conjunction: [Sound judgment task: high > low sound words] ∩ [Auditory localizer: Real sounds > Silence].

Region	**Cluster size (mm³)**	**x**	**y**	**z**	**T**
L aIFG, insula	6266				
L aIFG (pars triangularis)		-47	43	0	4.73
L aIFG (pars orbitalis)		-40	36	-18	4.60
L insula		-30	23	-5	4.19
L aIFG (pars orbitalis)		-50	20	-10	4.03
L aIFG, MFG / precentral sulcus	5391				
L aIFG (pars orbitalis)		-47	18	32	4.65
L aIFG (pars triangularis)		-50	26	18	4.21
L precentral sulcus		-37	3	38	3.34
L vmPFC	2156				
L vmPFC (Fo1)		-14	33	-20	4.09
L vmPFC (Fo1)		-7	50	-20	4.00
L vmPFC (Fo1)		-14	43	-18	3.55
L vmPFC (Fo1)		-10	33	-22	3.52
L vmPFC (Fo2)		-7	23	-20	3.48
L dmPFC (SFG)	1453	-2	28	48	4.54
L IPS (hIP3)	1047	-30	-57	40	4.22
L IPS (hIP3)		-32	-64	48	3.64
R cerebellum	516				
R cerebellum (crus I)		36	-70	-42	3.60
R cerebellum (crus II)		28	-74	-45	3.35
L pMTG	438	-62	-44	-12	3.93
L pMTG		-57	-47	-12	3.79

Table S8. Interaction: Action judgment task > Sound judgment task for high > low action words (inclusively masked with [Action judgment task: high > low action words]).

Region	**Cluster size (mm³)**	**x**	**y**	**z**	**T**
L PMv, pIFG, insula	6172				
L pIFG (pars opercularis)		-40	8	25	5.90
L PMv		-37	3	35	5.25
L insula		-34	20	-5	5.07
L insula		-30	18	2	4.76
L pIFG (pars opercularis)		-52	16	-2	4.46
L pIFG (pars opercularis)		-60	18	10	4.03
L pIFG (pars opercularis)		-57	10	22	3.40

L dmPFC	5484				
L dmPFC (SFG)		-4	28	42	6.89
L ACC		-7	40	20	3.69
L dmPFC (SFG)		-10	43	42	3.64
L dmPFC (SFG)		-14	33	58	3.64
R lingual gyrus (V3v)	2375	23	-94	-8	5.57
L middle occipital gyrus (h0c4lp)	2328	-24	-94	-2	5.41
L (pre-)SMA	1391	-14	16	68	3.37
L caudate nucleus	1344	-10	16	0	4.53
L caudate nucleus		-10	3	8	3.51
L ACC	1016	-4	0	30	4.17
L thalamus	516	-12	-27	-10	4.38
L thalamus		-7	-17	-2	3.44
R pallidum	359	8	0	-5	3.60

Table S9. Interaction: Action judgment task > Lexical decision task for high > low action words (inclusively masked with [Action judgment task: high > low action words]).

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L SMG/IPS, SPL	8938				
L IPS (hIP2)		-44	-50	50	5.00
L SPL (7A)		-34	-62	55	4.25
L IPS (hIP3)		-30	-64	40	4.13
L pMTG/LTO, pITG	5172				
L pMTG		-52	-40	-10	4.78
L pMTG/LTO		-52	-60	5	4.23
L pITG		-57	-62	-8	3.99
L anterior inferior frontal cortex	2891				
L frontal pole		-42	50	-10	5.30
L MFG		-44	50	5	3.99
L aIFG (pars orbitalis)		-52	38	-10	3.86
R cerebellum	1547				
R cerebellum (crus I)		40	-60	-42	4.46
R cerebellum (crus I)		40	-62	-32	3.72
L caudate nucleus	828	-10	13	0	5.12
L aIFG (pars orbitalis)	719	-17	26	-20	5.12
R pallidum	594	10	0	-5	6.51
L PMv, pIFG	500				
L pIFG (pars opercularis)		-60	18	8	4.11
L pIFG (pars opercularis)		-50	13	0	3.44

Table S10. Conjunction of interactions: [Action judgment task > Sound judgment task for high > low action words] ∩ [Action judgment task > Lexical decision task for high > low action words] (both inclusively masked with [Action judgment task: high > low action words]).

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L SMG/IPS, SPL	8625				
L IPS (hIP2)		-44	-50	50	5.00
L SPL (7A)		-34	-62	55	4.25
L SPL (7A)		-30	-64	52	4.24
L IPS (hIP3)		-30	-64	40	4.13
L aSMG (PF)		-60	-40	45	3.49
L pMTG/ITG	3547				
L pMTG		-54	-42	-10	4.73
L pITG		-54	-60	-10	3.81
L anterior inferior frontal cortex	2875				
L frontal pole		-44	50	-8	4.99
L aIFG (pars orbitalis)		-40	46	-12	4.68
L aIFG (pars triangularis)		-44	48	5	3.89
L aIFG (pars orbitalis)		-52	38	-10	3.81
R cerebellum (crus I)	1125	40	-60	-40	4.11
R cerebellum (crus I)		43	-60	-30	3.24
L caudate nucleus	719	-10	16	0	4.53
L vmPFC	688				
L vmPFC (Fo3)		-20	26	-20	4.56
L vmPFC (Fo2)		-17	23	-18	4.27
L pIFG (pars opercularis)	500	-54	16	10	3.54
L pIFG (pars opercularis)		-52	13	8	3.54
L pIFG (pars opercularis)		-60	18	8	3.32
L pMTG/LTO	406	-62	-50	2	3.48

Table S11. Interaction: Sound judgment task > Action judgment task for high > low sound words (inclusively masked with [Sound judgment task: high > low sound words]).

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
L dmPFC (SFG)	1406	-7	33	38	5.91
L aIFG (pars orbitalis)	891	-47	46	-8	5.61
L insula	94	-30	23	-10	4.58

Table S12. Interaction: Sound judgment task > Lexical decision task for high > low sound words (inclusively masked with [Sound judgment task: high > low sound words]).

Region	Cluster size (mm³)	x	y	z	T
L posterior IPL (AG, pSMG, pIPS)	5953				
L AG (PGa)		-44	-62	50	6.04
L IPS (hIP2)		-50	-44	50	4.10
L dmPFC (SFG)	3281	-4	33	38	5.96
L anterior inferior frontal cortex	2719				
L frontal pole		-47	46	-12	4.98
L aIFG (pars orbitalis)		-37	38	-15	4.63
L frontal pole		-40	56	-5	3.94
L aIFG (pars orbitalis)		-54	33	-8	3.59
L aIFG (pars orbitalis)	734	-40	20	-10	4.28
L aIFG (pars orbitalis)		-30	26	-10	4.27
L MFG / precentral sulcus	672				
L MFG		-42	13	48	4.05
L precentral sulcus		-40	6	40	3.73
L vmPFC (Fo2)	406	-12	18	-18	4.77
L pMTG	328	-57	-40	-12	4.26
L aIFG (pars triangularis)	328	-52	18	8	3.84

Table S13. Conjunction of interactions: [Sound judgment task > Action judgment task for high > low sound words] ∩ [Sound judgment task > Lexical decision task for high > low sound words] (both inclusively masked with [Sound judgment task: high > low sound words]).

Region	Cluster size (mm³)	x	y	z	T
L dmPFC (SFG)	1406	-7	33	38	5.91
L aIFG (pars orbitalis)	875	-47	46	-10	4.89

Table S14. Multimodal conceptual regions. Conjunction: [Action judgment task: high > low action words] ∩ [Sound judgment task: high > low sound words].

Region	Cluster size (mm³)	x	y	z	T
L posterior IPL (AG, pSMG, pIPS)	10578				
L SMG (PFm)		-44	-60	50	5.88
L IPS (hIP2)		-47	-44	50	4.87
L IPS (hIP3)		-32	-64	42	4.58
L aIFG, vmPFC	8484				
L aIFG (pars orbitalis)		-44	43	-15	5.44
L vmPFC (middle orbital gyrus)		-47	48	-5	5.26
L vmPFC (Fo2)		-14	20	-20	4.76
L vmPFC (Fo3)		-20	30	-20	4.73
L dmPFC	3859				
L dmPFC (SFG)		-4	33	32	4.30

L dmPFC (SFG)		-4	30	42	3.89
L dmPFC (SFG)		-14	48	40	3.77
L ACC		-7	38	25	3.57
L dmPFC (SFG)		-14	33	52	3.40
L dmPFC (SFG)		-14	38	50	3.39
L pMTG	1766	-57	-42	-12	4.83
R cerebellum (crus I/II)	1594	38	-77	-42	3.87
L aIFG (pars triangularis)	672	-52	16	8	3.52

Subject-specific fROI Analysis

The following tables show the results of the subject-specific functional region of interest (fROI) analysis. A 4-way repeated-measures ANOVA with the factors REGION (all fROIs), TASK (lexical decision, sound judgment, action judgment), SOUND (high, low), and ACTION (high, low) revealed a significant 4-way interaction (F(32,543)=2.074, p=.01). We resolved this interaction using step-down ANOVAs within each fROI (post-hoc comparisons were Bonferroni-Holm corrected). Bold font highlights significant effects, italic font highlights trends ($p < 0.1$ / did not survive correction). SF = sound feature; AF = action feature; L = lexical decision; S = sound judgment; A = action judgment.

Table S15. Motor fROIs (identified using the conjunction [Action judgment: high > low action words] ∩ [Motor localizer: hand movements > rest]).

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
Left aSMG/IPS	**TASK x ACTION (F(2,78)=3.886, p=.025)**	ACTION (F(1,39)=.046, p=.831)	ACTION (F(1,39)=.406, p=.528)	**ACTION (F(1,39)=11.070, p=.002)** Task-specificity: **A vs. S for high > low AF (t(39)=2.228, p=.032); A vs. L for high > low AF (t(39)=2.595, p=.013)**
Left pMTG/LTO	**TASK x ACTION (F(2,78)=3.190, p=.049)**	ACTION (F(1,39)=.606, p=.441)	ACTION (F(1,39)=.092, p=.764)	**ACTION (F(1,39)=6.617, p=.014)** Task-specificity: *A vs. S for high > low AF (t(39)=2.178, p=.035); A vs. L for high > low AF (t(39)=1.954, p=.058)*
Left PMv	**TASK x ACTION (F(2,78)=4.842, p=.024)**	ACTION (F(1,39)=.184, p=.670)	*ACTION (F(1,39)=5.629, p=.023)*	*ACTION (F(1,39)=3.191, p=.082)* Task-specificity: **[A vs. S for high > low AF (t(39)=2.440, p=.019)]**; [A vs. L for high > low AF (t(39)=1.565, p=.126)]
Right PMv	*TASK x ACTION (F(2,78)=2.498, p=.097)*	ACTION (F(1,39)=.784, p=.381)	ACTION (F(1,39)=.298, p=.588)	*ACTION (F(1,39)=3.593, p=.065)* Task-specificity: *A vs. S for high > low AF (t(39)=2.102, p=.042);* A vs. L for high > low AF (t(39)=1.379, p=.176)

Table S16. Auditory fROIs (identified using the conjunction [Sound judgment: high > low sound words] ∩ [Auditory localizer: real sounds > silence]).

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
Left aIFG	**TASK x SOUND x ACTION (F(2,78)=3.642, p=.032)**	SOUND (F(1,39)=.112, p=.740); ACTION (F(1,39)=.253, p=.618); SOUND x ACTION (F(1,39)=1.503, p=.228)	**SOUND x ACTION (F(1,39)=13.242, p<.001)** **[high SF, low AF] vs. [high SF, high AF] (t(39)=3.934, p<.001); [high SF, low AF] vs. [low SF, low AF] (t(39)=4.184, p<.001);** [high SF, high AF] vs. [low SF, high AF] (t(39)=-.625, p=.536); [low SF, high AF] vs. [low SF, low AF] (t(39)=.613, p=.543) Task-specificity: **S vs. A for high > low SF (t(39)=2.377, p=.022); S vs. L for high > low SF (t(39)=2.256, p=.03)**	SOUND (F(1,39)=.229, p=.635); ACTION (F(1,39)=.917, p=.344); SOUND x ACTION (F(1,39)=2.392, p=.13)
Left MFG	**TASK x SOUND (F(2,78)=6.750, p=0.003);** TASK x SOUND x ACTION (F(2,78)=2.332, p=0.105)	SOUND (F(1,39)=.204, p=.654)	**SOUND (F(1,39)=17.764, p<.001)** Task-specificity: **S vs. A for high > low SF (t(39)=2.378, p=.025); S vs. L for high > low SF (t(39)=3.344, p=.002)**	SOUND (F(1,39)=.794, p=.378)
Left precentral sulcus	**TASK x SOUND x ACTION (F(2,78)=4.476, p=.020)**	SOUND (F(1,39)=.064, p=.802); ACTION (F(1,39)=.089, p=.767); SOUND x ACTION (F(1,39)=.014, p=.905)	**SOUND x ACTION (F(1,39)=11.002, p=.002)** **[high SF, low AF] vs. [high SF, high AF] (t(39)=3.659, p<.001); [high SF, low AF] vs. [low SF, low AF] (t(39)=3.523, p=.001);** [high SF, high AF] vs. [low SF, high AF] (t(39)=-.220, p=.827); [low SF, high AF] vs. [low SF, low AF] (t(39)=.892, p=.378) Task-specificity: *S vs. A for high > low SF (t(39)=1.720, p=.093); S vs. L for high > low SF (t(39)=2.322, p=.026)*	SOUND (F(1,39)=.249, p=.620); ACTION (F(1,39)=.821, p=.370); SOUND x ACTION (F(1,39)=.004, p=.952)

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
Left dmPFC	*TASK x SOUND x ACTION (F(2,78)=3.259, p=.053);* **TASK x SOUND (F(2,78)=7.224, p=.002); TASK x ACTION (F(2,78)=4.891, p=.01)**	SOUND (F(1,39)=.288, p=.595); ACTION (F(1,39)=.131, p=.719); SOUND x ACTION (F(1,39)=.051, p=.823)	**SOUND x ACTION (F(1,39)=6.988, p=.012)** **[high SF, low AF] vs. [high SF, high AF] (t(39)=3.307, p=.002); [high SF, low AF] vs. [low SF, low AF] (t(39)=3.783, p<.001);** [high SF, high AF] vs. [low SF, high AF] (t(39)=.276, p=.791); [low SF, high AF] vs. [low SF, low AF] (t(39)=.712, p=.481) Task-specificity: **S vs. A for high > low SF (t(39)=2.909, p=.006); S vs. L for high > low SF (t(39)=3.250, p=.002)**	SOUND (F(1,39)=.068, p=.796); ACTION (F(1,39)=.911, p=.346); SOUND x ACTION (F(1,39)=1.909, p=.175)
Left pIPS	**TASK x SOUND (F(2,78)=9.098; p<.001); TASK x ACTION (F(2,78)=5.443; p=.007)**	SOUND (F(1,39)=.395, p=.534); ACTION (F(1,39)=.281, p=.599)	**SOUND (F(1,39)=23.250, p<.0001);** ACTION (F(1,39)=.014, p=.908) Task-specificity: **S vs. A for high > low SF (t(39)=2.558, p=.015); S vs. L for high > low SF (t(39)=4.227, p<.0001)**	*SOUND (F(1,39)=5.326, p=.026);* **ACTION (F(1,39)=11.157, p=.002)** Task-specificity: **A vs. S for high > low AF (t(39)=2.719, p=.01); A vs. L for high > low AF (t(39)=2.733, p=.009)**

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
Left pSTG/MTG	**TASK x SOUND (F(2,78)=3.916; p=.025);** **TASK x ACTION (F(2,78)=6.808; p=.002)**	SOUND (F(1,39)=.296, p=.589); ACTION (F(1,39)=1.904, p=.175)	**SOUND (F(1,39)=6.536, p=.015);** ACTION (F(1,39)=1.768, p=.191) [high SF, high AF] vs. [low SF, high AF] (t(39)=-.220, p=.827); [low SF, high AF] vs. [low SF, low AF] (t(39)=.892, p=.378) Task-specificity: **S vs. A for high > low SF (t(39)=2.466, p=.018);** **S vs. L for high > low SF (t(39)=2.280, p=.028)**	SOUND (F(1,39)=.153, p=.698); **ACTION (F(1,39)=8.991, p=.005)** Task-specificity: **A vs. S for high > low AF (t(39)=3.939, p<.001);** *A vs. L for high > low AF (t(39)=1.999, p=.053)*

Table S17. Multimodal fROIs (identified using the conjunction [Action judgment: high > low action words] ∩ [Sound judgment: high > low sound words]).

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
Left aIFG	**TASK x SOUND x ACTION (F(2,78)=3.712, p=.034)**	SOUND (F(1,39)=.007, p=.933); ACTION (F(1,39)=.044, p=.834); *SOUND x ACTION (F(1,39)=3.254, p=.079)*	**SOUND x ACTION (F(1,39)=12.458, p=.001)** **[high SF, low AF] vs. [high SF, high AF] (t(39)=3.491, p=.001);** **[high SF, low AF] vs. [low SF, low AF] (t(39)=4.365, p<.0001);** [high SF, high AF] vs. [low SF, high AF] (t(39)=-.082, p=.935); *[low SF, high AF] vs. [low SF, low AF] (t(39)=1.945, p=.059)* Task-specificity: **S vs. A for high > low SF (t(39)=3.605, p<.001); S vs. L for high > low SF (t(39)=3.271, p=.002)**	SOUND (F(1,39)=1.376, p=.248); **ACTION (F(1,39)=18.876, p<.0001);** SOUND x ACTION (F(1,39)=.521, p=.475) Task-specificity: **A vs. S for high > low AF (t(39)=4.046, p<.001); A vs. L for high > low AF (t(39)=3.537, p=.001)**
Left pIPL	**TASK x SOUND (F(2,78)=8.148; p=.001);** **TASK x ACTION (F(2,78)=7.478; p=.002)**	SOUND (F(1,39)=.308, p=.582); ACTION (F(1,39)=1.696, p=.2)	**SOUND (F(1,39)=21.818, p<.0001);** ACTION (F(1,39)=.535, p=.469)	SOUND (F(1,39)=.370, p=.546); **ACTION (F(1,39)=18.742, p<.001)**

Region	Full ANOVA	Lexical decision	Sound judgment	Action judgment
			Task-specificity: **S vs. A for high > low SF (t(39)=2.846, p=.007); S vs. L for high > low SF (t(39)=4.5, p<.0001)**	Task-specificity: **A vs. S for high > low AF (t(39)=3.132, p=.003); A vs. L for high > low AF (t(39)=3.069, p=.004)**
Left pMTG	**TASK x SOUND (F(2,78)=5.512; p=.006);** **TASK x ACTION (F(2,78)=6.222; p=.003)**	SOUND (F(1,39)=.187, p=.668); ACTION (F(1,39)=1.185, p=.283)	**SOUND (F(1,39)=11.425, p=.002);** ACTION (F(1,39)=.636, p=.430)	SOUND (F(1,39)=.035, p=.852); **ACTION (F(1,39)=10.265, p=.003)**
			Task-specificity: **S vs. A for high > low SF (t(39)=2.730, p=.009); S vs. L for high > low SF (t(39)=3.072, p=.004)**	Task-specificity: **A vs. S for high > low AF (t(39)=3.411, p<.002); A vs. L for high > low AF (t(39)=2.434, p=.02)**

Supplementary material for study 2 (fMRI connectivity)

Temporal Signal-to-Noise Ratio (tSNR)

We employed a dual-echo sequence to minimize susceptibility artifacts and maximize BOLD sensitivity throughout the entire brain (Poser et al. 2006; Halai et al. 2014), including in regions suffering from signal dropout in single-echo EPI, such as the anterior temporal lobe (ATL) (Devlin et al. 2000). To assess the signal quality in the ATL and other regions, we computed the temporal signal-to-noise ratio (tSNR) by dividing the mean signal in each voxel by the standard deviation of the voxel's signal over time (Friedman et al. 2006; Fairhall and Caramazza 2013). While signal quality was generally higher in regions outside vs. inside the ATL (Table S1), tSNR within the ATL was clearly above 20, which is considered the threshold for signal detection at 3T (Friedman et al. 2006; Binder et al. 2011).

Table S1. Temporal signal-to-noise ratio (tSNR) in anatomical regions-of-interest (ROIs). Bilateral ROIs were extracted from the Harvard-Oxford atlas (http://www.fmrib.ox.ac.uk/fsl/) and thresholded at 30% probability for a voxel to belong to a region.

Region	**mean tSNR (SD)**	**Region**	**mean tSNR (SD)**	**Region**	**mean tSNR (SD)**
Anterior temporal lobe (ATL)		**Posterior temporal lobe**		**Other regions**	
Temporal pole	61.62 (17.96)	Heschl's gyrus	80.93 (14.31)	AG	122.89 (17.59)
aSTG	85.89 (12.73)	pSTG	101.54 (13.47)	Occipital pole	108.39 (27.56)
aMTG	79.79 (9.63)	pMTG	94.36 (14.95)	Postcentral gyrus	120.16 (19.78)
aITG	62.99 (10.5)	pITG	67.61 (16.96)	aIFG	99.0 (30.36)
aFG	50.53 (12.64)			pIFG	103.26 (10.05)

STG = superior temporal gyrus; MTG = middle temporal gyrus; ITG = inferior temporal gyrus; FG = fusiform gyrus; AG = angular gyrus; IFG = inferior frontal gyrus; a (prefix) = anterior; p (prefix) = posterior.

Supplementary Results

Psychophysiological interactions (PPI)

“Amodal seed” (left ATL)

As the anterior temporal lobe (ATL) is widely considered a central, amodal “hub” of the conceptual system (Patterson et al. 2007; Jefferies 2013; Lambon Ralph et al. 2016), we performed a supplementary PPI analysis seeding in the amodal ATL. The “amodal seed” was defined as the ATL region most strongly engaged for “general” conceptual processing, using the contrast [lexical decision: words > pseudowords]. This region was located in the left ATL (containing parts of the anterior superior, middle, and inferior temporal gyri). All other methods were identical to our other PPI analyses (see Materials and Methods).

We found that during sound judgments, sound feature retrieval (high > low sound words) significantly increased coupling between the amodal seed (left ATL) and bilateral precuneus / posterior cingulate cortex (PC/PCC) (Figure S1A; Table S10). This PC/PCC region did not overlap with the auditory localizer (Figure S1B), indicating that it constitutes a higher-level, cross-modal region. Interaction analyses further revealed a significant TASK x SOUND interaction in bilateral PC/PCC, driven by a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during action judgments and lexical decisions (Figure S1C; Table S11). Action features (high > low action words) did not induce significant coupling changes during sound judgments.

During action judgments, we found no significant effects that survived stringent multiple comparisons correction (voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). However, an exploratory analysis at $p < 0.001$ uncorrected (extent > 10 voxels) showed that action feature retrieval (high > low action words) selectively increased coupling between the amodal seed (left ATL) and the left dmPFC (Figure S2A; Table S12). Left dmPFC did not overlap with the somatomotor localizer (Figure S2B), indicating that it represents a higher-level, cross-modal area. Interaction analyses revealed a TASK x ACTION interaction within left dmPFC, which was driven by a larger coupling increase for action features (high vs. low action words) during action judgments than sound judgments and lexical decisions (Figure S2C; Table S13). Sound features (high > low sound words) did not increase coupling during action judgments (even at $p < 0.001$ uncorrected).

We found no significant effects during lexical decisions (even at $p < 0.001$ uncorrected).

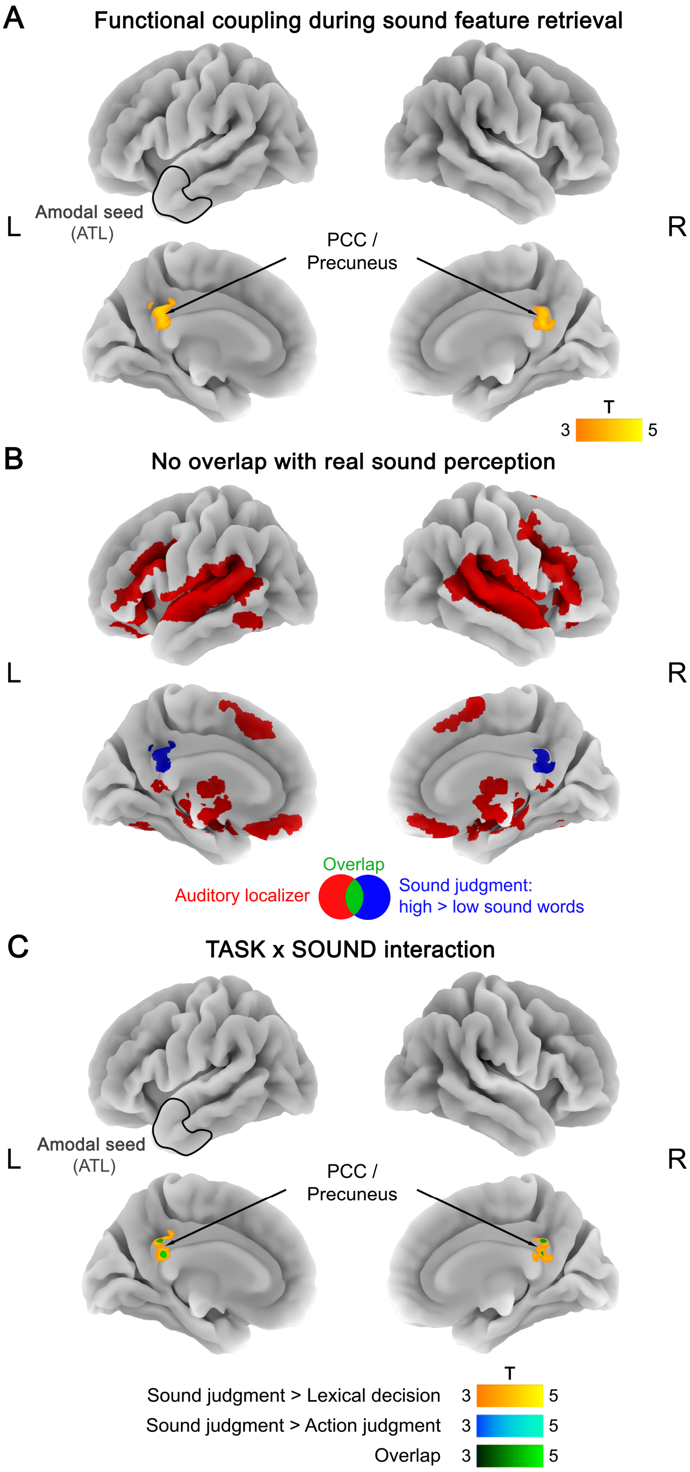

Figure S1. (A) Functional coupling with the amodal seed (left ATL) during sound feature retrieval (sound judgments: high > low sound words). (B) No overlap between functional coupling with the amodal seed during sound feature retrieval (blue) and activation for the auditory localizer (red; real sounds > silence). (C) TASK x SOUND interaction in functional coupling with the amodal seed, reflecting a stronger coupling increase for sound features (high vs. low sound words) during sound judgments than during lexical decisions (yellow), action judgments (blue), or both (green). All statistical maps were thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected.

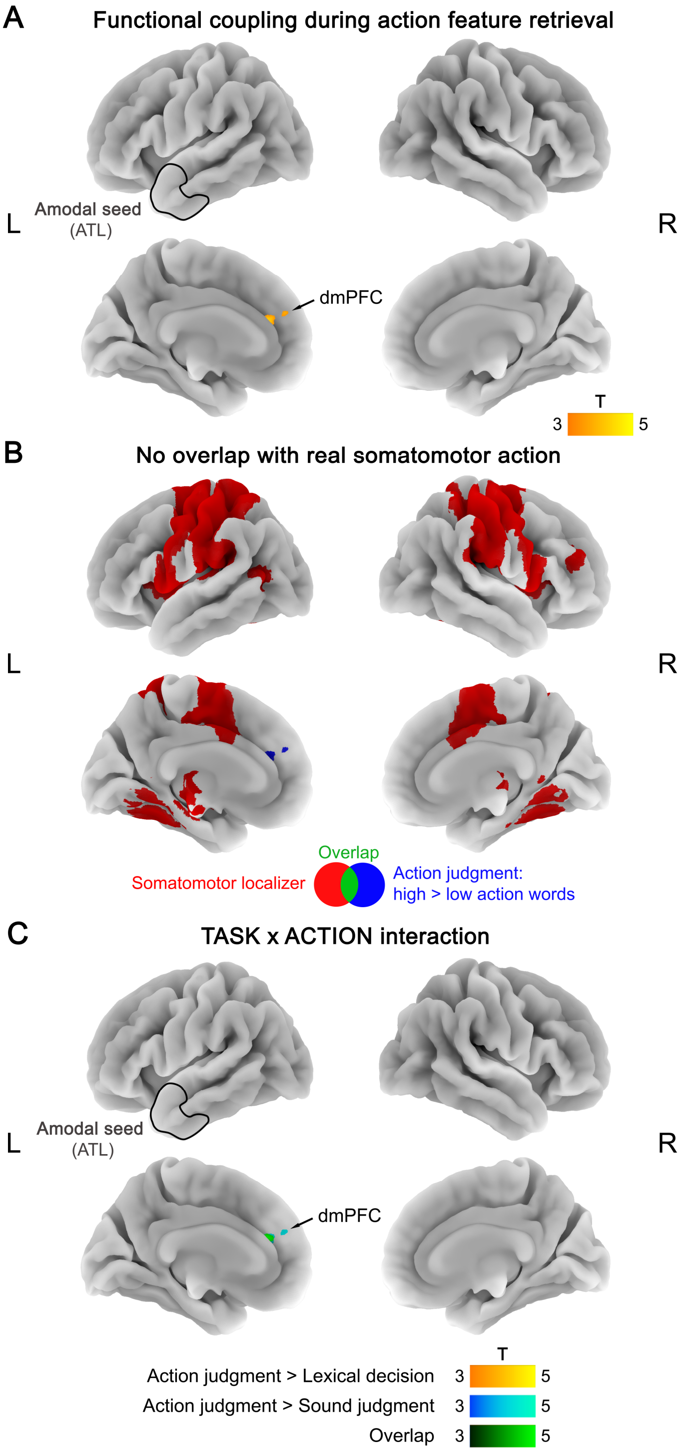

Figure S2. (A) Functional coupling with the amodal seed (left ATL) during action feature retrieval (action judgments: high > low action words). (B) No overlap between functional coupling with the amodal seed during action feature retrieval (blue) and activation for the somatomotor localizer (red; hand movements > rest). (C) TASK x ACTION interaction in functional coupling with the amodal seed, reflecting a stronger coupling increase for action features (high vs. low action words) during action judgments than during lexical decisions (yellow), sound judgments (blue), or both (green). Note that these results come from an exploratory analysis thresholded at $p < 0.001$ uncorrected (extent > 10 voxels).

Ratings–RT correlations

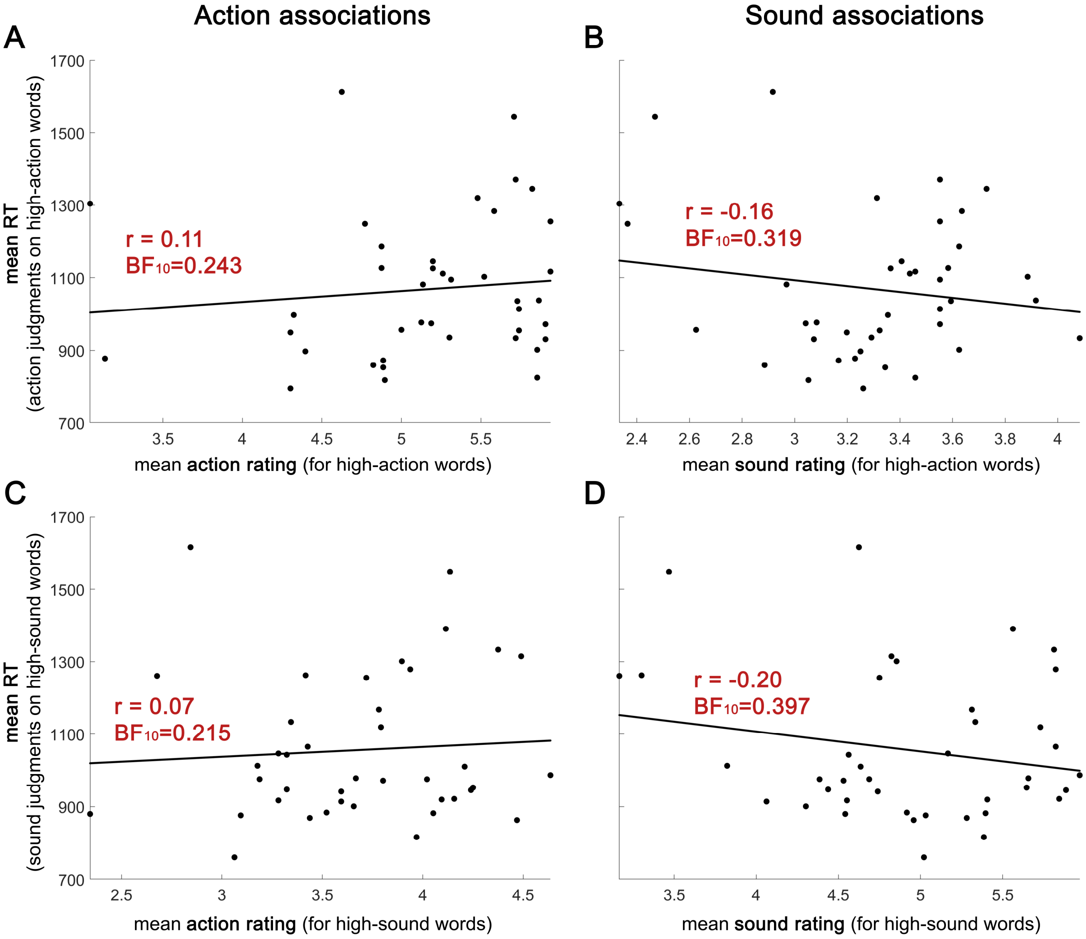

Figure S3. Mean response times (RTs) for action judgments on high-action words were not associated with the mean action (A) or sound (B) ratings for the same words. Similarly, mean RTs for sound judgments on high-sound words were not associated with the mean sound (D) or action (C) ratings for these words.

Tables of coordinates

The following tables report brain regions showing task-dependent functional coupling with a certain seed region during conceptual processing. Coordinates are in MNI space. Up to 3 peaks per cluster are reported (> 8 mm apart). AAC = auditory association cortex; ATL = anterior temporal lobe; dmPFC = dorsomedial prefrontal cortex; FG = fusiform gyrus; IFG = inferior frontal gyrus; IPL = inferior parietal lobe; ITG = inferior temporal gyrus; LOC = lateral occipital cortex; MCC = middle cingulate cortex; MTG = anterior middle temporal gyrus; M1 = primary motor cortex; PCC = posterior cingulate cortex; SPL = superior parietal lobe; S1 = primary somatosensory cortex; SPL = superior parietal lobe; STS = posterior superior temporal sulcus; a (prefix): anterior; p (prefix): posterior; L = left; R = right.

Table S2. Brain regions showing functional coupling with the motor seed (left aIPL/S1) during action feature retrieval.

Region	Cluster size (mm^3)	x	y	z	T
Action judgments: high > low action words					
L ATL	734				
L aITG		-62	-17	-25	4.57
L aMTG		-64	-10	-22	4.15
L aITG		-60	-27	-28	3.94

Table S3. TASK x ACTION interaction in functional coupling with the motor seed (left aIPL/S1).

Region	Cluster size (mm^3)	x	y	z	T
Action judgment > lexical decision for high vs. low action words					
L ATL (aITG)	94	-60	-27	-28	3.82
L ATL (aMTG)	31	-67	-14	-25	3.45

Table S4. Brain regions showing functional coupling with the auditory seed (left MFG/PreCS) during sound feature retrieval.

Region	Cluster size (mm^3)	x	y	z	T
(A) Sound judgments: high > low sound words					
L thalamus	1781				
L thalamus (temporal)		-4	-22	12	4.91
L thalamus (prefrontal)		-17	-17	12	4.79
L thalamus (parietal)		-17	-22	15	4.76
R SPL	750				
R SPL (7PC)		23	-54	58	4.66
R SPL (7A)		18	-62	55	4.52
R SPL (5L)		13	-50	58	3.52
R FG	703				
R FG2		-42	-70	-10	4.49

Region	Cluster size (mm³)	x	y	z	T
R FG4		-40	-60	-10	4.39
R FG2		-37	-67	-12	4.06
(B) Overlap with auditory localizer					
L thalamus	156				
L thalamus (temporal)		-7	-14	12	3.72
L thalamus (prefrontal)		-14	-10	12	3.52

Table S5. TASK x SOUND interaction in functional coupling with the auditory seed (left MFG/PreCS).

Region	Cluster size (mm³)	x	y	z	T
(A) Sound judgment > lexical decision for high vs. low sound words					
R SPL	531				
R SPL (7PC)		23	-54	58	4.79
R SPL (7A)		23	-60	58	4.68
R SPL (7A)		16	-60	58	4.01
L FG (FG4)	94	-40	-60	-10	4.01
L Thalamus (prefrontal)	47	-4	-20	8	3.94
L Thalamus (parietal)	31	-17	-22	12	3.43
L FG (FG2)	31	-34	-67	-12	3.83
(B) Sound judgment > action judgment for high vs. low sound words					
L FG	266				
L FG2	0	-42	-67	-10	4.62
L FG4	0	-40	-62	-10	4.28
R SPL (7A)	156	20	-57	58	3.95
(C) Overlap					
R SPL (7A)	156	20	-57	58	3.95

Table S6. Brain regions showing functional coupling with the multimodal seed (left PPC) during action feature retrieval.

Region	Cluster size (mm³)	x	y	z	T
(A) Action judgments: high > low action words					
R pSTS	1156				
R pSTS		50	-42	15	4.56
R pSTS		58	-44	5	4.07
L M1 / SPL	1000				
L SPL (5L)		-12	-50	75	4.33
L M1 (4a)		-7	-40	80	4.04
L M1 (4a)		-10	-37	72	4.00
L M1 / S1	828				

Region	Cluster size (mm^3)	x	y	z	T
L M1 (4a)		-22	-30	58	4.26
L M1		-30	-24	55	4.10
L S1 (3b)		-44	-22	58	3.82
(B) Overlap with motor localizer					
L M1 / S1	766				
L M1		-30	-24	55	4.10
L M1 (4p)		-24	-30	58	3.85
L S1 (3b)		-44	-22	58	3.82
L M1 (4a)	188	-20	-37	72	3.86

Table S7. TASK x ACTION interaction in functional coupling with the multimodal seed (left PPC).

Region	Cluster size (mm^3)	x	y	z	T
(A) Action judgment > lexical decision for high vs. low action words					
R pSTS	156	60	-44	2	4.10
(B) Action judgment > sound judgment for high vs. low action words					
R pSTS	844				
R pSTS		58	-47	10	4.58
R pSTS		56	-44	8	4.58
L M1/S1	172				
L M1 (4a)		-12	-40	72	3.84
L S1 (3b)		-17	-40	70	3.59
L M1	125				
L M1 (4a)		-40	-24	58	3.92
L M1 (4a)		-40	-24	65	3.47
L M1	94				
L M1 (4a)		-14	-32	80	3.99
L M1 (4a)		-20	-34	78	3.84
(C) Overlap					
R pSTS	156	60	-44	2	4.01

Table S8. Brain regions showing functional coupling with the multimodal seed (left PPC) during sound feature retrieval.

Region	Cluster size (mm^3)	x	y	z	T
(A) Sound judgments: high > low sound words					
L/R precuneus / medial SPL / MCC	11016				
R precuneus		3	-47	48	5.38
R SPL (5Ci)		10	-32	40	5.20
R MCC		3	-42	42	5.07
L/R dmPFC / MCC	10891				

Region	Cluster size (mm³)	x	y	z	T
L dmPFC		0	8	45	5.58
L MCC		0	-14	40	5.26
L MCC		-2	18	35	5.05
L cerebellum / high-level visual cortex	2016				
L cerebellum (lobule VI)		-2	-70	-12	4.85
L cerebellum (lobule VI)		-17	-72	-25	4.51
L V4 (hOc4v)		-20	-72	-15	4.49
L S1	1688				
L S1 (area 2)		-44	-37	58	4.75
L S1 (area 2)		-47	-34	55	4.47
L S1 (area 3b)		-42	-24	48	4.24
L/R early visual cortex	1641				
R V1 (hOc1)		8	-64	5	4.70
L V1 (hOc1)		-12	-82	10	4.08
R V2 (hOc2)		6	-74	12	4.01
R high-level visual cortex	1578				
R pITG		56	-62	-10	4.54
R pITG (hOc4la)		56	-64	-5	4.49
R pMTG		50	-44	-5	4.35
R LOC	1531				
R LOC (middle occipital)		38	-72	28	4.50
R LOC (middle occipital)		40	-70	25	4.29
R LOC (middle occipital)		33	-70	35	3.76
L/R thalamus	1516				
L thalamus (prefrontal)		-10	-12	10	5.01
R thalamus (temporal)		6	-24	15	4.57
L thalamus (prefrontal)		-7	-22	8	4.32
R IPL	1453				
R IPL (PFcm)		60	-30	25	4.85
R IPL (PFop)		58	-20	25	4.42
R IPL (PF)		68	-27	28	4.28
R dmPFC	1344				
R dmPFC (SFG)		20	10	65	4.54
R dmPFC (SFG)		18	6	70	4.06
R dmPFC (SFG)		16	0	72	3.96
L LOC	1125				
L LOC (middle occipital)		-24	-74	30	4.33
L LOC (superior occipital)		-24	-67	32	4.20
L precuneus		-14	-70	30	3.97
R IPL	938				
R IPL (PFm)		60	-47	32	4.46
R IPL (PFm)		50	-44	30	4.02
R IPL (PF)		63	-37	38	3.94
L LOC	891				
L LOC (middle occipital)		-27	-80	12	4.65

Region	Cluster size (mm^3)	x	y	z	T
L LOC (hOc4lp)		-32	-90	8	4.05
L LOC (hOc4lp)		-34	-87	10	3.89
L AAC / IFG	844				
L AAC (TE 3)		-52	10	-8	5.13
L IFG (pars triangularis)		-47	20	-2	3.49
(B) Overlap with auditory localizer					
R IPL (PFcm)	594				
R IPL (PFcm)		60	-30	25	4.55
R IPL (PFcm)		50	-32	22	4.09
L thalamus	391				
L thalamus (prefrontal)		-10	-12	10	4.57
L thalamus (prefrontal)		-14	-10	10	4.20
L/R dmPFC	344				
L/R dmPFC		0	8	58	3.94
R dmPFC		3	0	60	3.52
L AAC (TE 3)	344	-52	10	-8	5.13
L/R dmPFC	281	0	26	48	4.10
R thalamus (prefrontal)	234	10	-14	10	4.29
L cerebellum (lobule VI)	219	-24	-67	-22	4.32

Table S9. TASK x SOUND interaction in functional coupling with the multimodal seed (left PPC).

Region	Cluster size (mm^3)	x	y	z	T
(A) Sound judgment > lexical decision for high vs. low sound words					
R SPL / IPS	3047				
R SPL (7PC)		28	-52	55	5.66
R SPL (7A)		23	-64	58	5.65
R precuneus		13	-60	55	5.54
R high-level visual cortex	1422				
R LOC (hOc4la)		48	-74	-5	4.84
R ITG		53	-54	-10	4.81
R LOC (hOc4la)		50	-80	-8	4.61
R MCC / precuneus	1375				
R MCC		3	-42	42	4.74
R MCC (5M)		6	-37	50	4.11
R precuneus (5Ci)		8	-44	50	4.09
L S1	1297				
L S1 (area 1)		-32	-42	65	4.94
L S1 (area 3b)		-42	-22	50	4.66
L S1 (area 2)		-40	-42	55	4.30
R LOC	750				
R LOC (superior occipital)		30	-74	40	5.40
R LOC (middle occipital)		36	-72	25	3.73

Region	**Cluster size (mm³)**	**x**	**y**	**z**	**T**
L MCC	719				
L MCC		0	8	32	4.33
L MCC		-2	16	35	4.29
R MCC		6	16	38	3.92
L SPL	609				
L SPL (5L)		-17	-42	75	5.10
L Paracentral Lobule		-10	-37	70	4.83
L Paracentral Lobule		-10	-40	78	4.45
L LOC / precuneus	484				
L LOC (middle occipital)		-24	-74	30	5.13
L precuneus		-14	-70	32	3.91
L LOC (superior occipital)		-17	-77	30	3.89
L LOC	453				
L LOC (middle occipital)		-34	-80	10	4.23
L LOC (hoc4la)		-40	-82	10	4.06
L LOC (hoc4lp)		-32	-90	8	3.82
R MCC	422	10	-34	35	5.31
R early visual cortex	422				
R V1 (hOc1)		8	-70	5	4.01
R V2 (hOc2)		6	-74	12	3.93
L/R dmPFC	375				
R dmPFC		6	0	62	4.06
L/R dmPFC		0	6	58	3.74
R dmPFC		3	-4	60	3.73
L AAC (TE 3)	328	-52	10	-5	4.54
L/R dmPFC	297				
R dmPFC		3	-4	70	4.22
L dmPFC		-7	-2	70	4.18
L MCC	297				
L MCC		-7	-32	35	4.24
L MCC		-12	-24	38	4.18
L MCC		-4	-34	38	3.71
L MCC	281				
L MCC		-7	-10	45	4.09
L MCC		-10	-2	42	3.72
R IPL	266				
R IPL (PFt)		58	-17	30	3.77
R IPL (PFt)		56	-20	32	3.64
R IPL (PFop)		63	-24	25	3.59
(B) Sound judgment > action judgment for high vs. low sound words					
R SPL / IPS	1359				
R SPL (7A)		26	-64	55	4.90
R SPL (7PC)		30	-50	55	4.12

Region	Cluster size (mm³)	x	y	z	T
R IPS (hIP3)		28	-57	52	4.07
L LOC (middle occipital)	469	-27	-67	30	4.69
(C) Overlap					
R SPL / IPS	1281				
R SPL (7A)		26	-64	55	4.65
R IPS (hIP3)		28	-57	52	4.07
R SPL (7PC)		30	-50	55	4.02
L LOC (middle occipital)	125	-27	-72	28	3.83

Table S10. Brain regions showing functional coupling with the amodal seed (left ATL) during sound feature retrieval.

Region	Cluster size (mm³)	x	y	z	T
Sound judgments: high > low sound words					
L/R Precuneus/PCC	1094				
R PCC		8	-44	22	4.44
L PCC		-2	-44	22	4.10
R Precuneus		6	-50	20	3.93

Table S11. TASK x SOUND interaction in functional coupling with the amodal seed (left ATL).

Region	Cluster size (mm³)	x	y	z	T
(A) Sound judgment > lexical decision for high vs. low sound words					
L PCC	219	-4	-44	22	4.71
L/R MCC	188				
L MCC		-2	-44	35	4.00
L/R MCC		0	-47	32	3.66
R Precuneus	109	6	-52	20	3.80
(B) Sound judgment > action judgment for high vs. low sound words					
L/R MCC	16	0	-47	32	3.82
L PCC	16	-2	-44	22	3.44

Table S12. Brain regions showing functional coupling with the amodal seed (left ATL) during action feature retrieval.

Region	Cluster size (mm³)	x	y	z	T
Action judgments: high > low action words					
L dmPFC	156	-12	48	25	4.34
L dmPFC	156	-12	38	22	4.25

Note that these results come from an exploratory analysis at $p < 0.001$ uncorrected (extent > 10 voxels).

Table S13. TASK x ACTION interaction in functional coupling with the amodal seed (left ATL).

Region	**Cluster size (mm^3)**	**x**	**y**	**z**	**T**
(A) Action judgments > lexical decisions for high vs. low action words					
L dmPFC	78	-12	38	22	4.12
L dmPFC	16	-12	46	25	3.55
(B) Action judgments > sound judgments for high vs. low action words					
L dmPFC	156	-14	36	22	5.33
L dmPFC	109	-10	48	25	4.29

Supplementary material for study 3 (TMS)

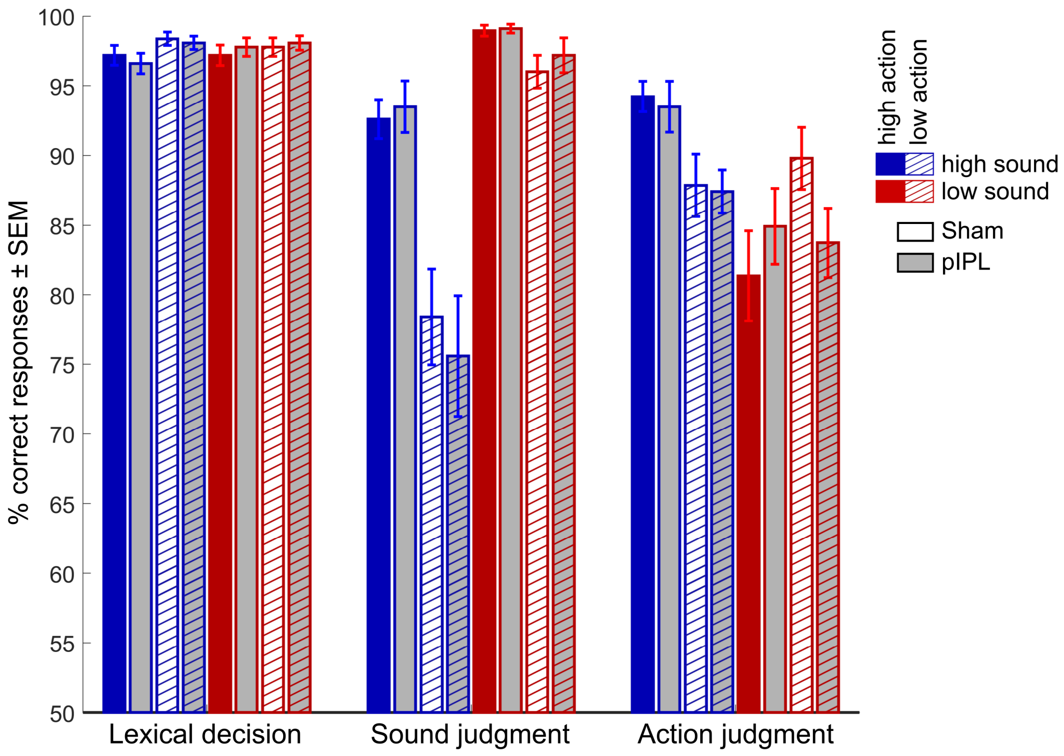

Figure S1. Response accuracies (% correct responses). Error bars represent standard error of the mean (SEM).

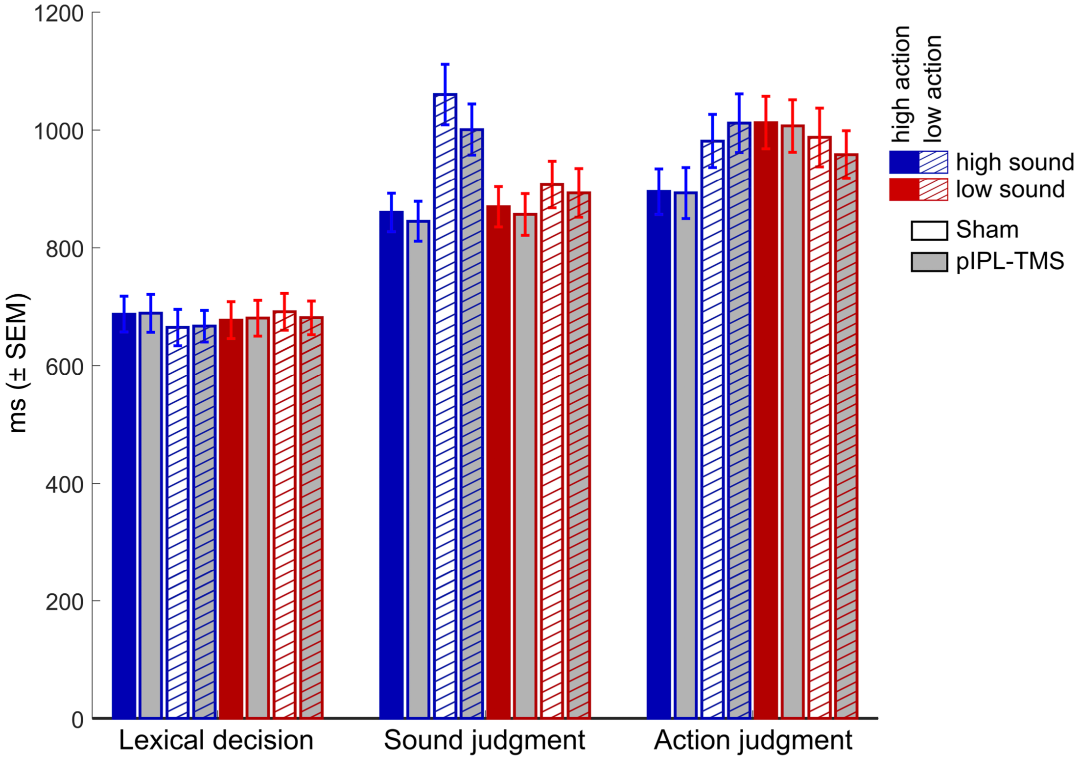

Figure S2. Response times for correct trials (in ms). rTMS over left pIPL did not significantly alter response times, as compared to sham stimulation. Error bars represent standard error of the mean (SEM).

Table S1. Results of the mixed ANOVA on sham-normalized response accuracies (testing for session order effects).

	F	**p**	**partial-η^2**
ORDER	0.034	0.86	0.001
TASK	0.246	0.72	0.010
TASK x ORDER	0.271	0.70	0.011
SOUND	0.248	0.62	0.010
SOUND x ORDER	0.032	0.86	0.001
ACTION	2.650	0.12	0.099
ACTION x ORDER	0.033	0.86	0.001
TASK x SOUND	0.472	0.60	0.019
TASK x SOUND x ORDER	0.092	0.88	0.004
TASK x ACTION	1.454	0.25	0.057
TASK x ACTION x ORDER	2.619	0.09	0.098
SOUND x ACTION	1.526	0.23	0.060
SOUND x ACTION x ORDER	0.170	0.68	0.007
TASK x SOUND x ACTION	**3.811**	**0.04**	**0.137**
TASK x SOUND x ACTION x ORDER	0.577	0.53	0.023

The table shows the results of a mixed ANOVA with within-subject factors TASK (lexical decision, sound judgment, action judgment), SOUND (high, low association) and ACTION (high, low association), and between-subject factor ORDER (sham first, pIPL-rTMS first). P-values are Huhyn-Feldt corrected for non-sphericity. Bold font highlight significant effects.

Table S2. Results of the Bayesian analysis on sham-normalized response times for correct trials (in ms).

	Mean	**95% credible interval**	**BF_{10}**	**BF_{01}**
L: high SF, high AF	3.844	[-25.769, 33.457]	0.214	**4.670**
L: high SF, low AF	5.692	[-21.812, 33.197]	0.225	**4.440**
L: low SF, high AF	8.615	[-22.765, 39.995]	0.240	**4.169**
L: low SF, low AF	-16.062	[-48.019, 15.862]	0.336	**2.977**
S: high SF, high AF	-5.781	[-37.423, 25.862]	0.221	**4.522**
S: high SF, low AF	-55.84	[-120.432, 8.751]	0.820	**1.219**
S: low SF, high AF	-13.106	[-57.588, 31.377]	0.245	**4.079**
S: low SF, low AF	-20.81	[-67.175, 25.554]	0.305	**3.277**
A: high SF, high AF	15.002	[-44.122, 74.125]	0.235	**4.259**
A: high SF, low AF	26.456	[-29.814, 82.726]	0.317	**3.159**
A: low SF, high AF	-2.117	[-68.998, 64.764]	0.208	**4.817**
A: low SF, low AF	-43.943	[-105.394, 17.509]	0.540	**1.851**

L: lexical decision; S: sound judgment; A: action judgment; SF: sound feature; AF: action feature; BF_{10}: Bayes Factor for the alternative hypothesis; BF_{01}: Bayes Factor for the null hypothesis (where $BF_{01} = 1/BF_{10}$). Bold font highlights evidence in favor of one hypothesis over the other.

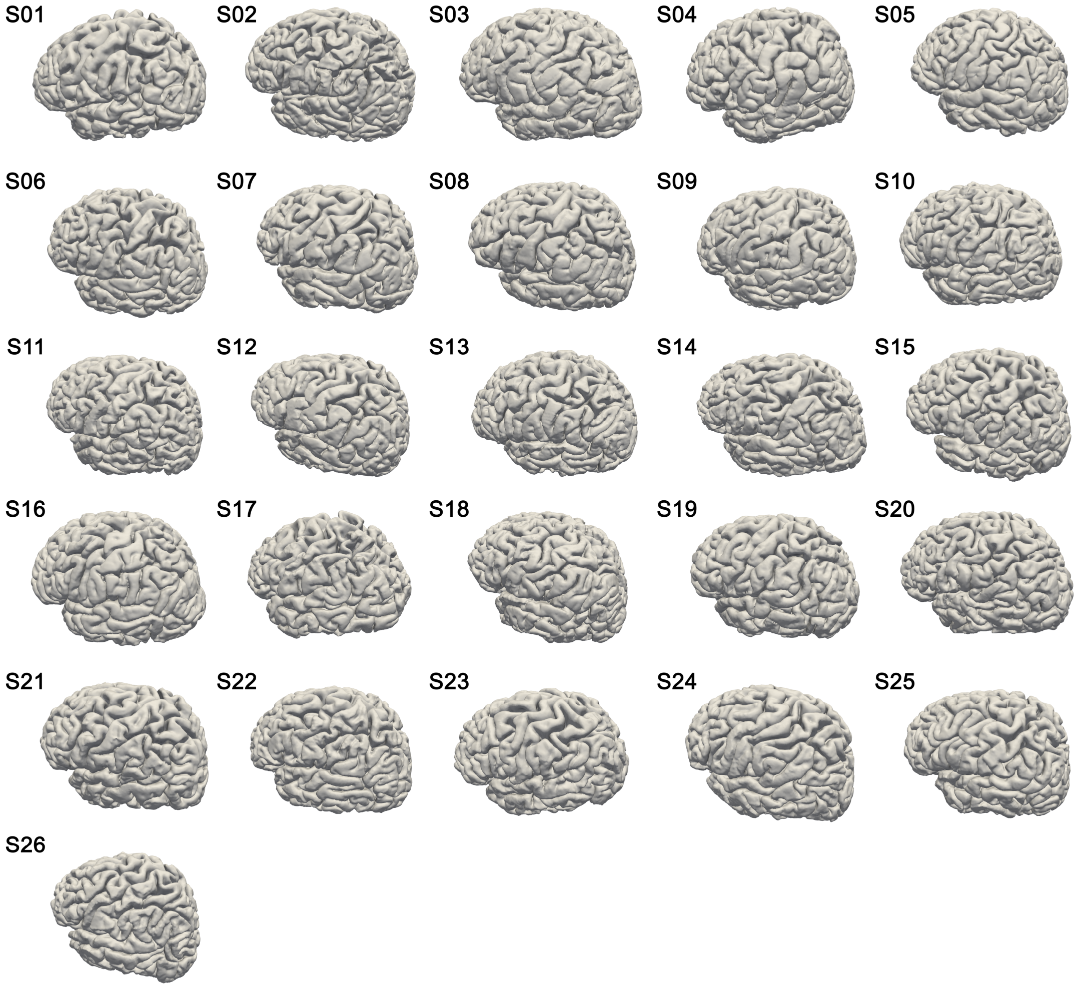

Figure S3. Reconstructions of the cortical surface for each individual subject. Head models were created for electrical field simulations based on subject-specific T1-weighted MR images using the mri2mesh pipeline (Nielsen et al., 2018).

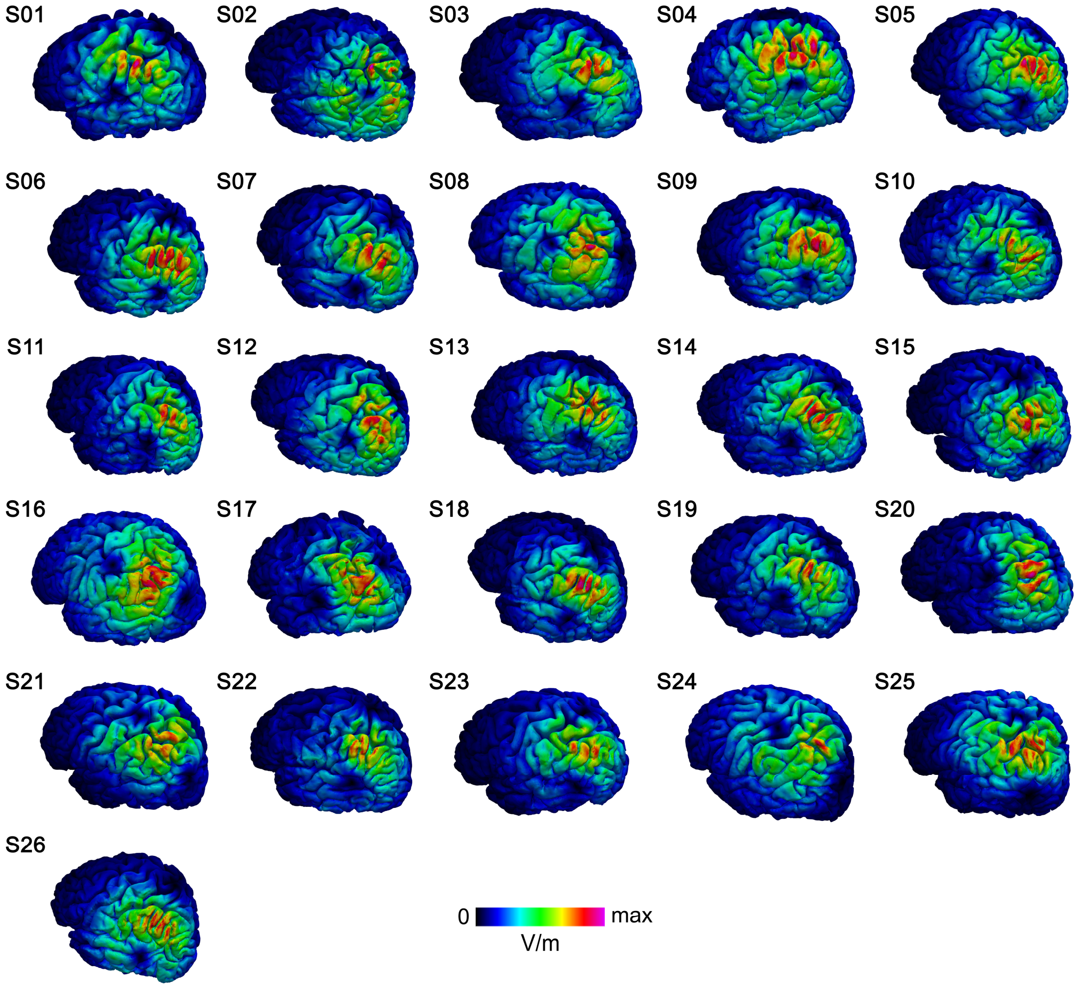

Figure S4. Electrical field simulations for each individual subject. Simulations were performed using SimNIBS v3.1 with high-resolution isotropic finite element models (FEMs; Saturnino et al., 2019; Thielscher et al., 2015) and leveraged the actual position and orientation of the coil recorded during the experiment. The colormap is scaled from 0 V/m to the individual maximum field strength.

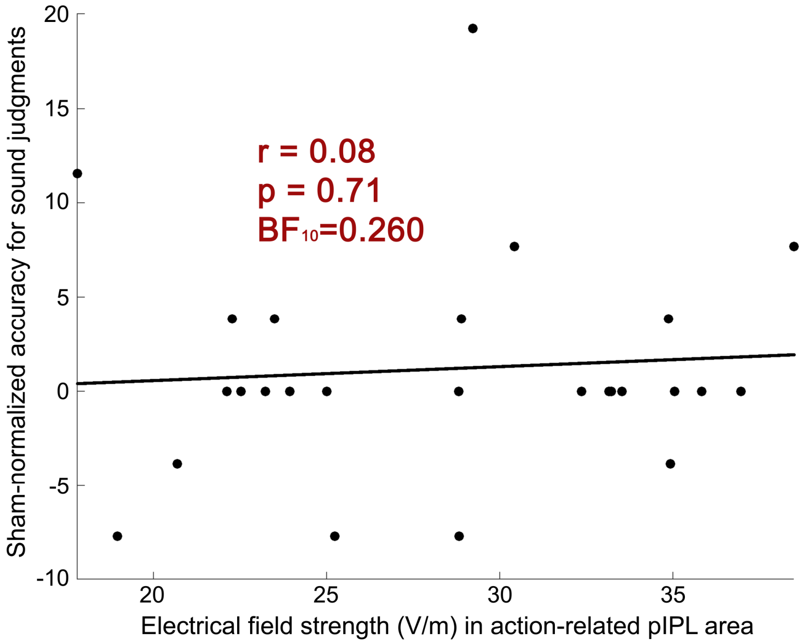

Figure S5. Electrical field strength in action-related left pIPL was not associated with behavioral performance for sound judgments on low sound–low action words (i.e. accuracy change in % for pIPL-rTMS vs. sham stimulation). The Bayes Factor BF_{10}=0.260, or equivalently BF_{01}=1/0.260=3.847, means that the data were ~4 times more likely under the null hypothesis than alternative hypothesis.

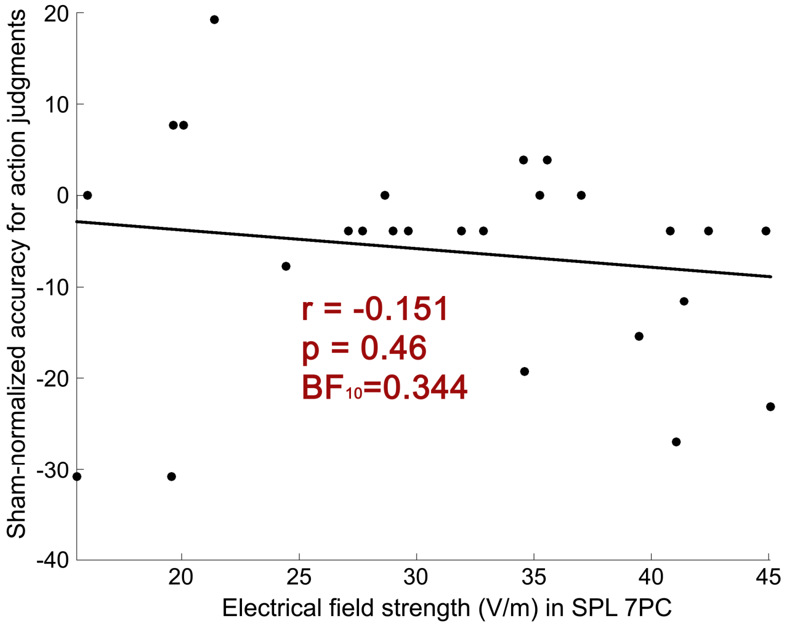

Figure S6. Electrical field strength in left SPL (area 7PC) was not associated with behavioral performance for action judgments on low sound–low action words (i.e. accuracy change in % for pIPL-rTMS vs. sham stimulation). The Bayes Factor BF_{10}=0.344, or equivalently BF_{01}=2.907, means that the data were ~3 times more likely under the null hypothesis than alternative hypothesis.

Table S3. Psycholinguistic measures for stimuli list 1 (means; SD in parentheses).

	low sound	high sound	p	low action	high action	p
Sound rating	1.31 (0.27)	4.95 (0.64)	**<0.0001**	2.94 (1.68)	3.32 (2.08)	0.3
Action rating	3.2 (1.63)	3.37 (1.64)	0.59	1.74 (0.53)	4.83 (0.46)	**<0.0001**
Visual rating	4.17 (0.56)	4.01 (0.8)	0.24	4.13 (0.82)	4.05 (0.54)	0.57
Familiarity rating	5.52 (0.41)	5.41 (0.43)	0.17	5.39 (0.42)	5.54 (0.42)	0.07
Letters	6.25 (1.58)	6.5 (1.91)	0.47	6.35 (1.9)	6.4 (1.61)	0.87
Syllables	2.25 (0.76)	2.31 (0.76)	0.7	2.31 (0.78)	2.25 (0.74)	0.7
Lemma freq.	5.38 (6.66)	4.9 (11.06)	0.79	4.16 (5.75)	6.11 (11.48)	0.28
Bigram freq.	259978.98 (136575.41)	232187.54 (112079.53)	0.26	258438.85 (124835.14)	233727.67 (125352.69)	0.32
Trigram freq.	150264.45 (80960.2)	126896.58 (68690.91)	0.12	143733.6 (72156.54)	133427.43 (79313.69)	0.49
Orthographic neighbors	7.5 (7.35)	5.74 (6.53)	0.2	7.01 (7.58)	6.23 (6.37)	0.57

Ratings were obtained from a total of 163 subjects who did not participate in the fMRI experiment. All other psycholinguistic measures were extracted from the dlexDB database (http://dlexdb.de/). Lemma, bigram and trigram frequencies and number of orthographic neighbors are given per one million words.

Table S4. Psycholinguistic measures for stimuli list 2 (means; SD in parentheses).

	low sound	**high sound**	**p**	**low action**	**high action**	**p**
Sound rating	1.37 (0.32)	4.86 (0.62)	**<0.0001**	2.89 (1.6)	3.35 (2.01)	0.2
Action rating	3.13 (1.66)	3.37 (1.67)	0.47	1.65 (0.44)	4.84 (0.44)	**<0.0001**
Visual rating	4.3 (0.54)	4.14 (0.83)	0.22	4.25 (0.86)	4.19 (0.51)	0.66
Familiarity rating	5.53 (0.37)	5.45 (0.45)	0.32	5.48 (0.41)	5.5 (0.42)	0.86
Letters	6.27 (1.57)	6.25 (2.01)	0.96	6.19 (1.99)	6.33 (1.59)	0.7
Syllables	2.27 (0.79)	2.25 (0.65)	0.89	2.15 (0.67)	2.37 (0.77)	0.14
Lemma freq.	4.82 (5.65)	5.79 (9.01)	0.51	4.89 (6.58)	5.72 (8.37)	0.57
Bigram freq.	248388.44 (130276.27)	228512.52 (129617.31)	0.44	250520.71 (145416.39)	226380.25 (111941.64)	0.35
Trigram freq.	144697.4 (85115.5)	134251.38 (85110.76)	0.53	149516.31 (92936.99)	129432.47 (75506.29)	0.23
Orthographic neighbors	6.72 (5.69)	6.12 (4.86)	0.57	6.66 (5.64)	6.18 (4.92)	0.65

Table S5. Psycholinguistic measures for all stimuli across both lists (means; SD in parentheses).

	low sound	**high sound**	**p**	**low action**	**high action**	**p**
Sound rating	1.34 (0.3)	4.9 (0.63)	**<0.0001**	2.91 (1.63)	3.33 (2.03)	0.1
Action rating	3.17 (1.64)	3.37 (1.65)	0.37	1.7 (0.49)	4.84 (0.45)	**<0.0001**
Visual rating	4.24 (0.55)	4.07 (0.82)	0.09	4.19 (0.84)	4.12 (0.53)	0.48
Familiarity rating	5.53 (0.39)	5.43 (0.44)	0.09	5.44 (0.41)	5.52 (0.42)	0.15
Letters	6.26 (1.57)	6.38 (1.96)	0.64	6.27 (1.94)	6.37 (1.6)	0.7
Syllables	2.26 (0.78)	2.28 (0.7)	0.85	2.23 (0.73)	2.31 (0.75)	0.45
Lemma freq.	5.1 (6.16)	5.34 (10.05)	0.83	4.53 (6.16)	5.92 (10)	0.23
Bigram freq.	254183.71 (132941.15)	230350.03 (120590.66)	0.18	254479.78 (134916.26)	230053.96 (118315.82)	0.17
Trigram freq.	147480.93 (82706.94)	130573.98 (77050.16)	0.13	146624.95 (82844.21)	131429.95 (77082.72)	0.17
Orthographic neighbors	7.11 (6.55)	5.93 (5.73)	0.17	6.83 (6.65)	6.21 (5.66)	0.47