Meta-analytic evidence for a novel hierarchical model of conceptual processing

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Abstract

Conceptual knowledge plays a pivotal role in human cognition. Grounded cognition theories propose that concepts consist of perceptual-motor features represented in modality-specific perceptual-motor cortices. However, it is unclear whether conceptual processing consistently engages modality-specific areas. Here, we performed an activation likelihood estimation (ALE) meta-analysis across 212 neuroimaging experiments on conceptual processing related to 7 perceptual-motor modalities (action, sound, visual shape, motion, color, olfaction-gustation, and emotion). We found that conceptual processing consistently engages brain regions also activated during real perceptual-motor experience of the same modalities. In addition, we identified multimodal convergence zones that are recruited for multiple modalities. In particular, the left inferior parietal lobe (IPL) and posterior middle temporal gyrus (pMTG) are engaged for three modalities: action, motion, and sound. These "trimodal" regions are surrounded by "bimodal" regions engaged for two modalities. Our findings support a novel model of the conceptual system, according to which conceptual processing relies on a hierarchical neural architecture from modality-specific to multimodal areas up to an amodal hub.

Keywords: concepts, grounded cognition, language, semantic memory, fMRI

Introduction

Conceptual knowledge about objects, people, and events in the world is crucial for core human cognitive abilities, such as object recognition and use, problem solving, as well as language comprehension (Lambon Ralph, 2013; van Elk et al., 2014). Therefore, a central question in cognitive neuroscience has been how concepts are represented and processed in the human brain.

According to the traditional view in cognitive science—amodal theories—concepts can be considered as entirely abstract, amodal symbols (Fodor, 1975; Pylyshyn, 1984). Thus, under this view, the conceptual system is completely separated from the modality-specific systems for perception and action. In contrast, grounded theories of cognition propose that concepts consist of perceptual and motor features represented in modality-specific perceptual-motor brain regions (Barsalou, 2008; Kiefer and Barsalou, 2013). For example, concepts like 'dog' are assumed to comprise visual shape, color, and motion features represented in visual brain areas, sound features represented in auditory areas, action features in somatomotor regions, as well as olfaction and emotion features in olfactory-gustatory and emotion-related brain regions, respectively (Binder and Desai, 2011; Fernandino et al., 2016b, 2016a). While a common terminology is still lacking in the field, we refer to "perceptual-motor modalities" as the brain's major input and output channels of perception and action (cf. Kuhnke et al., 2021). 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) as well as motor action (Kiefer and Harpaintner, 2020). Moreover, some senses (e.g. vision) may contain several sub-modalities (e.g. color, shape, and motion). We call brain regions "modality-specific" if they represent information related to a single perceptual-motor modality (Kiefer and Pulvermüller, 2012). Grounded cognition theories are mainly supported by neuroimaging studies demonstrating that conceptual processing related to a certain perceptual-motor modality activates the corresponding modality-specific areas (for reviews, see Hauk and Tschentscher, 2013; Kiefer and Harpaintner, 2020; Kiefer and Pulvermüller, 2012; Meteyard et al., 2012).

In addition to modality-specific regions, previous evidence suggests an involvement of "cross-modal convergence zones" which integrate multiple different modality-specific features into more abstract conceptual representations (Binder et al., 2009; Binder and Desai, 2011; Lambon Ralph et al., 2016). We recently proposed a distinction among cross-modal convergence zones between "multimodal" regions which retain modality-specific information, and "amodal" regions which completely abstract away from modality-specific input (Kuhnke et al., 2021, 2020b). Multimodal regions seem to include the left inferior parietal lobe (IPL), posterior middle temporal gyrus (pMTG), and medial prefrontal cortex (mPFC) (Fernandino et al., 2016b, 2016a; Kuhnke et al., 2021, 2020b). In contrast, the anterior temporal lobe (ATL)

appears to act as an amodal hub of the conceptual system (Jefferies, 2013; Lambon Ralph et al., 2016; Patterson et al., 2007).

However, several issues remain open. First, it is unknown whether conceptual processing consistently engages modality-specific perceptual-motor regions across neuroimaging studies. Several studies failed to find modality-specific perceptual-motor activity during conceptual tasks (e.g. Bedny et al., 2008; Postle et al., 2008; Raposo et al., 2009) and the involvement of modality-specific regions in conceptual processing remains controversial (Kompa, 2021; Kompa and Mueller, 2020; Mahon, 2015; Mahon and Caramazza, 2008). Second, it is unknown which modalities robustly overlap in multimodal convergence zones. In particular, it is unclear which cross-modal regions are multimodal (rather than amodal), as well as *how many* and *which* modalities are integrated in each multimodal area. A better understanding of the overlap and dissociation within and between areas would advance the current knowledge of the neural basis of conceptual processing.

Coordinate-based meta-analyses allow to formally assess the consistency of functional activations across numerous neuroimaging experiments, capitalizing on the common reporting of activation coordinates in standard space (Fox et al., 2014; Yarkoni et al., 2010). However, previous meta-analyses have mainly investigated conceptual processing in general (i.e. regardless of perceptual-motor content; Binder et al., 2009; Visser et al., 2010) or executive control during concept retrieval (Jackson, 2021; Noonan et al., 2013). No meta-analysis has systematically tested the grounded cognition hypothesis that conceptual processing related to a certain perceptual-motor modality recruits the respective modality-specific perceptual-motor regions. Two meta-analyses focused on action-related conceptual processing (Binder et al., 2009; Watson et al., 2013) and identified consistent engagement of left pMTG and anterior supramarginal gyrus (aSMG). However, neither study tested for overlap with real action execution (also see Giacobbe et al., 2022). Likewise, a previous meta-analysis on emotion-related concepts (Desai et al., 2018) did not test for overlap with real emotion perception. In addition, no meta-analysis has simultaneously investigated conceptual processing related to multiple different modalities.

To address these issues, we performed an activation likelihood estimation (ALE) meta-analysis across a total of 212 neuroimaging experiments (3893 participants, 3101 activation foci) on conceptual processing related to 7 perceptual-motor modalities (action, sound, visual shape, motion, color, olfaction-gustation, and emotion). We also performed ALE meta-analyses on real perception or action in each modality (studies identified using the BrainMap database; total of 1582 experiments, 21,349 participants, 39,221 foci) and tested for overlap with conceptual processing. This design allowed us to investigate several modalities simultaneously, thereby dissociating modality-specific brain areas and multimodal convergence zones. To test modality specificity, we directly contrasted the meta-analytic maps

between conceptual modalities. Finally, to identify multimodal convergence zones, we investigated the conjunctions between all modalities, and analyzed how many and which modalities overlap in each multimodal area.

Following grounded cognition theories, we hypothesized that conceptual processing should engage brain regions that are also activated during real perceptual-motor experience of the same modalities. These perceptual-motor regions should exhibit a high modality specificity. Regarding multimodal convergence zones, we predicted that several modalities should overlap in the “multimodal” left IPL, pMTG and mPFC, but not in the “amodal” ATL.

Materials and Methods

Literature search

We performed a systematic literature search using the PubMed, Web of Science, and BrainMap databases, as well as manual reference tracing (through reviews and original research articles). Table S30 shows a checklist following the guidelines for neuroimaging meta-analyses by Müller et al. (2018), which includes the employed search queries. Figure 1 presents a flowchart following the PRISMA guidelines (Page et al., 2021).

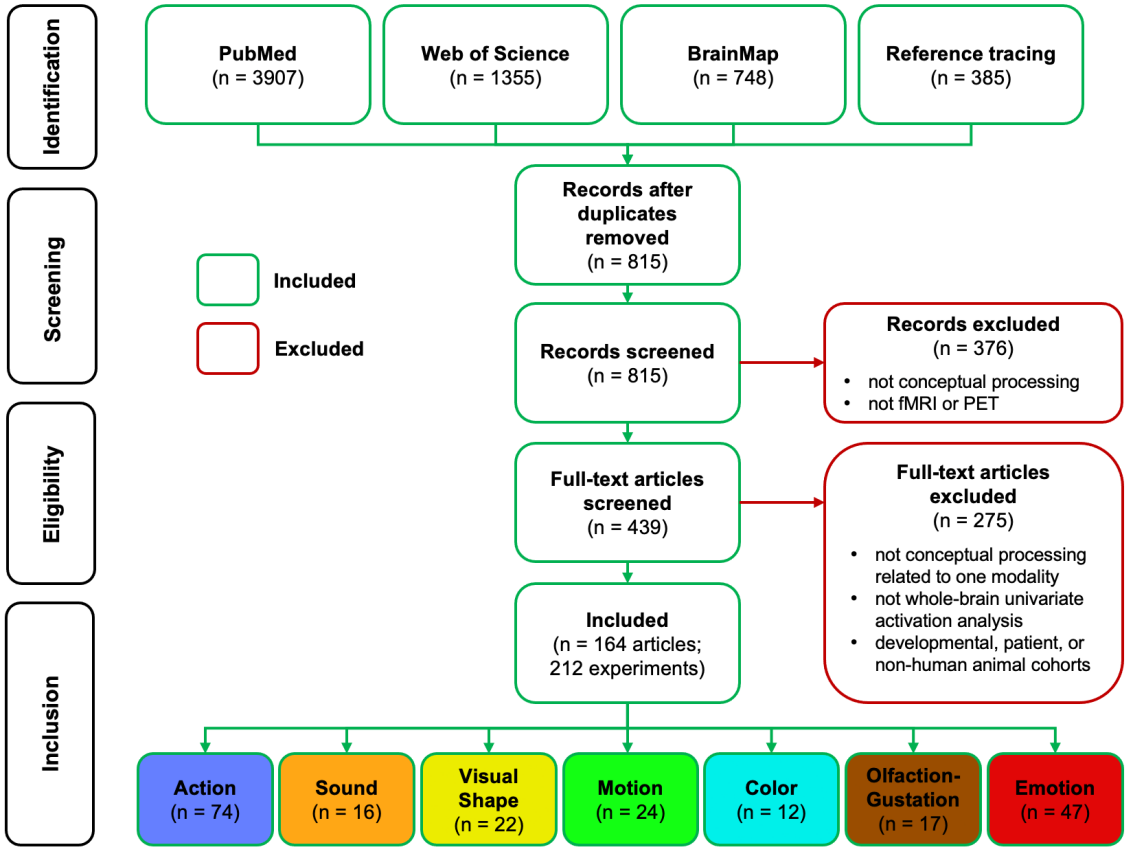

Figure 1. Flowchart illustrating the inclusion-exclusion process leading to the datasets included in the meta-analyses (following the PRISMA guidelines; Page et al., 2021). Before the final "inclusion" stage, *n* represents the number of articles. At the "inclusion" stage, *n* represents the number of experiments per modality (where one article could contain multiple experiments).

We included functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies that reported peak coordinates from voxel-wise, whole-brain activation analyses in Montreal Neurological Institute (MNI) or Talairach (TAL) space. Therefore, we excluded non-whole-brain (e.g. region-of-interest), non-voxel-wise (e.g. multivariate), and non-activation (e.g. connectivity) analyses. Study participants had to be healthy, right-handed human adults; developmental, patient, and non-human animal cohorts were excluded. In studies using language stimuli, only native-speaker samples were included.

Appropriate experiments asked participants to perform implicit or explicit conceptual tasks on pictures, sounds, words, sentences, or stories. We selectively included activation contrasts that targeted conceptual processing related to one of the 7 perceptual-motor modalities (action, sound, visual shape, color, motion, olfaction-gustation, or emotion). To this end, we carefully ensured that the relationship between stimuli and perceptual-motor modality was purely conceptual-semantic (not perceptual). Therefore, we excluded all contrasts with a potential stimulus difference in the same modality as the targeted conceptual modality (e.g. visual-shape stimuli for visual-shape related conceptual processing).

To enable tests for modality specificity and overlap across modalities, every contrast was assigned to only one modality. To completely distinguish the modalities action and motion, action was defined as object manipulation, whereas motion subsumed all other (non-object-directed) movements (cf. Fernandino et al., 2016; van Elk et al., 2014). Contrasts that could not be assigned to only one modality were excluded.

Our primary analysis included both high-level and low-level contrasts to maximize statistical power, which is considered crucial for the sensitivity and specificity of neuroimaging meta-analyses (Eickhoff et al., 2016; Müller et al., 2018). However, only high-level contrasts between different experimental conditions (e.g. action words > abstract words) can isolate brain activity specific to conceptual processing. Contrasts against a low-level baseline (e.g. action words > fixation) may yield concomitant activation for non-conceptual processes (e.g. orthographic or phonological processing). Therefore, to test the robustness of our meta-analytic results to baseline differences, we complemented our primary analysis with a supplementary analysis that excluded low-level contrasts (cf. Diveica et al., 2021).

Table 1 provides an exemplary overview of the included experiments for each modality. Tables S2-S8 present the full datasets for action (74 experiments, 1378 subjects, 1118 foci), sound (16 experiments, 323 subjects, 275 foci), visual shape (22 experiments, 342 subjects, 256 foci), motion (24 experiments, 450 subjects, 220 foci), color (12 experiments, 207 subjects, 154 foci), olfaction-gustation (17 experiments, 330 subjects, 167 foci), and emotion (47 experiments, 863 subjects, 911 foci).

Table 1. Examples of studies included in the meta-analysis.

Study	Method	N	Task	Stimuli	Contrast	Space	Foci
Action							
Damasio et al. (2001)	PET	20	naming	pictures	tool action > face orientation naming	TAL	21
Tettamanti et al. (2008)	fMRI	18	passive listening	spoken sentences	action > abstract sentences	MNI	10
van Dam et al. (2010)	fMRI	14	semantic decision	written words	action > abstract verbs	MNI	5
Sound							
Kuhnke et al. (2020)	fMRI	40	semantic decision	written words	high-sound > low-sound words	MNI	21
Popp et al. (2019a)	fMRI	22	lexical decision	written words	sound > action verbs	MNI	18
Zvyagintsev et al. (2013)	fMRI	15	mental imagery	none	auditory > visual imagery	TAL	15
Visual Shape							
Cappa et al. (1998)	PET	13	semantic decision	written words	visual > associative semantics	TAL	12
Fernandino et al. (2016)	fMRI	44	semantic decision	written words	shape associations > other associations	TAL	24
Nagels et al. (2013)	fMRI	17	perceptual decision	videos, spoken sentences	shape-related > space-related speech-gesture pairs	MNI	10
Motion							
Deen & McCarthy (2010)	fMRI	15	passive reading	written sentences	motion > non-motion sentences	MNI	13
Humphreys et al. (2013)	fMRI	10	semantic decision	pictures, spoken sentences	motion > static sentences	MNI	1
Vigliocco et al. (2006)	PET	12	passive listening	spoken words	motion > sensory words	MNI	2
Color							
Goldberg et al. (2006b)	fMRI	14	semantic decision	written words	color words > auditory, gustatory, tactile words	TAL	3
Kellenbach et al. (2001)	PET	10	semantic decision	written words	color > sound verifications	MNI	3
Martin et al. (1995)	PET	12	word generation	(colorless) pictures	color > action word generation	TAL	5

Olfaction-Gustation							
Barros-Loscertales et al. (2011)	fMRI	59	passive reading	written words	taste-related > taste-unrelated words	MNI	11
Fairhall (2020)	fMRI	16	semantic decision	written words	food words > people and place words	MNI	3
Ghio et al. (2016b)	fMRI	16	episodic recall	pictures	olfactory > visual-only objects	MNI	1
Emotion							
Isenberg et al. (1999)	PET	6	perceptual decision	written words	threat > neutral words	TAL	4
Kedia et al. (2008)	fMRI	29	mental imagery	written sentences	emotional > neutral sentences	TAL	5
Phillips et al. (1998)	fMRI	6	perceptual decision	pictures	disgusted > neutral faces	TAL	18

N = number of participants; fMRI = functional magnetic resonance imaging; PET = positron emission tomography; MNI = Montreal Neurological Institute space; TAL = Talairach space.

Activation Likelihood Estimation (ALE)

We performed a coordinate-based activation likelihood estimation (ALE) meta-analysis using *GingerALE* version 3.0 (https://brainmap.org/ale). ALE treats reported activation coordinates as centers of 3D Gaussian probability distributions, whose width depends on an empirical model of between-template and between-participant variance (Eickhoff et al., 2012, 2009; Turkeltaub et al., 2012). In practice, larger samples receive tighter distributions. For each experiment, these probability distributions are combined into a "modelled activation" (MA) map. Taking the voxel-wise union of all MA maps yields the ALE map, which quantifies the convergence of activations across experiments (Eickhoff et al., 2012). The ALE map is compared to a null distribution reflecting random spatial association between experiments. This results in a random-effects inference, allowing for generalization to the entire population of studies (Eickhoff et al., 2009).

Main ALE analyses for each conceptual modality

Our primary goal was to identify brain regions that are consistently engaged across neuroimaging studies for conceptual processing related to one of the 7 perceptual-motor modalities (action, sound, visual shape, motion, color, olfaction-gustation, or emotion). Therefore, we first ran an ALE meta-analysis for each modality separately. To minimize within-sample effects, we used the conservative Turkeltaub ALE method, and pooled together multiple contrasts from the same study and sample (Turkeltaub et al., 2012). All meta-analyses were performed in MNI space; TAL coordinates were converted to MNI space using the *tal2icbm* algorithm in *GingerALE* (Lancaster et al., 2007). ALE maps were thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected for multiple comparisons using Monte Carlo simulation (10,000 permutations; as proposed by Müller et al., 2018).

Overlap between conceptual and perceptual-motor regions

Second, we aimed to test the key prediction of grounded cognition theories that conceptual processing related to a certain perceptual-motor modality involves brain regions also engaged during real perception or action in that modality. To this end, we first searched the *BrainMap* database (using the *Sleuth* software; http://www.brainmap.org/sleuth/) for neuroimaging studies on actual perception or action in each modality. We queried the following behavioral domains restricted to activation-based experiments on healthy human participants: for action execution = Action.Execution (451 experiments, 5037 subjects, 12241 foci); auditory perception = Perception.Audition (152 experiments, 2068 subjects, 3670 foci); visual shape perception = Perception.Vision.Shape (147 experiments, 1869 subjects, 3074 foci); visual motion perception = Perception.Vision.Motion (97 experiments, 1019 subjects, 2703 foci); color perception = Perception.Vision.Color (40 experiments, 665 subjects, 835 foci); olfaction-

gustation = Perception.Olfaction or Perception.Gustation (98 experiments, 1420 subjects, 1980 foci); and emotion = Emotion (597 experiments, 9271 subjects, 14718 foci). For each modality, we then performed an ALE meta-analysis using the same ALE methods and thresholding as our conceptual processing analyses. Finally, we computed the overlap between the meta-analytic maps for conceptual processing related to a certain modality (e.g. sound) and real perception/action in that modality (e.g. auditory perception) via minimum-statistic conjunction (testing the conjunction null; Nichols et al., 2005).

Contrast analyses for modality specificity

Third, we investigated the modality specificity of the brain regions engaged for conceptual processing related to a certain modality. To this end, we performed direct contrasts between the ALE maps for one modality vs. every other modality (e.g. for action: action > sound; action > visual shape; action > motion; action > color; action > olfaction-gustation; and action > emotion). *GingerALE* employs the following procedure for contrast analysis (Eickhoff et al., 2011; Langner and Eickhoff, 2013): First, the voxel-wise difference between ALE maps is computed. To account for sample size differences, the two datasets are pooled and randomly divided into two new datasets of equal sizes. An ALE image is then created for each new dataset and subtracted from the other. We repeated this procedure 10,000 times to create a null distribution of ALE-value differences, which was used to threshold the observed difference map at a posterior probability of $P > 0.95$ for a true difference (Cieslik et al., 2016; Hardwick et al., 2018). To quantify modality specificity, we then tested how many contrasts were significant in each voxel. All contrasts were inclusively masked by regions that were significantly engaged only for the respective modality (e.g. action) and no other modality (cf. Hardwick et al., 2018; Rottschy et al., 2012). Hence, we exclusively called regions “modality-specific” if they showed significant convergence for only a single modality *and* higher activation likelihood for that modality than for the other modalities.

Conjunction analyses for multimodal convergence zones

Fourth, we aimed to identify “multimodal convergence zones”—brain regions engaged in conceptual processing related to multiple different perceptual-motor modalities. To this end, we computed the overlap (using minimum-statistic conjunctions) between the ALE maps for all conceptual modalities. We then tested *how many* modalities overlap in which areas to determine “bimodal” (2 modalities), “trimodal” (3 modalities) areas, and so on. Finally, we analyzed *which* modalities overlap in the different multimodal areas.

Results

Action

Across neuroimaging studies, action-related conceptual processing consistently engaged the left inferior frontal gyrus (IFG) and premotor cortex (PMC), anterior supramarginal gyrus (aSMG) extending into primary somatosensory cortex (S1) and intraparietal sulcus (IPS), the lateral temporal-occipital junction (LTO) including parts of posterior middle and inferior temporal gyri (pMTG/ITG) and superior temporal sulcus (pSTS), as well as the bilateral (pre-)supplementary motor area (SMA) (Figure 2A; Table S1).

Real action execution robustly activated the bilateral primary motor cortex (M1), PMC, (pre-)SMA, aSMG extending into IPS and S1, pSTG/STS, thalamus, and cerebellum (Figure 2B red; Table S2). Action-related conceptual processing overlapped with real action execution in left IFG/PMC, aSMG/S1 and IPS, pSTS, and in bilateral (pre-)SMA (Figure 2B purple; Table S3).

Left aSMG/S1 and pITG were action-specific (Figure 2C; Table S4): These regions were significantly engaged only for action and no other modality, and contrast analyses revealed significantly higher activation likelihood for action than every other modality. Weaker evidence for action specificity was found in left IFG/PMC, IPS, LTO, and bilateral (pre-)SMA: These areas showed significant engagement selectively for action, and a higher activation likelihood for action than for several, but not all, other modalities.

A supplementary analysis that excluded low-level contrasts (e.g. action words > fixation) yielded qualitatively similar results (Figure S1), confirming their robustness to baseline differences. In particular, left aSMG/S1, IPS, IFG/PMC, LTO/pSTS, and pMTG/ITG (but not pre-SMA) were robustly engaged in action-related conceptual processing. Left aSMG/S1 and pITG showed high action specificity.

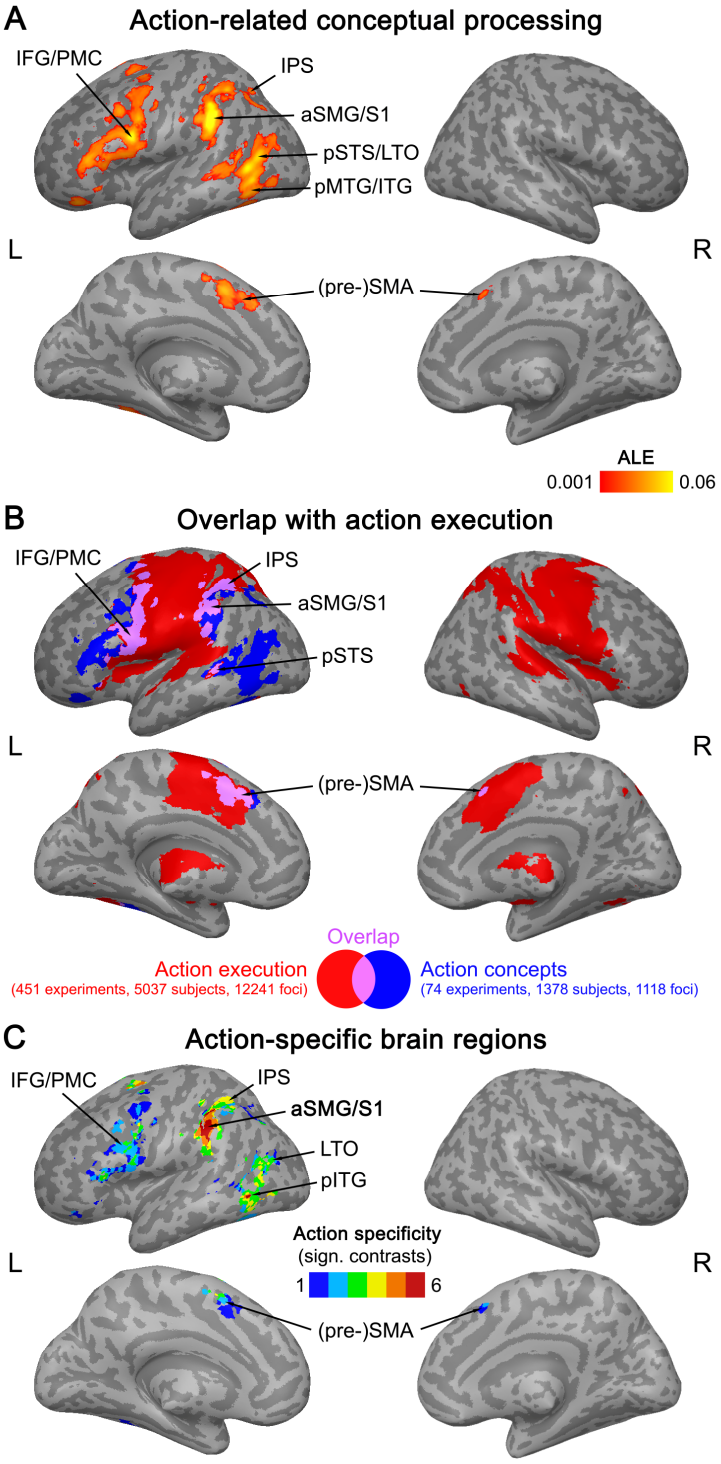

Figure 2. (A) ALE meta-analytic map for action-related conceptual processing (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for action-related conceptual processing (blue) and real action execution (red). (C) Regions showing consistent engagement for conceptual processing related to action and no other modality, and higher activation likelihood for action than the other modalities (number of significant contrasts is displayed).

Sound

Sound-related conceptual processing consistently activated the bilateral pSTS (extending into pMTG in the left hemisphere), as well as left pSMG and dorsomedial prefrontal cortex (dmPFC) (Figure 3A; Table S5).

Real auditory perception robustly engaged the bilateral early auditory cortex and surrounding STG/MTG, IFG (extending into insula), middle frontal gyrus (MFG) and precentral sulcus (PreCS), dmPFC, thalamus, and right IPS (Figure 3B red). Sound-related conceptual processing overlapped with real auditory perception in bilateral pSTS (Figure 2B purple). Left dmPFC and pSMG areas engaged for sound-related conceptual processing were adjacent to, but non-overlapping with regions engaged for auditory perception.

The right pSTS was sound-specific (Figure 3C), showing consistent engagement exclusively for sound (and no other modality) and higher activation likelihood for sound than every other modality. Left pMTG, pSMG, and dmPFC showed weaker evidence for sound specificity, with significant convergence selectively for sound and higher activation likelihood for sound than multiple, but not all, other modalities.

A supplementary analysis without low-level contrasts (e.g. sound-related words > fixation) yielded very similar results (Figure S2). Indeed, this analysis provided even stronger evidence for sound specificity in right pSTS, left pMTG, and pSMG. In contrast, left dmPFC was not robustly engaged.

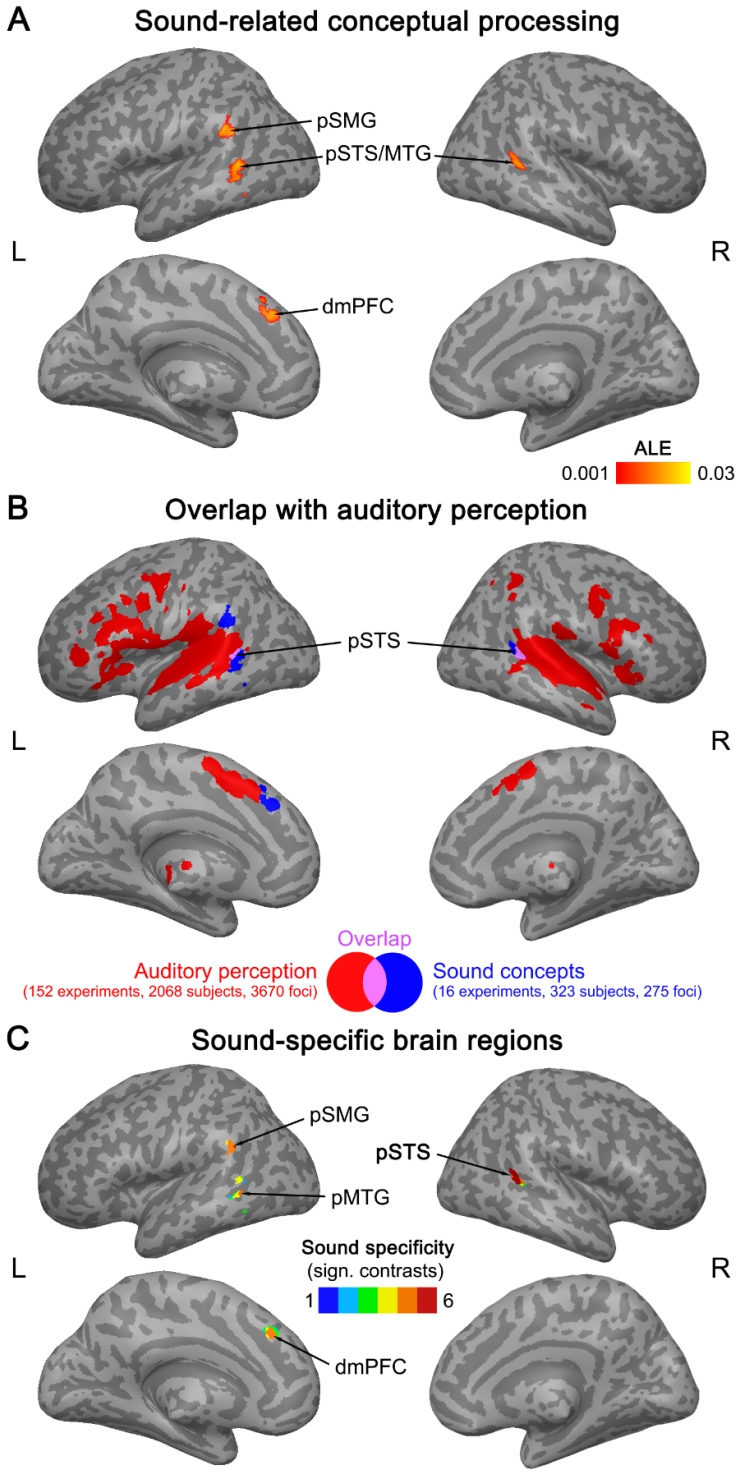

Figure 3. (A) ALE meta-analytic map for sound-related conceptual processing (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for sound-related conceptual processing (blue) and real auditory perception (red). (C) Regions showing consistent engagement for conceptual processing

related to sound and no other modality, and higher activation likelihood for sound than the other modalities (number of significant contrasts is displayed).

Visual shape

Conceptual processing related to visual shape consistently activated the left precentral sulcus (PreCS), lateral occipital cortex (LOC; area hOc4la), and anterior FG (Figure 4A).

Real visual shape perception robustly engaged the bilateral early visual cortex (V1/V2/V3/V4), LOC (hOc4la/p), IPS/SPL, FG, PreCS extending into PMC, IFG, and insula (Figure 4B red). Shape-related conceptual processing overlapped with real visual shape perception in left PreCS and LOC (hOc4la), whereas the FG clusters were directly adjacent but non-overlapping (Figure 4B purple).

Left LOC (hOc4la) and aFG showed evidence for shape specificity, with consistent engagement selectively for shape (and no other modality) and higher activation likelihood for shape than most other modalities (Figure 4C).

A supplementary analysis that excluded low-level contrasts (e.g. shape-related words > fixation) provided even stronger evidence that left LOC (hOc4la) was robustly and selectively engaged in shape-related conceptual processing (Figure S3). However, left aFG did not show significant convergence in this analysis.

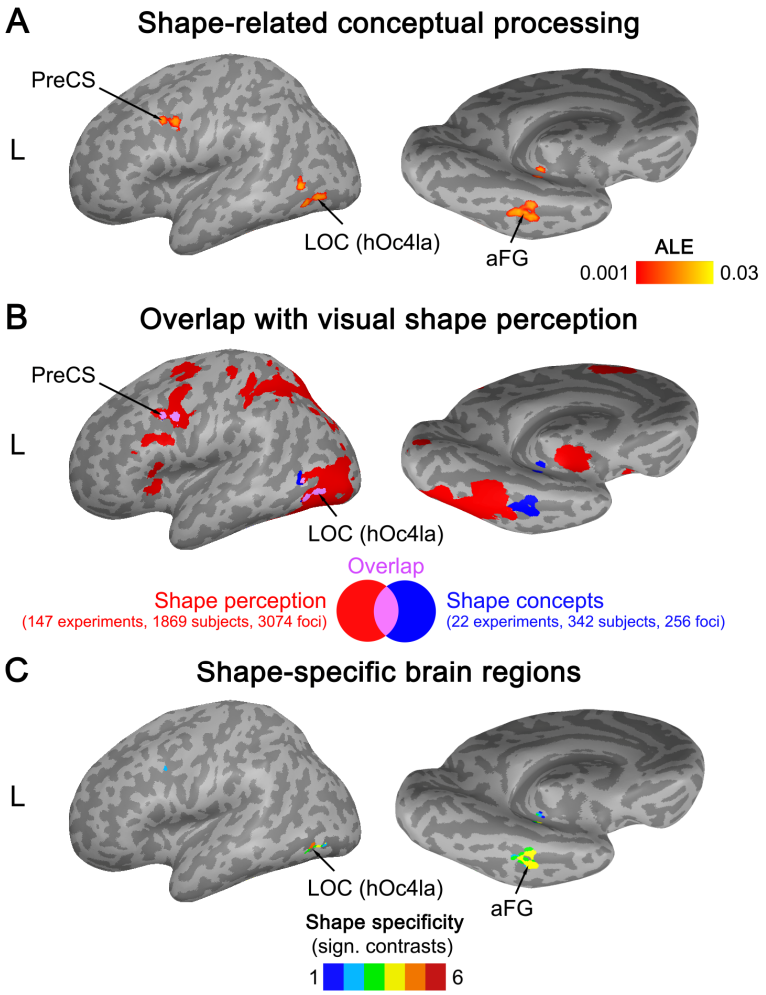

Figure 4. (A) ALE meta-analytic map for conceptual processing related to visual shape (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for shape-related conceptual processing (blue) and real visual shape perception (red). (C) Regions showing consistent engagement for conceptual processing related to visual shape and no other modality, and higher activation likelihood for shape than the other modalities (number of significant contrasts is displayed).

Motion

Motion-related conceptual processing consistently recruited the left pSTS extending into pMTG and aSMG, as well as left IFG and dorsal FG (Figure 5A).

Motion-related conceptual processing did not overlap with real motion perception, which robustly recruited the bilateral early visual cortex (V1/V2), LOC, area V5/MT, SPL/IPS, PMC, and SMA (Figure S8). However, motion-related conceptual processing overlapped with real action execution in left pSTS and aSMG (Figure 5B).

Left pSTS was motion-specific (Figure 5C): A cluster in left pSTS was consistently engaged only for motion (and no other modality) and showed significantly higher activation likelihood for motion than all other modalities. Left dFG showed weaker evidence for motion specificity, with significant convergence only for motion and higher activation likelihood for motion than some, but not all, other modalities.

A supplementary meta-analysis excluding low-level contrasts (e.g. motion words > fixation) revealed highly similar results (Figure S4), confirming that left pSTS and dFG are robustly engaged for motion-related conceptual processing, where left pSTS is motion-specific. In contrast to the full analysis, left IFG was not consistently engaged.

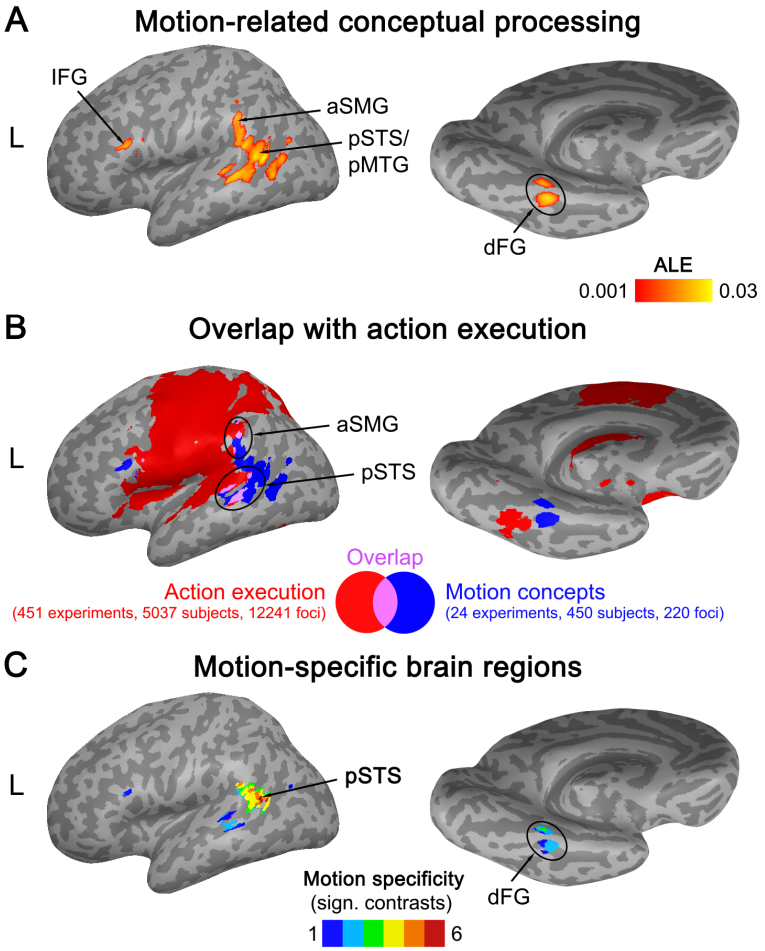

Figure 5. (A) ALE meta-analytic map for motion-related conceptual processing (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for motion-related conceptual processing (blue) and real action execution (red). (C) Regions showing consistent engagement for conceptual processing related to motion and no other modality, and higher activation likelihood for motion than the other modalities (number of significant contrasts is displayed).

Color

Color-related conceptual processing robustly engaged the left IPS and ventral FG across neuroimaging experiments (Figure 6A).

Real color perception consistently activated bilateral IPS (extending into SPL), insula, pre-SMA, left precuneus, and right LOC (Figure 6B red). Color-related conceptual processing and real color perception overlapped in left IPS (Figure 5B). The left vFG region engaged for color concepts was not consistently engaged for color perception.

Left vFG was color-specific (Figure 6C), with significant convergence selectively for color (and no other modality) and higher activation likelihood for color than all other modalities. Left IPS showed weaker evidence for color specificity: This area was consistently engaged only for color, and more consistently activated for color than several, albeit not all, other modalities.

A supplementary analysis excluding low-level contrasts (e.g. color words > fixation) provided qualitatively identical results (Figure S3), confirming that color-related conceptual processing robustly engages left IPS and vFG, where vFG is color-specific.

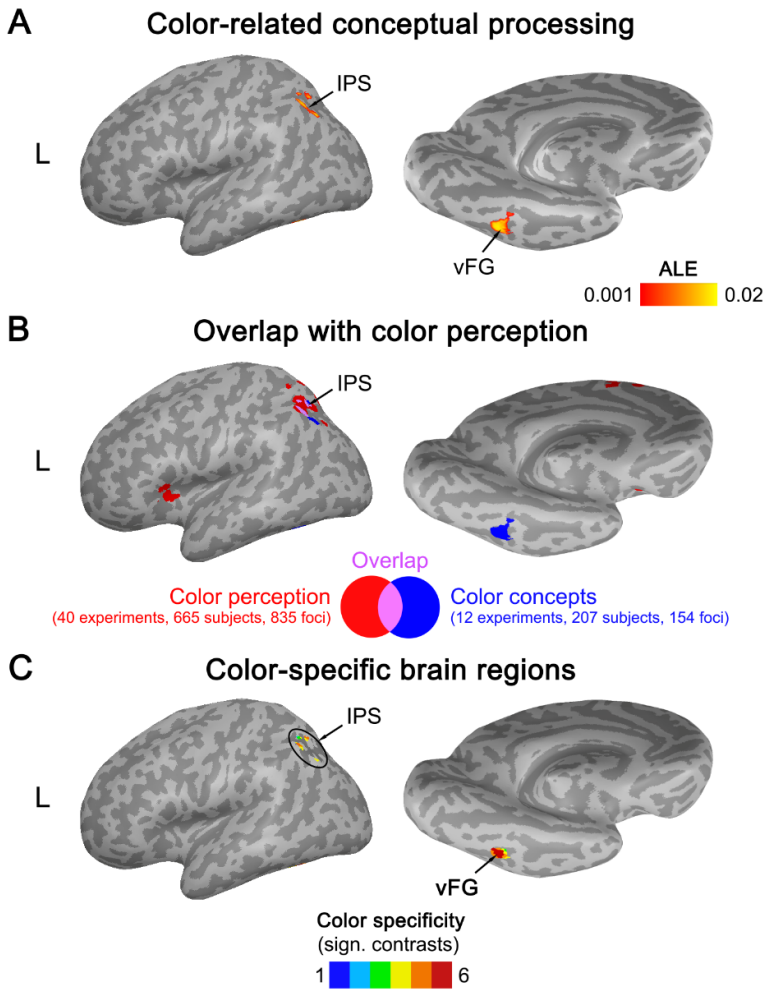

Figure 6. (A) ALE meta-analytic map for color-related conceptual processing (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for color-related conceptual processing (blue) and real color perception (red). (C) Regions showing consistent engagement for conceptual processing related to color and no other modality, and higher activation likelihood for color than the other modalities (number of significant contrasts is displayed).

Olfaction-Gustation

Conceptual processing related to olfaction-gustation was associated with consistent activation in left orbitofrontal cortex (OFC) (Figure 7A).

Real olfactory-gustatory perception robustly activated the bilateral OFC, insula, IFG, anterior cingulate, thalamus, basal forebrain, as well as the amygdala, hippocampus, entorhinal cortex, and subiculum (Figure 7B red). Conceptual processing related to olfaction-gustation and real olfactory-gustatory perception overlapped in the left OFC (Figure 7B purple).

Left OFC was specific to olfactory-gustatory conceptual processing (Figure 7C): This area showed significant convergence only for olfaction-gustation (and no other modality) and higher activation likelihood for olfaction-gustation than every other modality.

A supplementary analysis that excluded low-level contrasts (e.g. food words > rest) yielded highly similar results (Figure S6), confirming that left OFC is robustly and selectively engaged in conceptual processing related to olfaction-gustation.

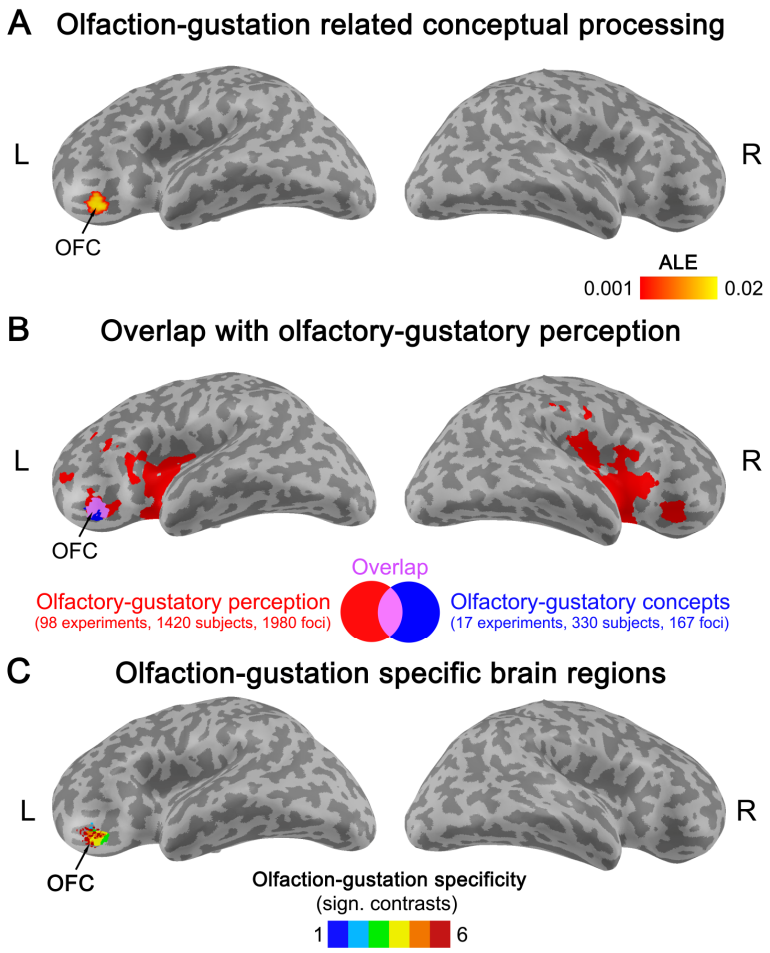

Figure 7. (A) ALE meta-analytic map for conceptual processing related to olfaction-gustation (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap

(purple) between meta-analytic maps for olfaction-gustation related conceptual processing (blue) and real olfactory-gustatory perception (red). (C) Regions showing consistent engagement for conceptual processing related to olfaction-gustation and no other modality, and higher activation likelihood for olfaction-gustation than the other modalities (number of significant contrasts is displayed).

Emotion

Emotion-related conceptual processing consistently activated the bilateral amygdala and medial prefrontal cortex (mPFC), as well as the left angular gyrus (AG) and temporal pole (TP) (Figure 8A).

Real emotion perception robustly recruited the bilateral amygdala and hippocampus, thalamus, basal forebrain, IFG and insula, PreCS, FG, LOC, cingulate and mPFC (Figure 8B red). Emotion-related conceptual processing overlapped with real emotion perception in the bilateral amygdala, mPFC, and left AG (Figure 8B purple). Left TP was not consistently engaged for real emotion perception.

Bilateral amygdala and left TP were emotion-specific (Figure 8C), showing significant engagement selectively for emotion (and no other modality) and higher activation likelihood for emotion than all other modalities. Weaker evidence for emotion specificity was found in left AG and bilateral mPFC, which were consistently engaged exclusively for emotion and more consistently engaged for emotion than several, but not all, other modalities.

A supplementary analysis without low-level contrasts (e.g. emotionally-connotated words > fixation) provided similar results (Figure S7), confirming the consistent engagement of left AG, bilateral amygdala and mPFC, as well as the emotion specificity of bilateral amygdala. However, left TP did not show significant convergence in this analysis.

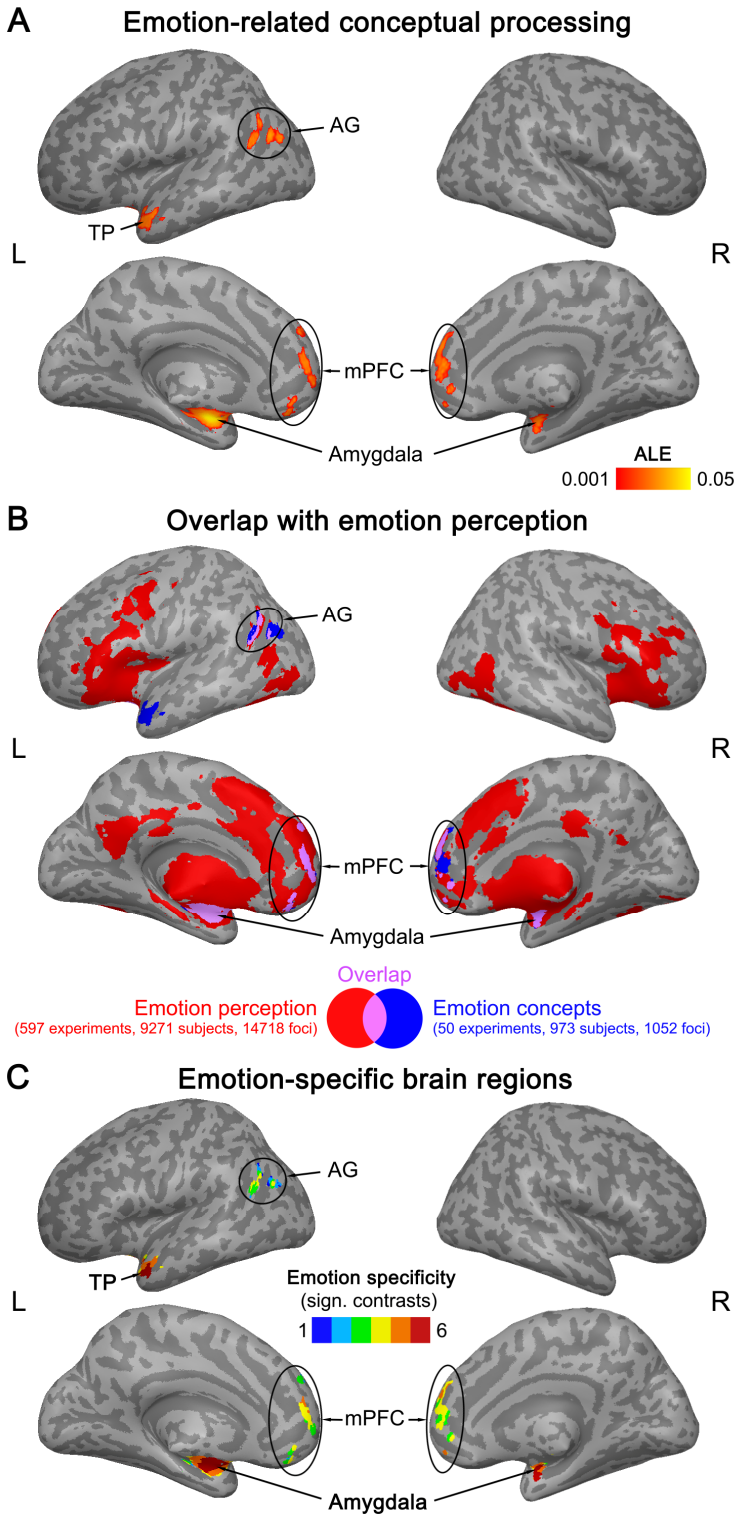

Figure 8. (A) ALE meta-analytic map for emotion-related conceptual processing (thresholded at a voxel-wise $p < 0.001$, cluster-wise $p < 0.05$ FWE-corrected). (B) Overlap (purple) between meta-analytic maps for emotion-related conceptual processing (blue) and real emotion perception (red). (C) Regions showing consistent engagement for conceptual processing

related to emotion and no other modality, and higher activation likelihood for emotion than the other modalities (number of significant contrasts is displayed).

Multimodal convergence zones

To identify “multimodal” brain regions consistently engaged for conceptual processing related to multiple modalities, we performed conjunction analyses between all possible combinations of modalities. We found that several brain regions were recruited for two (“bimodal”), or three (“trimodal”) modalities (Figure 9A). No region was engaged for more than three modalities.

In particular, the left posterior middle temporal gyrus (pMTG) and inferior parietal lobe (IPL; area PF/PFcm) contained “trimodal” convergence zones engaged for action, motion, and sound (Figure 9B). These trimodal areas were surrounded by “bimodal” regions for action and motion (blue), motion and sound (red), and action and sound (orange).

Other bimodal regions were distributed throughout the left hemisphere—for action and shape (green; LOC, PreCS, aFG), action and color (cyan; IPS, vFG), action and emotion (purple; pAG), action and olfaction-gustation (brown; OFC), and motion and emotion (yellow, TPJ).

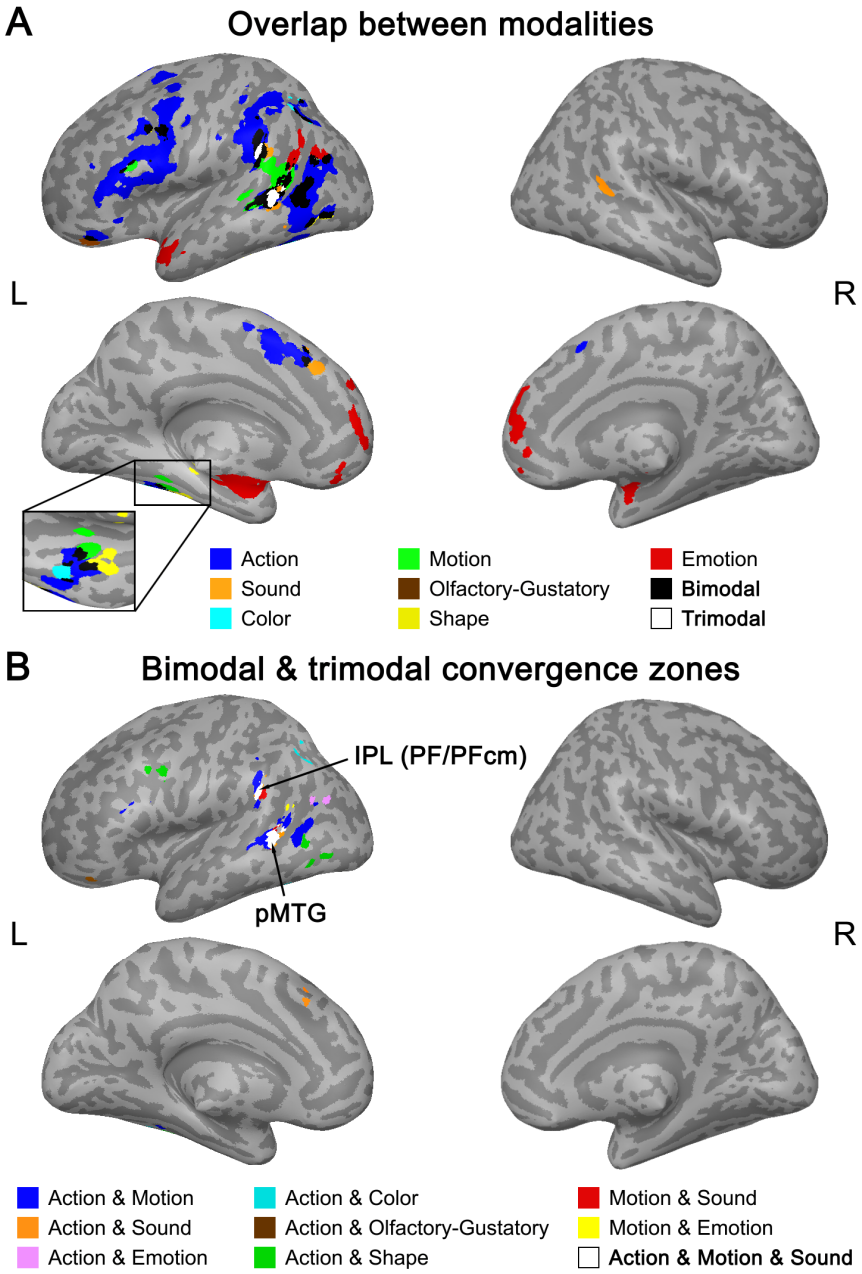

Figure 9. (A) Overlap between meta-analytic maps for conceptual processing related to the different perceptual-motor modalities. All maps were thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected. (B) Multimodal convergence zones that were consistently engaged for multiple modalities. Trimodal regions in left IPL and pMTG were surrounded by bimodal areas.

Discussion

Here, we investigated the neural basis of conceptual processing in the healthy human brain. Specifically, we (1) tested the grounded cognition hypothesis that conceptual processing consistently recruits modality-specific perceptual-motor regions, and (2) investigated whether and which modalities overlap in multimodal convergence zones. To this end, we performed an activation likelihood estimation (ALE) meta-analysis across 212 functional neuroimaging experiments on conceptual processing related to 7 perceptual-motor modalities: action, sound, visual shape, motion, color, olfaction-gustation, and emotion.

We found that conceptual processing consistently engages brain regions that are also activated during real perceptual-motor experience of the same modalities. These perceptual-motor areas exhibit a strong modality specificity, that is, a higher activation likelihood for the respective modality than for the other modalities. These results support grounded cognition theories: Conceptual processing robustly recruits modality-specific perceptual-motor regions.

In addition to modality-specific perceptual-motor areas, we identified multimodal convergence zones that are robustly engaged for multiple modalities. In particular, the left inferior parietal lobe (IPL) and posterior middle temporal gyrus (pMTG) are activated for three modalities: action, motion, and sound. These “trimodal” areas are surrounded by “bimodal” areas engaged for two modalities. Taken together, our findings support “hybrid theories” of conceptual processing which propose an involvement of both modality-specific and cross-modal brain regions.

Modality-specific perceptual-motor regions

Action

Action-related conceptual processing overlapped with real action execution in high-level somatomotor regions, including left aSMG/S1, IPS, PMC, and (pre-)SMA. These regions are recruited during real tool use (Goldenberg, 2009; Johnson-Frey, 2004; Lewis, 2006), as well as during action observation, pantomime and imagery (Hardwick et al., 2018; Papitto et al., 2019). Left aSMG/S1 showed the strongest evidence for action specificity, that is, a higher activation likelihood for conceptual processing related to action than all other modalities. Left aSMG is implicated in the visual-motor control of object-directed actions (Haaland et al., 2000; Turella and Lingnau, 2014). In particular, ideomotor apraxia—a deficit in producing skilled object-directed movements (Culham and Valyear, 2006)—is specifically associated with damage in and near left aSMG (Buxbaum et al., 2005a, 2005b; Haaland et al., 2000). These observations suggest that left aSMG stores high-level representations of object-use motor skills (Culham and Valyear, 2006; Johnson-Frey, 2004; van Elk et al., 2014). Overall, our results indicate that action-related conceptual processing involves high-level somatomotor representations that are also engaged during real object-directed actions.

Sound

Sound-related conceptual processing and real auditory perception overlapped in the bilateral pSTS. The pSTS is implicated in high-level auditory processes, such as environmental sound recognition (Lewis et al., 2004), sound recall (Wheeler et al., 2000), music imagery (Zatorre et al., 1996), and voice perception (Belin et al., 2000; Specht and Reul, 2003). Right pSTS showed the strongest evidence for sound specificity, with a higher activation likelihood for sound than all other modalities. This finding converges with a right-hemispheric dominance for non-linguistic environmental sounds, such as music (Halpern et al., 2004), human voices (Belin et al., 2000), and animal vocalizations (Lewis et al., 2009). In contrast, speech perception is strongly left-lateralized (Friederici, 2012, 2002). This suggests that auditory features of concepts comprise high-level environmental sound representations (e.g. barking), and not internal verbalizations (e.g. “dog”). Overall, these results indicate that sound-related conceptual processing involves brain regions that are also engaged in high-level auditory processing.

Visual shape

Both shape-related conceptual processing and real visual shape perception consistently activated the left LOC (area hOc4la). Left LOC (hOc4la) was also shape-specific, being selectively and more consistently recruited for shape than for the other modalities. The LOC is part of extrastriate visual cortex, situated downstream from early visual cortex (V1-V3) and implicated in visual object perception (Malikovic et al., 2016; Weiner and Grill-Spector, 2011). The LOC responds to differences in the perceived 3D shape of objects (Kourtzi et al., 2003; Murray et al., 2002), as well as the 2D shapes of familiar and illusory objects (Stanley and Rubin, 2005). Area hOc4la of the LOC can be structurally and functionally distinguished from its neighbors hOc4lp and V5/MT: While both hOc4la and hOc4lp are associated with visual shape perception, only hOc4la contains object-selective representations (Sayres and Grill-Spector, 2008). In contrast to V5/MT, hOc4la is not motion-sensitive, but strongly responds to images of intact vs. scrambled objects (Larsson and Heeger, 2006). Taken together, these results suggest that shape-related conceptual processing recruits high-level representations of object shape.

Left aFG was also consistently engaged in shape-related conceptual processing. This converges with several neuroimaging studies indicating that the shape properties of animals and tools are represented in the FG in both perceptual and conceptual tasks (for a review, see Martin, 2007). However, in this meta-analysis, the FG area engaged in conceptual processing did not overlap with, but lay directly anterior to the FG area engaged in real visual shape

perception. This may reflect abstraction from low-level visual shape information (Thompson-Schill, 2003; see discussion of “anterior shift” below).

Motion

Motion-related conceptual processing did not overlap with real visual motion perception, but with action execution in left pSTS and aSMG. At first glance, this result might suggest that motion concepts are more related to movement execution than perception. This view is supported by the fact that left aSMG is implicated in tool-use motor skills (Johnson-Frey, 2004; van Elk et al., 2014; see section on Action).

However, left pSTS is rather implicated in movement perception than execution (Pitcher and Ungerleider, 2021). Indeed, a cluster within left pSTS showed strong evidence for motion specificity, that is, a higher activation likelihood for motion than for all other modalities, including action. Moreover, this motion-specific cluster did not overlap with real action execution. Left pSTS is known to be specialized for biological (i.e. human and animal) motion perception (for a review, see Saygin, 2012). The pSTS receives input from the classical motion-sensitive area V5/MT which does not distinguish different types of movement (Boussaoud et al., 1990; Ungerleider and Desimone, 1986). Together with these previous findings, our results suggest that motion-related conceptual processing involves high-level representations of (biological or action-related) motion.

Color

Color-related conceptual processing consistently engaged the left IPS and vFG. Remarkably, overlap with real color perception was found in left IPS, but not in vFG. Left IPS is not typically implicated in color perception. However, left IPS is implicated in storing individual object features in visual working memory, including color features (Galeano Weber et al., 2016; Xu, 2007). Thus, the left IPS recruitment during color-related conceptual processing may reflect the online working-memory storage of color representations, rather than color representation *per se*. In line with this view, left IPS showed only weak evidence for color specificity and virtually the same region was also engaged in action-related conceptual processing.

In contrast, left vFG showed strong evidence for color specificity. Left vFG is specifically implicated in active color perception (e.g. color discrimination tasks; Beauchamp, 1999; Simmons et al., 2007), and receives input from area V4 implicated in passive color perception (Conway, 2009). However, left vFG was not consistently activated during real color perception in our meta-analysis. As a potential explanation, the *BrainMap* dataset possibly included too few active color perception tasks to engage left vFG. Notably, several individual studies demonstrated direct activation overlap between color-related conceptual processing

and active color perception in left vFG (Hsu et al., 2012, 2011; Simmons et al., 2007). Therefore, we conclude that color-related conceptual processing involves high-level color perception areas.

Olfaction-Gustation

Conceptual processing related to olfaction-gustation and real olfactory-gustatory perception overlapped in left OFC. Left OFC was also highly specific to olfactory-gustatory processing, with significant engagement selectively for olfaction-gustation and a higher activation likelihood for olfaction-gustation than for all other modalities.

The OFC is implicated in both olfaction and gustation, receiving input from both primary olfactory and gustatory cortices (de Araujo et al., 2003; Small and Prescott, 2005). Specifically, the OFC is involved in the recognition of odors and flavors, as well as the computation of their reward value, which translates to degrees of (un-)pleasantness on the behavioral level (Kemmerer, 2014; Small et al., 2007). Therefore, our results indicate that conceptual processing related to olfaction-gustation involves high-level components of the olfactory-gustatory system.

Emotion

Emotion-related conceptual processing overlapped with real emotion perception in the left TPJ, bilateral mPFC and amygdala. The TPJ is involved in social-emotional processes, particularly in theory-of-mind or mentalizing—representing the mental states of others (Saxe and Kanwisher, 2003; Schurz et al., 2020; Van Overwalle and Baetens, 2009). The mPFC is implicated in social-emotional event representation and simulation (Benoit et al., 2011; Schacter et al., 2017). Finally, the amygdala is well-known for its central role in emotion perception (Cheung et al., 2019; LeDoux, 2007), especially fear and anxiety (Davis, 1992). Unsurprisingly, the amygdala showed the strongest evidence for emotion specificity out of all regions.

However, strong emotion specificity was also found in the left TP. The TP is implicated in high-level social-emotional processing, receiving affective input from the amygdala and mPFC (Olson et al., 2007; Ross and Olson, 2010). In our meta-analysis, this region was not consistently engaged in real emotion perception, suggesting that it stores highly abstract social-emotional representations. Moreover, although the TP is located in the ATL, our findings support the view that the TP is not cross-modal, but emotion-specific (cf. Binder and Desai, 2011). Crucially, however, this result does not refute the idea that the ATL contains the cross-modal hub of the conceptual system. It only implies that the cross-modal hub is not located in the TP, but it could be located in other parts of the ATL. Indeed, some previous work suggests

that the most critical and modality-invariant hub region is located in the anterior fusiform and/or inferior temporal gyri (Binney et al., 2010; Lambon Ralph et al., 2016; Mion et al., 2010).

Conceptual processing engages high-level, rather than low-level, perceptual-motor regions

Overall, we found strong evidence for a consistent involvement of modality-specific perceptual-motor areas in conceptual processing. Importantly, however, conceptual processing mainly recruited *high-level* (e.g. secondary or association), rather than low-level (e.g. primary) regions of the modality-specific perceptual-motor systems. For instance, sound-related conceptual-processing engaged the right pSTS, not primary auditory cortex. This indicates that low-level perceptual-motor areas are not consistently recruited across conceptual tasks (Fernandino et al., 2016a; Martin, 2016; Thompson-Schill, 2003). However, several individual studies found conceptual effects in low-level perceptual-motor areas (e.g. Harpaintner et al., 2020; Hauk et al., 2004). As a potential explanation for the lack of consistent recruitment, the engagement of low-level perceptual-motor areas might be particularly task-dependent. Various authors propose that low-level perceptual-motor areas are selectively engaged when the task explicitly requires the retrieval of detailed perceptual-motor information (Binder and Desai, 2011; Kemmerer, 2015; Kuhnke et al., 2020b; Willems and Casasanto, 2011; Yee and Thompson-Schill, 2016). This view is supported by several functional neuroimaging studies (Hoenig et al., 2008; Hsu et al., 2011; Kuhnke et al., 2020b; van Dam et al., 2012). Moreover, low-level perceptual-motor areas may influence the activity of higher-level cortical areas via functional connections, even if low-level areas are not strongly activated themselves (Fiori et al., 2018; Ward et al., 2010). In line with both of these proposals, we recently found that multimodal IPL interacted with primary motor and somatosensory cortices (M1/S1) selectively when action knowledge was task-relevant, and with a low-level auditory area in the thalamus selectively when sound knowledge was task-relevant (Kuhnke et al. 2021). These connectivity effects occurred even though M1/S1 and thalamus did not show significant functional activation during the conceptual tasks.

Notably, not all perceptual-motor areas were modality-specific, and vice versa. This indicates that perceptual-motor involvement and modality specificity are two distinct issues, and it was crucial to analyze them separately. As an example, the left mid-FG contained a fine-grained parcellation into modality-specific regions for color (ventral), motion (dorsal), shape (anterior), and action (middle) (see Figure 9A). However, none of these regions overlapped with real perceptual-motor experience. The FG regions engaged in conceptual processing generally lay directly anterior to the regions engaged in perception or action. This finding is in line with the “anterior shift” hypothesis that brain regions involved in conceptual

processing often lie directly anterior to perceptual-motor areas, potentially reflecting abstraction from basic perceptual-motor information (Thompson-Schill, 2003).

Multimodal convergence zones for conceptual processing

In addition to modality-specific areas, we identified several multimodal convergence zones that were consistently engaged for conceptual processing related to multiple modalities. In particular, the left IPL and pMTG were robustly engaged for 3 modalities: action, sound, and motion. These "trimodal" areas were surrounded by "bimodal" areas engaged for 2 modalities. Bimodal areas were in turn surrounded by modality-specific areas. This concentric anatomical organization suggests a neural hierarchy, where modality-specific areas converge onto bimodal areas which converge onto trimodal areas (Damasio, 1989; Margulies et al., 2016; Mesulam, 1998). Such a hierarchy of convergence zones may implement multiple levels of abstraction from low-level perceptual-motor information, in line with several previous proposals (Binder and Desai, 2011; Fernandino et al., 2016a; Kuhnke et al., 2021, 2020b; Simmons and Barsalou, 2003).

Notably, the anterior temporal lobe (ATL) did not emerge as a multimodal convergence zone in our meta-analysis, even though the ATL is widely considered as the key cross-modal hub of the conceptual system (for a review, see Lambon Ralph et al., 2016). In support of this view, evidence from semantic dementia (Jefferies, 2013; Patterson et al., 2007), functional neuroimaging (Rice et al., 2015; Visser et al., 2010), and TMS (Pobric et al., 2010a, 2010b) indicates a crucial role of the ATL in processing various types of conceptual information, regardless of perceptual-motor content. As a potential explanation for the lack of consistent ATL engagement, we propose that the ATL is an "amodal" hub. That is, the ATL completely abstracts away from modality-specific perceptual-motor information to highly abstract conceptual representations (Lambon Ralph et al., 2010; Patterson and Lambon Ralph, 2016). This renders the "amodal" ATL insensitive to modality-specific conceptual content. In contrast, "multimodal" hubs like left IPL and pMTG retain modality-specific perceptual-motor information about the individual modalities that they bind (Fernandino et al., 2016b; Kuhnke et al., 2022, 2021, 2020b; Reilly et al., 2016; Seghier, 2013). Alternatively, these multimodal regions may code a knowledge type common to all involved conceptual features. For instance, action-related motion representations may be equally relevant for coding action and motion features, as well as sound features (as actions often elicit sounds; Lemaitre et al., 2018).

The multimodal—amodal hub theory is supported by several studies. For example, Kuhnke et al. (2020b) demonstrated that left IPL and pMTG respond to both sound and action features of concepts when these are task-relevant. In contrast, the ATL was not engaged for individual features, but for general abstract conceptual information (words vs. pseudowords). In a follow-up study (Kuhnke et al., 2021), left IPL was functionally coupled with auditory brain

regions during sound feature retrieval, and with somatomotor regions during action feature retrieval. In contrast, the ATL interacted with other high-level cross-modal areas, but not modality-specific cortices. In line with these results, Fernandino et al. (2016a) found that activity in the IPL during word reading correlated with the strength of sensory-motor associations for all modalities tested (action, sound, shape, color, motion). Again, ATL activity did not correlate with individual sensory-motor associations. Finally, TMS over left IPL (Ishibashi et al., 2011; Kuhnke et al., 2020a; Pobric et al., 2010a) and pMTG (Davey et al., 2015; Whitney et al., 2012) can selectively disrupt the retrieval of individual task-relevant semantic features. In contrast, TMS over ATL typically impairs semantic processing for all types of concepts (Pobric et al., 2010a, 2010b).

Evidence for hybrid theories of conceptual processing

Theories of conceptual representation can be organized on a continuum between strong embodied and strong amodal views (Kiefer and Harpaintner, 2020; Meteyard et al., 2012). Strong embodied views—the extreme version of grounded cognition theories—hold that conceptual processing relies exclusively on distributed and interconnected modality-specific perceptual-motor areas (e.g. Allport, 1985). In contrast, strong amodal views assume that concepts consist entirely of abstract, amodal symbols represented outside the perceptual-motor systems (Fodor, 1975; Pylyshyn, 1984).

Our results oppose both of these extremes. In contrast to strong embodied views, we found consistent engagement of multimodal convergence zones, not only modality-specific perceptual-motor regions. Contrary to strong amodal views, we found that conceptual processing robustly recruits modality-specific perceptual-motor areas. Moreover, conceptual processing engages multimodal, not only amodal, hubs. Taken together, our results support so-called “hybrid theories” of conceptual processing, which assume an involvement of both modality-specific perceptual-motor cortices and cross-modal convergence zones (Binder and Desai, 2011; Fernandino et al., 2016a; Kiefer and Harpaintner, 2020; Kuhnke et al., 2021, 2020b; Simmons and Barsalou, 2003).

Based on our findings, we now propose a new model of the conceptual system—a refined and extended version of our previous account (Kuhnke et al., 2021, 2020b). According to this model, conceptual processing relies on a hierarchical neural architecture from modality-specific to bimodal to trimodal regions, up to an amodal hub in the ATL (Figure 10). At the functional level, the neural hierarchy implements abstraction of conceptual representations from basic perceptual-motor information (Binder and Desai, 2011; Fernandino et al., 2016a; Kiefer and Harpaintner, 2020). At the structural level, representational convergence is implemented via a concentric anatomical organization, where trimodal areas are surrounded by bimodal areas which are surrounded by modality-specific areas (Damasio, 1989; Margulies

et al., 2016; Mesulam, 1998). Our model can account for all key results of the current meta-analysis: (1) The consistent recruitment of modality-specific perceptual-motor regions, (2) the overlap of multiple modalities in multimodal (i.e. bimodal and trimodal) convergence zones, and (3) the absence of ATL recruitment for modality-specific contrasts, despite overwhelming evidence for a crucial role of the ATL in semantic cognition. Moreover, our model is supported by a recent computational modeling study which revealed that the core functions of the conceptual system—conceptual abstraction and flexibility—are best achieved by a hierarchical multi-level architecture composed of a modality-specific layer, an intermediate layer (~multimodal regions), and a single top-level hub (~amodal ATL) (Jackson et al., 2021; also see Garagnani and Pulvermüller, 2016).

Our model is related to two prominent theories of conceptual representation: The "hub-and-spokes" (Lambon Ralph et al., 2016; Patterson et al., 2007) and "embodied abstraction" (Binder and Desai, 2011; Fernandino et al., 2016a) models. According to the hub-and-spokes model, modality-specific "spoke" regions converge onto a single cross-modal "hub" in the ATL. In contrast, 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 assumes multiple levels of cross-modal convergence zones. In line with the hub-and-spokes model, our model proposes the ATL to constitute the most abstract cross-modal hub. However, in contrast to both theories, our model distinguishes among cross-modal areas between "multimodal" regions which retain modality-specific information and the "amodal" ATL which does not. In addition, our model makes more precise functional-anatomical predictions: (1) Multimodal areas are restricted to bimodal and trimodal zones, whereas no multimodal area binds more than three modalities. (2) Trimodal areas are exclusively located in the left IPL and pMTG. (3) Trimodal, bimodal and modality-specific areas show a concentric anatomical organization. (4) Only the ATL functions as amodal hub. These predictions could be directly tested in future research to further develop and refine theories of conceptual representation in the human brain.

Conclusion

In conclusion, this meta-analysis of >200 functional neuroimaging studies revealed that conceptual processing robustly recruits both modality-specific perceptual-motor regions and multimodal convergence zones. These results support "hybrid theories" of conceptual processing which propose an involvement of both modality-specific and cross-modal cortices. We propose a novel model of the conceptual system, according to which conceptual processing relies on a hierarchical neural architecture from modality-specific to bimodal to trimodal areas (left IPL, pMTG) up to an amodal hub in the ATL.

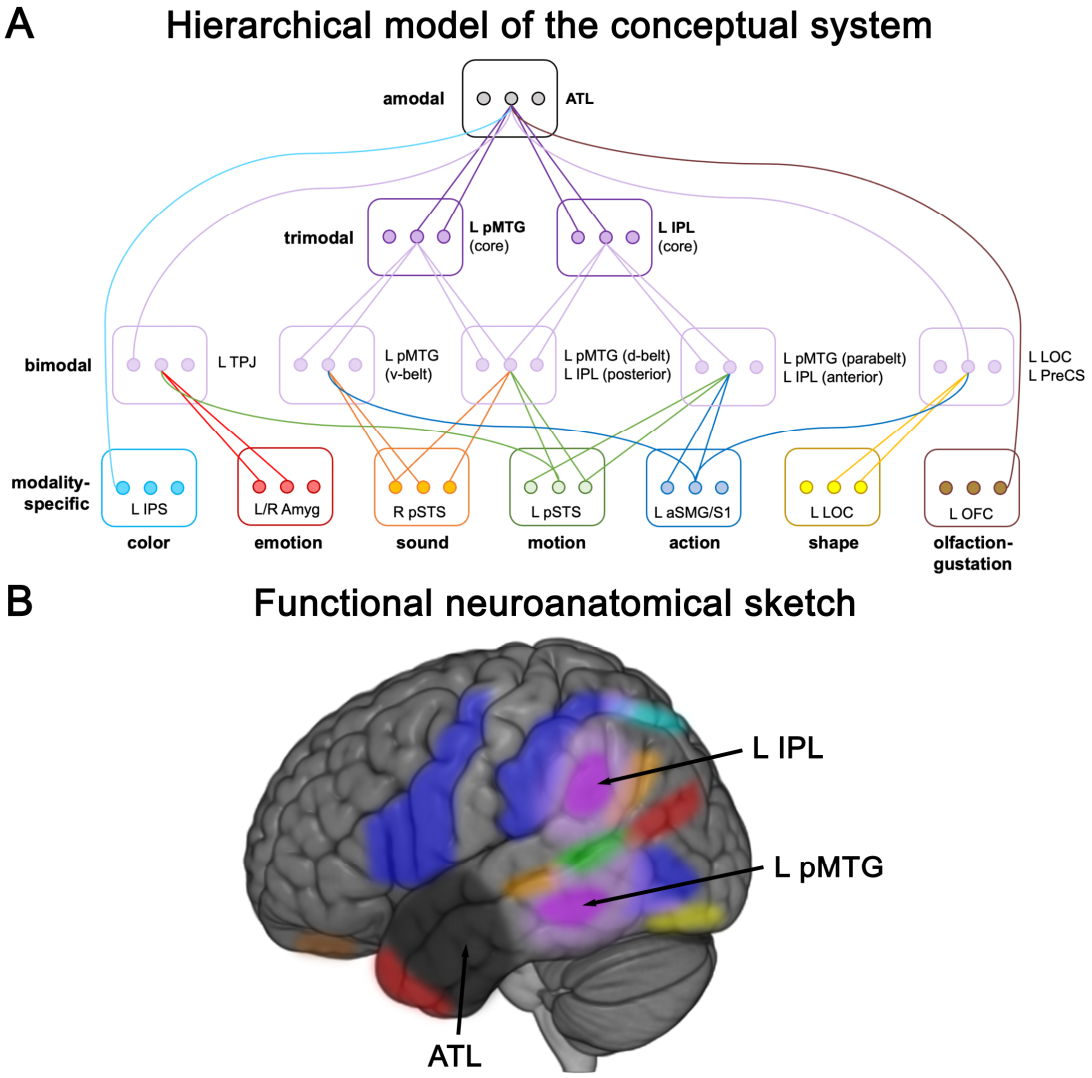

Figure 10. Novel model of the conceptual system. (A) Conceptual processing relies on a hierarchical neural architecture from modality-specific to bimodal to trimodal areas, up to an amodal hub. Boxes represent brain regions and dots represent individual representational units that converge onto a more abstract representation at a higher level. (B) Functional neuroanatomical sketch illustrating the proposed locations of the different components of our model on the cerebral cortex. The color code is identical to panel A.

Statements & Declarations

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Competing Interests

The authors declare no competing interests.

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Author Contributions (CRediT)

Philipp Kuhnke: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Visualization, Writing—original draft, Writing—review and editing;

Marie C. Beaupain: Investigation, Data curation, Methodology, Writing—review and editing;

Johannes Arola: Investigation, Data curation, Methodology;

Markus Kiefer: Conceptualization, Writing—review and editing.

Gesa Hartwigsen: Conceptualization, Funding acquisition, Supervision, Project administration, Writing—review and editing.

Data Statement

All meta-analytic maps and raw datasets will be made openly available via the Archive of Neuroimaging Meta-Analyses (ANIMA): https://anima.fz-juelich.de/

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