Conceptual representations in the default, control and attention networks are task-dependent and cross-modal

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Abstract

Conceptual knowledge is central to human cognition. Neuroimaging studies suggest that conceptual processing involves modality-specific and multimodal brain regions in a task-dependent fashion. However, it remains unclear (1) whether conceptual representations *within* these regions are also modulated by the task, (2) whether conceptual representations in multimodal areas are indeed cross-modal, and (3) how the conceptual system relates to the large-scale functional brain networks. To address these issues, we conducted multivariate pattern analyses on fMRI data. 40 participants performed three tasks—lexical decision, sound judgment, and action judgment—on written words. We found that (1) conceptual representations are strongly modulated by the task, (2) conceptual representations in several multimodal regions are cross-modal, and (3) conceptual feature retrieval involves the default, frontoparietal control, and dorsal attention networks. Conceptual representations in these large-scale networks are task-dependent and cross-modal. Our findings support theories that assume conceptual processing to rely on a flexible, multi-level architecture.

1. Introduction

Conceptual knowledge is crucial for many cognitive abilities, such as word comprehension and object recognition (Lambon Ralph, 2014; van Elk et al., 2014). Previous neuroimaging studies indicate that conceptual processing involves both modality-specific perceptual-motor regions and cross-modal convergence zones (for a meta-analysis, see Kuhnke et al., 2023; for reviews, see Binder & Desai, 2011; Borghesani & Piazza, 2017; Kiefer & Pulvermüller, 2012; Lambon Ralph et al., 2016). Modality-specific regions represent perceptual-motor features of concepts. For instance, action features are represented in somatomotor regions (Hauk et al., 2004; Tettamanti et al., 2005; Vukovic et al., 2017), while sound features are represented in auditory areas (Bonner and Grossman, 2012; Kiefer et al., 2012, 2008; Trumpp et al., 2013). Cross-modal convergence zones integrate modality-specific features into more abstract, cross-modal representations (Binder, 2016; Fernandino et al., 2016a; Kuhnke et al., 2023, 2020b; Tong et al., 2022). We previously 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., 2023, 2022, 2020b). Multimodal regions seem to include the left inferior parietal lobe (IPL) and posterior middle temporal gyrus (pMTG) (Fernandino et al., 2022, 2016a; Kuhnke et al., 2023, 2020b), whereas the anterior temporal lobe (ATL) acts as an amodal hub of the conceptual system (Jefferies, 2013; Lambon Ralph et al., 2016; Patterson et al., 2007).

While a common terminology is currently lacking in the field, we refer to "perceptual-motor modalities" as the brain's major input and output channels of perception and action (Kuhnke et al., 2023, 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). We call brain regions "modality-specific" if they represent information related to a single perceptual-motor modality (Barsalou, 2016; Kiefer and Pulvermüller, 2012).

Crucially, the recruitment of both modality-specific and multimodal regions is task-dependent. Several studies indicate that modality-specific perceptual-motor regions are selectively engaged when the task requires the retrieval of perceptual-motor features of concepts (Borghesani et al., 2019; Hoenig et al., 2008; Hsu et al., 2011; Kemmerer, 2015; Kuhnke et al., 2020b; van Dam et al., 2012). For example, we previously showed that auditory regions are selectively recruited for sound features during sound judgments, whereas somatomotor regions are selectively engaged for action features during action judgments (Kuhnke et al., 2021, 2020b). Remarkably, multimodal regions (e.g., left IPL and pMTG) also showed a task-dependent activation profile, responding to sound features during sound judgments and to action features during action judgments.

However, several issues remain unclear. First, it is unknown whether conceptual representations *within* modality-specific and multimodal regions are also modulated by the task. Previous neuroimaging studies have exclusively investigated task-dependent changes in general recruitment of brain regions, that is, changes in mean activation magnitude via univariate analyses (Borghesani et al., 2019; Hsu et al., 2011; Kemmerer, 2015; Kuhnke et al., 2020b; van Dam et al., 2012). However, neural representations of mental contents are generally assumed to be encoded in "population codes"—patterns of activity distributed across multiple representational units within a specific region (Connolly et al., 2012; Haxby et al., 2014; Ritchie et al., 2019). Whereas univariate analyses are insensitive to such fine-grained activity patterns, population codes can be studied using multivariate pattern analyses (MVPA) of functional neuroimaging data (Haxby, 2012; Mur et al., 2009). MVPA decoding aims to predict a mental content based on the activity patterns within a brain region (Haynes, 2015; Norman et al., 2006).

Second, it is unclear whether neural representations in multimodal convergence zones are indeed cross-modal, that is, similar for different modalities. As multimodal areas are typically identified via conjunctions of brain activation maps (Fernandino et al., 2016a; Kuhnke et al., 2020b), it is possible that multimodal overlap reflects spatially overlapping but distinct fine-grained activity patterns for different modalities (Downing et al., 2007; Haxby et al., 2001).

Third, it remains unknown how the conceptual system is related to the large-scale functional networks of the human brain, as identified using resting-state functional connectivity MRI (Buckner et al., 2009; Yeo et al., 2011). Several authors have noted the topographical similarity of the conceptual system, especially cross-modal areas, to the default mode network (DMN) (Binder et al., 2009, 1999; Fernandino et al., 2016a). The DMN is a set of brain regions that show deactivation during attention-demanding tasks (as compared to rest), and strong functional coupling during the resting state (Buckner et al., 2008; Raichle et al., 2001). The DMN is engaged in spontaneous thought, self-referential and autobiographical processes, as well as mentalizing (Andrews-Hanna, 2012; Smallwood et al., 2021). These forms of introspective information may contribute to conceptual knowledge (Kiefer et al., 2022; Ulrich et al., 2022). In addition, conceptual processing is frequently assumed to involve domain-general executive control or "multiple demand" systems, such as the frontoparietal control network (FPN) and/or the dorsal attention network (DAN) (Hodgson et al., 2021; Noonan et al., 2013; Wang et al., 2021). Specifically, FPN and DAN may support the controlled retrieval and/or selection of task-relevant conceptual representations (Noonan et al., 2013; Thompson-Schill et al., 1999; Wagner et al., 2001).

Here, we asked (1) whether conceptual representations in modality-specific and cross-modal brain regions are modulated by the task, (2) whether conceptual representations in putative multimodal convergence zones are indeed cross-modal, and (3) how the brain regions

engaged in conceptual processing relate to large-scale functional brain networks. To this end, we conducted MVPA decoding analyses on our previous fMRI data (Kuhnke et al., 2021, 2020b). 40 participants performed three different tasks—lexical decision, sound judgment, and action judgment—on written words with a high or low association to sounds and actions (e.g., "telephone" is a high sound–high action word).

First, in "searchlight" decoding analyses, we localized brain regions enabling above-chance decoding of sound and action features of concepts. In each task, we trained a machine-learning classifier to decode high vs. low action or sound words based on the local activity patterns. We compared the results for searchlight MVPA to classical univariate analysis to identify additional information represented in fine-grained activity patterns. Next, to test for cross-modal representations of task-relevant conceptual features, we trained a classifier on sound features (high vs. low sound words) during sound judgments, and tested the classifier on action features (high vs. low action words) during action judgments, and vice versa. Finally, we investigated the involvement of the large-scale functional brain networks, as characterized in the resting-state network parcellation by Yeo et al. (2011). To this end, we assessed the spatial overlap between the MVPA searchlight maps and each functional network, and performed MVPA decoding analyses using the activity patterns within each network separately.

We hypothesized that conceptual representations are modulated by the task: In both modality-specific and multimodal brain regions, activity patterns for sound and action features should be most distinctive when they are task-relevant. Secondly, multimodal convergence zones should contain cross-modal conceptual representations, enabling cross-decoding between task-relevant sound and action features. Finally, we expected that conceptual feature retrieval involves the DMN, and possibly domain-general control (FPN) and attention (DAN) networks.

2. Methods

2.1. Subjects

Data from 40 healthy native German speakers (22 female; mean age: 26.6 years; SD: 4.1; range: 19-33) were analyzed. 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.

2.2. Experimental procedures

The experimental procedure is reported in detail in Kuhnke et al. (2020), and summarized here. We used a 3 x 2 x 2 within-subject design with the factors TASK (lexical decision, sound judgment, action judgment), SOUND (high, low association), and ACTION (high, low association). During event-related fMRI, participants performed three different tasks—lexical decision, sound judgment, and action judgment—on 192 written words with a high or low association to sounds and actions (Figure 1). In the lexical decision task, participants had to decide 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. In the action judgment task, participants judged whether the object was strongly associated with actions. Whereas the lexical decision task acted as an implicit 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 to sounds, while high and low action words selectively differed in their association to actions, as determined by the ratings of a different group of 163 volunteers (cf. Fernandino et al., 2016; Trumpp et al., 2014). Word types 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., 2020). Stimuli for all conditions 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 using the *Wuggy* software (Keuleers and Brysbaert, 2010; http://crr.ugent.be/Wuggy).

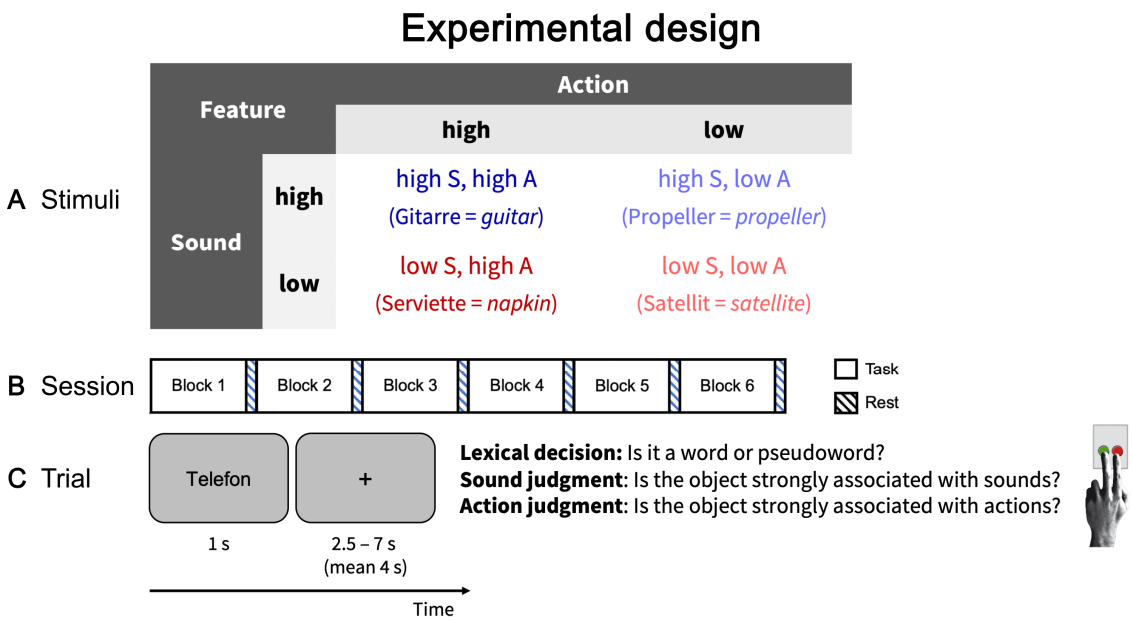

Figure 1. Experimental design. (A) Participants were presented with written words that had a high or low association to sounds and actions. (B) Stimuli were presented in random order within 6 blocks (64 trials each). Blocks were separated by 20-s rest periods (blue-striped bars). Sound and action judgment tasks were performed in mini-blocks of 16 trials. (C) On each trial, a word was shown for 1 s, followed by an inter-trial interval (fixation cross) of 2.5-7 s. Participants responded via left-handed button press.

2.3. fMRI acquisition and preprocessing

fMRI data were collected on a 3T 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-echo EPI sequence (repetition time (TR): 2 s; echo times (TE): 12 & 33 ms; flip angle: 90°; field of view (FoV): 204 mm; voxel size: 2.5 x 2.5 x 2.5 mm; slice gap: 0.25 mm; bandwidth: 1966 Hz/Px; phase encoding direction: A/P; multiband factor 2). We used a dual-echo sequence (Halai et al., 2014; Poser et al., 2006) and tilted slices 10° up from the AC-PC 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 & 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 x 1 x 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 9.10). 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, and normalized to MNI space (via normalization of the coregistered structural image).

2.4. Univariate analyses

Univariate analysis employed the classical two-level approach in SPM. At the first level, individual subject data smoothed with a 5 mm^3 FWHM Gaussian kernel were modeled using the general linear model (GLM). The subject-level GLM included one regressor for each experimental condition, 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). Nuisance regressors included the 6 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. The data were subjected to an AR(1) auto-correlation model to account for temporal auto-correlations, and high-pass filtered (cutoff 128 s) to remove low-frequency noise.

Contrast images were computed at the first level for each participant. At the second (group) level, these contrast images were submitted to non-parametric permutation tests (5000 permutations; *SnPM toolbox*; https://warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/software/snpm/). To identify brain regions sensitive to action or sound features of concepts in each task (lexical decisions, action judgments, sound judgments), we compared activation for high > low action words, and high > low sound words in each task. To localize “multimodal convergence zones” engaged in both sound and action feature retrieval, we performed conjunction analyses between [sound judgment: high > low sound words] ∩ [action judgment: high > low action words] via minimum-statistic conjunctions (testing the conjunction null; Nichols et al., 2005). All activation maps were thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected for multiple comparisons. Notably, to optimally match the univariate and MVPA decoding analyses. our current univariate analyses slightly differ from those in our previous publication (Kuhnke et al., 2020b) in smoothing (5 vs. 8 mm^3) and thresholding (cluster-wise FWE vs. voxel-wise FDR correction).

2.5. MVPA searchlight analyses

To allow for valid comparison to our univariate analyses, searchlight MVPA was performed with as similar parameters as possible. As for univariate analysis, individual subject data were modeled separately using the GLM. The subject-level GLM for MVPA was identical to the univariate GLM (i.e., same HRF model, same nuisance regressors, same auto-correlation model and high-pass filtering), with two exceptions: First, MVPA was performed on unsmoothed subject-level data as is common for MVPA to retain fine-grained multi-voxel activity patterns (Haxby et al., 2014; Raizada and Lee, 2013). Moreover, the subject-level GLM for MVPA included one regressor for each trial to obtain trial-wise activity estimates (betas).

Next, these subject-specific trial-wise estimates were used as input for MVPA decoding using *The Decoding Toolbox* (version 3.999E; Hebart et al., 2015) implemented in *Matlab* (version 9.10). For searchlight MVPA, we moved a spherical region-of-interest (or "searchlight") of 5 mm radius through the entire brain (Kriegeskorte et al., 2006). At each searchlight location, a machine-learning classifier (an L2-norm support vector machine; C=1) aimed to decode between high vs. low action words, as well as high vs. low sound words, within each task. We performed leave-one-block-out cross validation, training on the activity patterns for 5 blocks, and testing on the remaining 6th block (Hebart et al., 2015).

To identify cross-modal representations of task-relevant conceptual features, we performed "cross-decoding" (i.e., training and testing the classifier on different experimental conditions; Skerry & Saxe, 2014; Wurm & Lingnau, 2015). Specifically, we trained the classifier on high vs. low sound words in the sound judgment task, and tested the classifier on high vs. low action words in the action judgment task. We also performed training and testing in the reverse direction, and averaged the results for each subject before group analysis.

Subject-specific classification accuracy maps (minus chance accuracy of 50%) were smoothed with a 5 mm^3 FWHM Gaussian kernel, matching the smoothing level for our univariate analyses. Finally, the smoothed subject-specific accuracy maps were entered into non-parametric permutation tests at the group level (5000 permutations; *SnPM toolbox*). The right somatomotor cortex was masked out to remove brain activity related to left-handed button presses (using a mask of right M1/S1/PMC/SMA from the human motor area template; Mayka et al., 2006). As for our univariate analyses, all MVPA searchlight maps were thresholded at a voxel-wise $p < 0.001$ and cluster-wise $p < 0.05$ FWE-corrected.

2.6. Spatial relationship between conceptual processing and large-scale functional networks

To assess the spatial relationship between conceptual brain regions revealed by searchlight MVPA and large-scale functional brain networks, we tested the overlap of our MVPA searchlight maps with the resting-state networks by Yeo et al. (2011). This functional overlap analysis was performed with both the 7-network and 17-network parcellations by Yeo et al. (2011). Specifically, we computed the percentage of voxels in our MVPA searchlight maps for action and sound feature retrieval, as well as cross-modal areas that fell into each large-scale network. As a measure for above-chance contribution of a functional network, the percentage overlap was compared to a baseline of equal contribution of each network (7-network parcellation: 100 / 7 = 14.29%; 17-network parcellation: 100 / 17 = 5.88%) using χ^2-tests, correcting for multiple comparisons using Bonferroni correction.

2.7. ROI-based MVPA decoding in large-scale functional networks

As a more direct test of the involvement of each large-scale functional network in conceptual processing, we also performed MVPA decoding in regions-of-interest (ROIs) corresponding to each functional network by Yeo et al. (2011). Our main analyses focused on the 7-network parcellation; the 17-network parcellation was tested in supplementary analyses (see Supplementary Material). Subject-level ROI-based decoding employed the same methods as our searchlight analyses, with the exception that the activation pattern across all voxels of the network was used for classification (Mur et al., 2009). As for our searchlight analyses, the right somatomotor cortex was masked out of the network ROIs to remove button press related activity.

At the group level, classification accuracies for each ROI and condition were entered into one-sample t-tests (vs. chance level of 50%). Moreover, we performed (two-tailed) paired t-tests for differences in decoding accuracy between conditions for a given ROI, and between ROIs for a given condition. P-values were corrected for multiple comparisons via Bonferroni correction for the number of ROIs.

3. Results

3.1. Whole-brain analyses: Univariate vs. MVPA

For both univariate analysis and searchlight MVPA, brain activity for action and sound features was strongly task-dependent.

3.1.1. Action feature retrieval

During lexical decisions, neither univariate analysis nor MVPA revealed any significant brain activity for action features (high vs. low action words). During sound judgments, both univariate analysis and MVPA yielded activity differences for action features selectively in the left AG, and no other brain region (Figure S1 A-C).

During action judgments, however, both univariate analysis and MVPA yielded widespread activity for action features. Univariate analysis (Figure 2A; Table S1) revealed action-related activations in left anterior inferior frontal gyrus (aIFG), inferior parietal lobe (IPL) / intraparietal sulcus (IPS), posterior middle and inferior temporal gyri (pMTG/ITG), posterior cingulate cortex (PCC), caudate, and cerebellum.

Searchlight MVPA (Figure 2B; Table S2) found action-related activity in left IFG, IPL/IPS, pMTG/ITG, PCC and precuneus (PC), the lateral temporo-occipital junction (LTO), premotor cortex (PMC), dorsomedial prefrontal cortex (dmPFC), and cerebellum.

Comparison between univariate analysis and searchlight MVPA revealed overlap in left IPL/IPS, aIFG, pMTG/ITG, PCC, and cerebellum (Figure 2C purple; Table S3). However, MVPA activity patterns were broader in these regions, and only MVPA revealed recruitment of the right cerebral hemisphere, specifically in right IPL (area PGp), IFG, and LTO (Figure 2C red). Moreover, only MVPA found action-related activity in left posterior IFG, PMC, LTO, PC, and dmPFC.

3.1.2. Sound feature retrieval

During lexical decisions, neither univariate analysis nor MVPA revealed any significant brain activity for sound features (high vs. low sound words). During action judgments, small clusters emerged in left IPL and bilateral PC/PCC, and no other area (Figure S1 D-F).

During sound judgments, both univariate analysis and MVPA revealed widespread activity for sound features. Univariate analysis (Figure 2D; Table S4) showed sound-related activations in left pMTG/ITG, IPL/IPS, aIFG, middle frontal gyrus (MFG) / precentral sulcus (PreCS), dmPFC, and right cerebellum.

Searchlight MVPA (Figure 2E; Table S5) detected sound-related activity in bilateral IPL/IPS, pMTG/ITG, IFG, MFG/PreCS, mPFC, PC/PCC, cerebellum, as well as auditory association cortex (AAC; area TE3).

Comparison between univariate analysis and searchlight MVPA showed overlap in left IPL/IPS, aIFG, pMTG/ITG, and dmPFC (Figure 2F purple; Table S6). However, MVPA activity patterns were more extensive in these areas, and only MVPA revealed engagement of the right cerebral hemisphere, specifically in right IPL/IPS, pMTG, and aIFG (Figure 2F red). Moreover, only MVPA revealed sound-related activity in bilateral PC/PCC, mPFC, and AAC (area TE3).

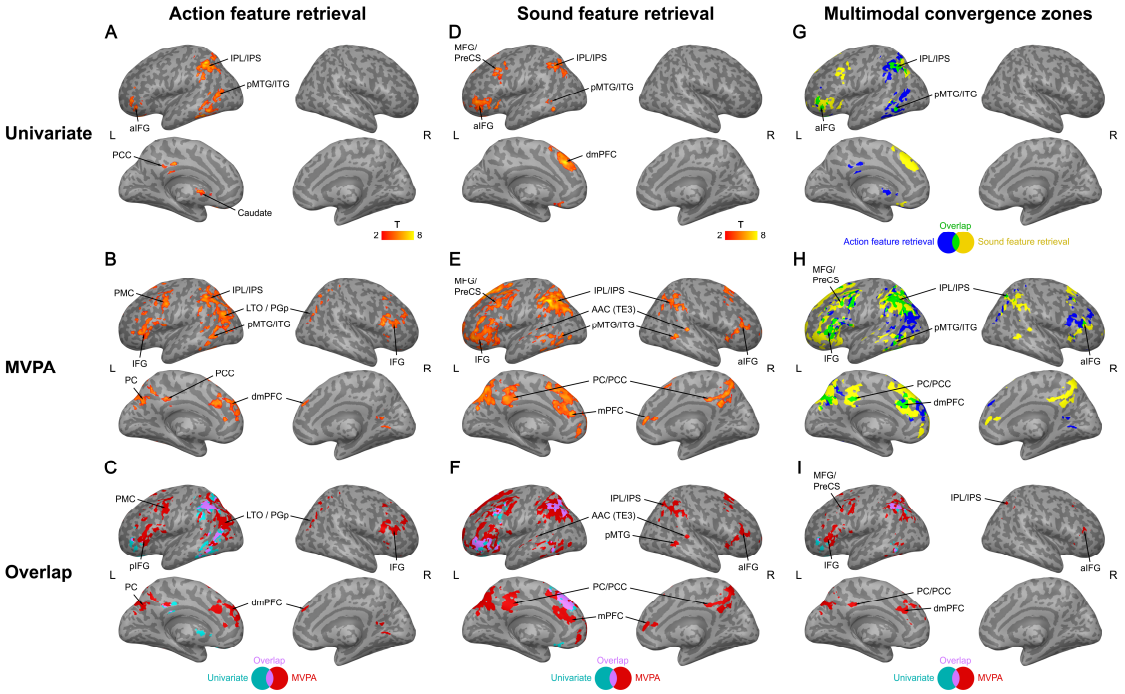

Figure 2. Comparison of results for whole-brain univariate analysis vs. searchlight MVPA on task-relevant conceptual feature retrieval. Both univariate and MVPA subject-specific maps were smoothed with a 5 mm^3 FWHM Gaussian kernel. All group-level maps were thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected using non-parametric permutation tests.

3.1.3. Multimodal convergence zones

To identify multimodal convergence zones engaged in both action and sound feature retrieval, we performed conjunction analyses between [action judgments: high vs. low action words] and [sound judgments: high vs. low sound words] for both univariate analyses and searchlight MVPA.

Univariate analysis (Figure 2G; Table S7) identified multimodal areas in left IPL/IPS, pMTG/ITG, aIFG, and right cerebellum. Searchlight MVPA (Figure 2H; Table S8) found multimodal regions in left pMTG/ITG, MFG/PreCS, dmPFC, cerebellum, as well as in bilateral IPL/IPS and IFG.

Direct comparison between univariate analysis and MVPA revealed overlap in left IPL/IPS, pMTG/ITG, and aIFG (Figure 2I purple; Table S9). However, MVPA multimodal clusters were broader in all of these areas, and only MVPA yielded multimodal regions in the right cerebral hemisphere, specifically in right IPL/IPS, and aIFG (Figure 2I red). In addition, only MVPA revealed multimodal overlap in left MFG/PreCS, PC/PCC and dmPFC.

3.2. Cross-modal conceptual representations

Next, we assessed whether "multimodal" overlap between sound and action feature retrieval was indeed based on cross-modal conceptual representations. As the machine-learning classifier was trained and tested on sound and action features separately, it is possible that successful decoding relied on spatially overlapping but distinct activity patterns. We reasoned that if these regions indeed hold cross-modal conceptual representations, it should be possible to train a classifier on sound features during sound judgments, and test it on action features during action judgments, and vice versa.

We found that cross-decoding of task-relevant conceptual features was possible (i.e., significant above chance level) in bilateral IPL/IPS, as well as in left PC and dmPFC (Figure 3; Table S10).

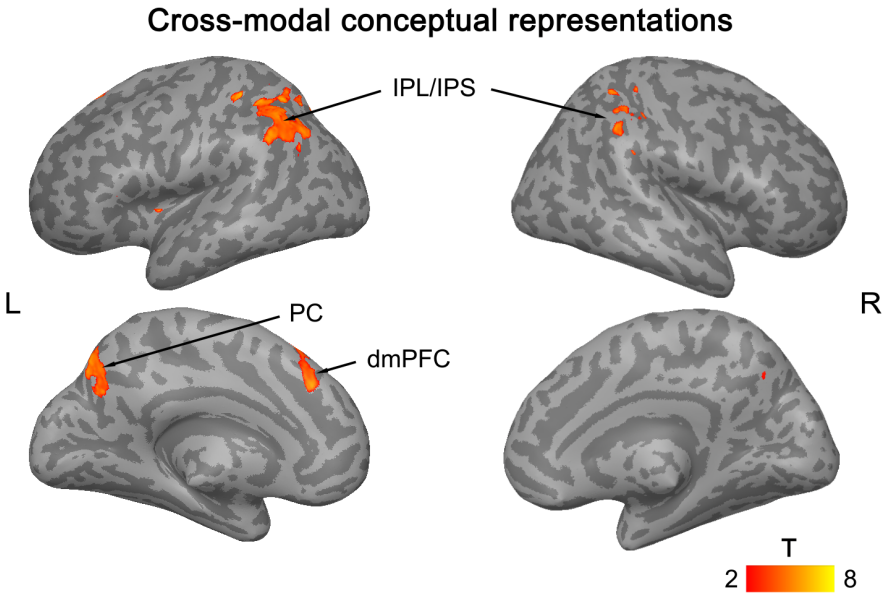

Figure 3. Brain regions showing significant cross-decoding of task-relevant conceptual features. The classifier was trained on activation patterns for task-relevant sound features (sound judgments: high vs. low sound words) and tested on task-relevant action features (action judgments: high vs. low action words), and vice versa. The searchlight map was thresholded at a voxel-wise $p < 0.001$ and a cluster-wise $p < 0.05$ FWE-corrected using non-parametric permutation tests.

3.3. Relationship between conceptual processing and large-scale functional networks

To investigate the relationship between brain regions engaged during conceptual feature retrieval and the large-scale functional networks of the human brain, we analyzed the overlap between our MVPA searchlight maps and the resting-state networks by Yeo et al. (2011).

3.3.1. Action feature retrieval

In the 7-network parcellation, action feature retrieval (action judgments: high vs. low action words) mainly involved parts of the default (27.6% voxels; $\chi^2 = 335.13$, $p < 0.001$), frontoparietal control (24.9%; $\chi^2 = 223.20$, $p < 0.001$), and dorsal attention (18.4%; $\chi^2 = 38.93$, $p < 0.001$) networks (Figure 4A and C).

In the 17-network parcellation, action feature retrieval overlapped with the dorsal attention A (13.5%; $\chi^2 = 207.01$, $p < 0.001$), control B (17.5%; $\chi^2 = 407.36$, $p < 0.001$) and control C (9.8%; $\chi^2 = 67.36$, $p < 0.001$), as well as the default C (10.6%; $\chi^2 = 91.45$, $p < 0.001$) and temporo-parietal (12.4%; $\chi^2 = 160.16$, $p < 0.001$) networks (Figure 4B).

3.3.2. Sound feature retrieval

In the 7-network parcellation, sound feature retrieval (sound judgments: high vs. low sound words) mainly involved the default (34.9% voxels; $\chi^2 = 335.13$, $p < 0.001$) and frontoparietal control (26.7%; $\chi^2 = 223.20$, $p < 0.001$) networks (Figure 5A and C). The dorsal attention network also showed some overlap (13.1%), but below the baseline level of equal overlap with each network (14.29%).

In the 17-network parcellation, sound feature retrieval overlapped with the control B (14.8%; $\chi^2 = 473.58$, $p < 0.001$) and control C (13.6%; $\chi^2 = 371.55$, $p < 0.001$), default C (14.8%; $\chi^2 = 474.36$, $p < 0.001$) and temporo-parietal (13.7%; $\chi^2 = 379.51$, $p < 0.001$), as well as the saliency ventral attention B (8.1%; $\chi^2 = 42.41$, $p < 0.001$) networks (Figure 5B).

3.3.3. Cross-modal conceptual representations

Finally, we compared the searchlight MVPA map for cross-decoding of task-relevant conceptual features to the resting-state networks. In the 7-network parcellation, cross-modal decoding mainly overlapped with the default (31.67%; $\chi^2 = 125.94$, $p < 0.001$), frontoparietal control (35.38%; $\chi^2 = 175.99$, $p < 0.001$) and dorsal attention (19.72%; $\chi^2 = 15.30$, $p < 0.001$) networks (Figure 6A and C).

In the 17-network parcellation, cross-decoding overlapped with the control A (10.74%; $\chi^2 = 22.98$, $p < 0.001$), control B (11.75%; $\chi^2 = 31.80$, $p < 0.001$) and control C (22.38%; $\chi^2 = 167.89$, $p < 0.001$), default C (14.18%; $\chi^2 = 56.62$, $p < 0.001$) and temporo-parietal (9.59%; $\chi^2 = 14.32$, $p = 0.003$), and dorsal attention A (8.91%; $\chi^2 = 9.98$, $p = 0.03$) networks (Figure 6B). Involvement of the dorsal attention B network was not significantly above baseline level of equal overlap with each network (5.88%) (7.09%; $\chi^2 = 1.80$, $p > 0.05$).

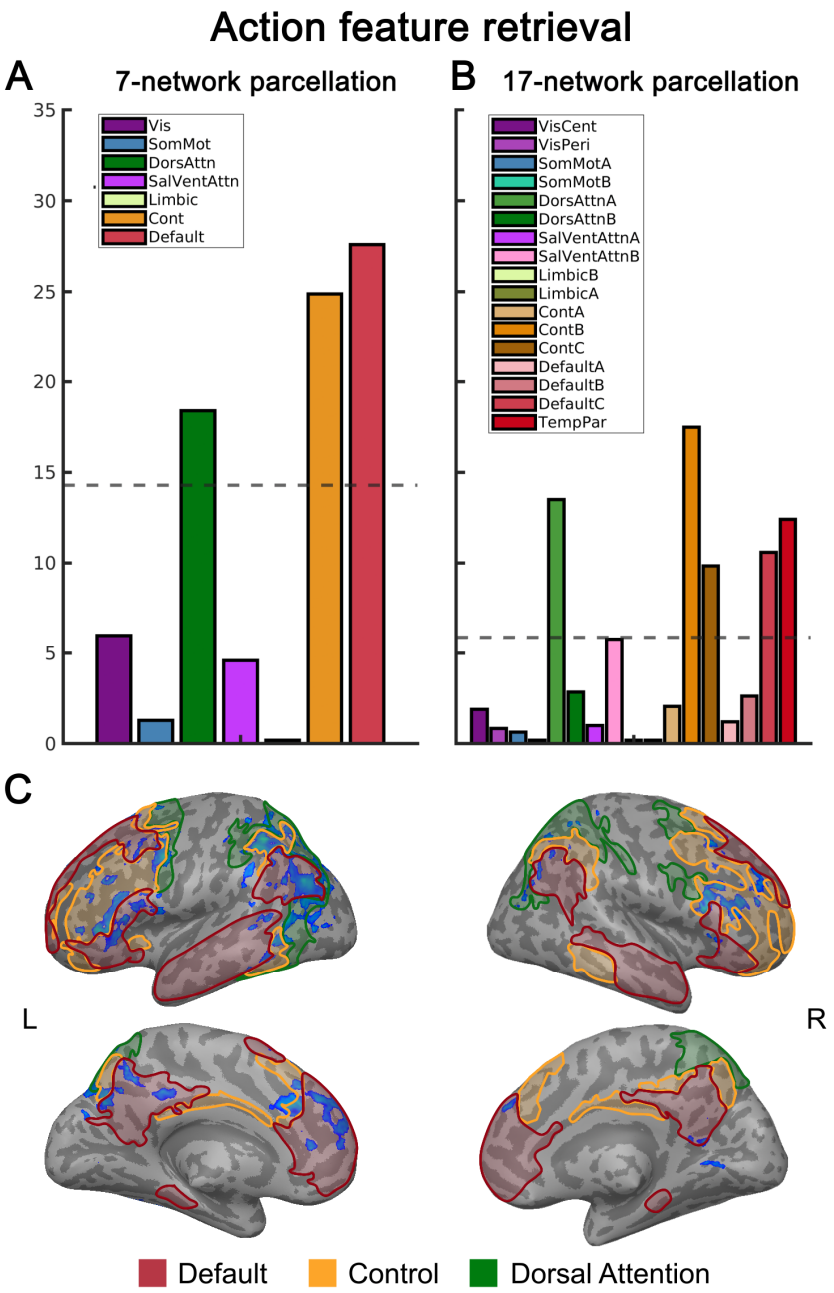

Figure 4. Overlap between the MVPA searchlight map for action feature retrieval and the resting-state networks by Yeo et al. (2011). We investigated both the 7-network (A) and 17-network (B) parcellations. Dashed lines represent the baseline level of equal overlap with each network. (C) Illustration of the three core networks from the 7-network parcellation that overlap with the MVPA searchlight map for action feature retrieval (blue; action judgments: high vs. low action words). Vis = visual; SomMot = somatomotor; DorsAttn = dorsal attention; SalVentAttn = salience ventral attention; Cont = frontoparietal control; VisCent = visual center; VisPeri = visual periphery; TempPar = temporo-parietal.

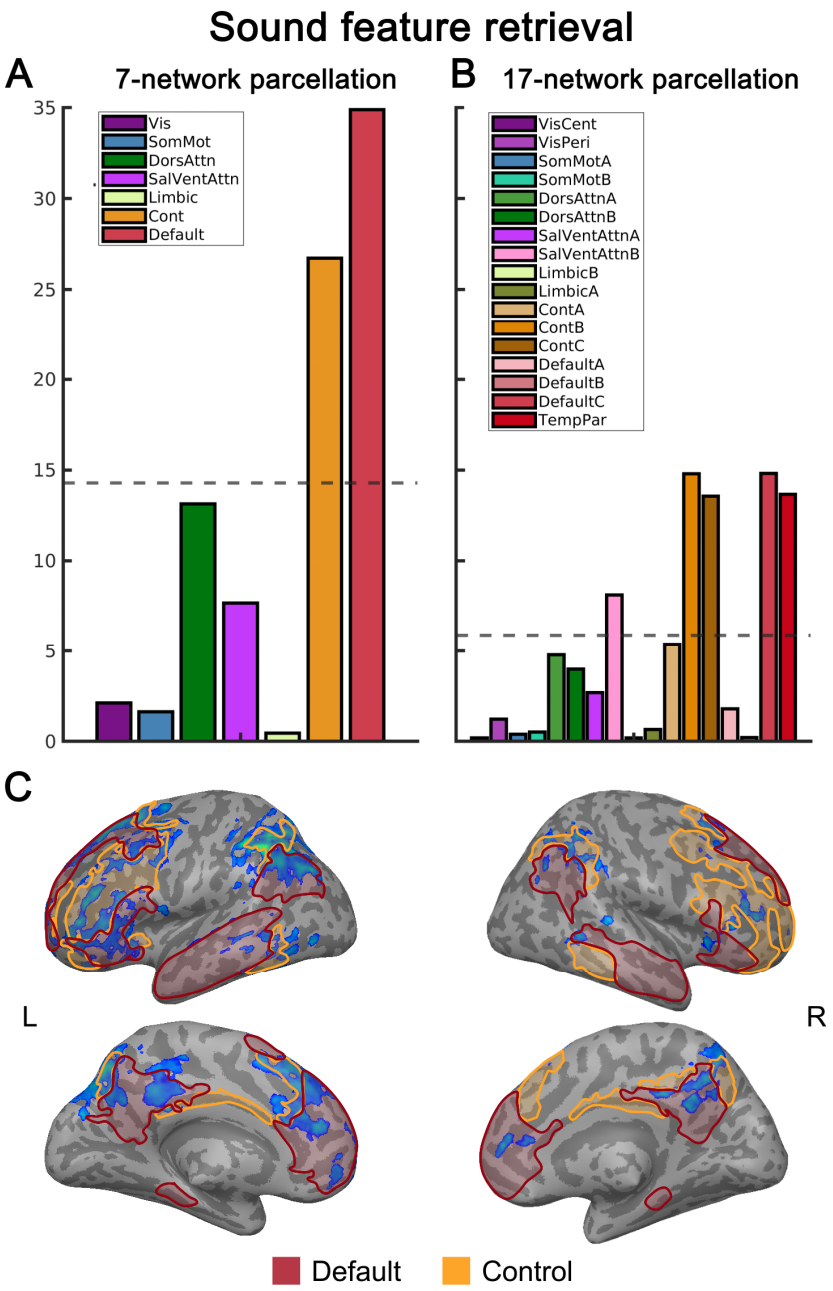

Figure 5. Overlap between the MVPA searchlight map for sound feature retrieval and the resting-state networks by Yeo et al. (2011). We investigated both the 7-network (A) and 17-network (B) parcellations. Dashed lines represent the baseline level of equal overlap with each network. (C) Illustration of the two core networks from the 7-network parcellation that overlap with the MVPA searchlight map for sound feature retrieval (blue; sound judgments: high vs. low sound words). Vis = visual; SomMot = somatomotor; DorsAttn = dorsal attention; SalVentAttn = salience ventral attention; Cont = frontoparietal control; VisCent = visual center; VisPeri = visual periphery; TempPar = temporo-parietal.

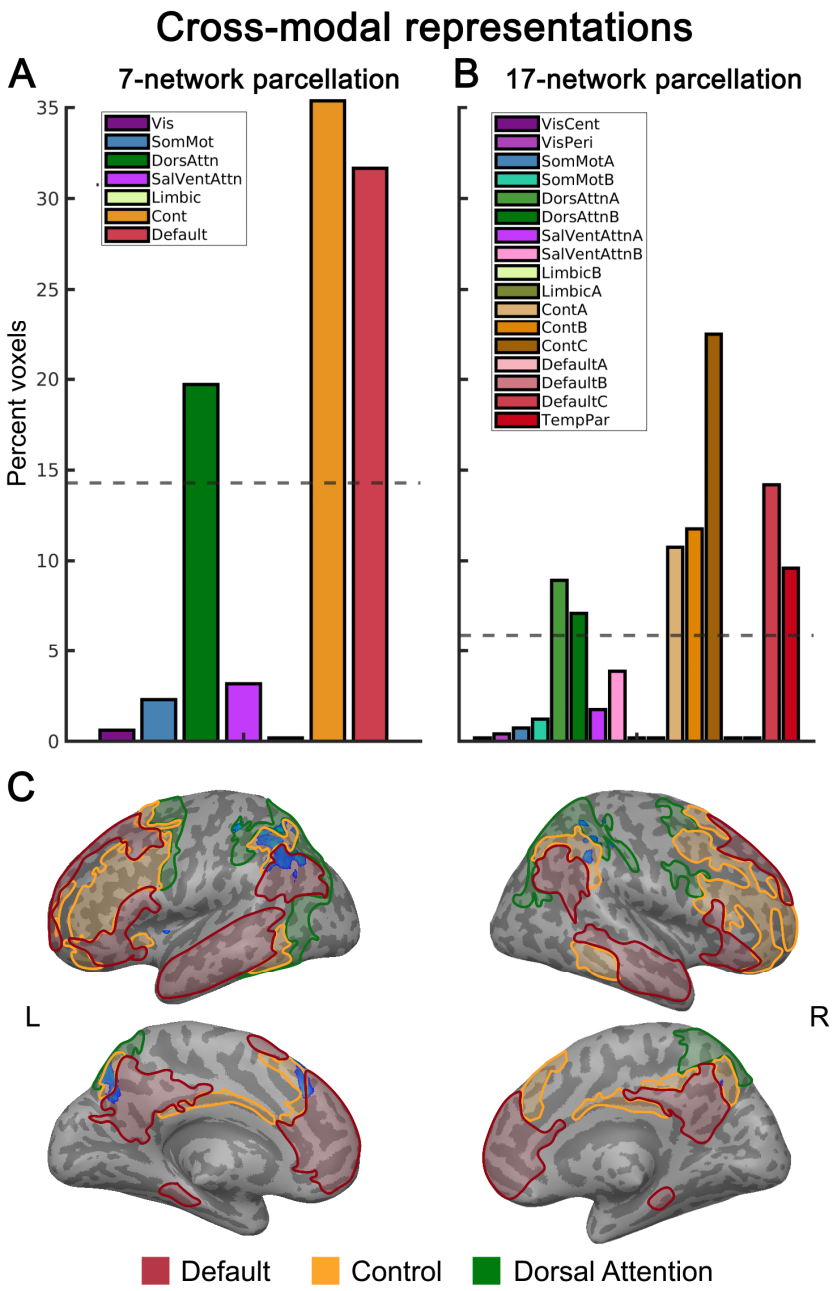

Figure 6. Overlap between the MVPA searchlight map for cross-modal conceptual representations and the resting-state networks by Yeo et al. (2011). We investigated both the 7-network (A) and 17-network (B) parcellations. Dashed lines represent the baseline level of equal overlap with each network. (C) Illustration of the three core networks from the 7-network parcellation that overlap with the MVPA searchlight map for cross-decoding (blue). Vis = visual; SomMot = somatomotor; DorsAttn = dorsal attention; SalVentAttn = salience ventral attention; Cont = frontoparietal control; VisCent = visual center; VisPeri = visual periphery; TempPar = temporo-parietal.

3.4. MVPA decoding in large-scale functional networks

As a more direct test of the involvement of large-scale functional networks in conceptual processing, we performed MVPA decoding based on the activation patterns in each network of the 7-network parcellation by Yeo et al. (2011).

Mirroring our searchlight analyses, we found that neural representations for sound and action features were strongly task-dependent (Figure 7; see Table S11 for statistics). During lexical decisions, no network displayed above-chance decoding of sound features (high vs. low sound words) or action features (high vs. low action words).

In contrast, all networks showed significant decoding of task-*relevant* conceptual features: sound features during sound judgments (Figure 7 yellow), and action features during action judgments (Figure 7 cyan). However, decoding accuracies for task-relevant features were higher in the default, frontoparietal control, and dorsal attention networks than in the other networks (visual, somatomotor, saliency ventral attention, limbic) (Table S12).

Moreover, selectively the default, frontoparietal control, and dorsal attention networks enabled above-chance decoding of task-*irrelevant* conceptual features in both judgment tasks: action features during sound judgments (Figure 7 purple), and sound features during action judgments (Figure 7 green). Nonetheless, in all three networks, decoding accuracies were higher for task-relevant than -irrelevant features (Table S13).

The 17-network parcellation yielded similar results at a higher granularity (Figure S2).

3.4.1. Cross-modal representations in large-scale functional networks

Finally, we also performed cross-decoding of task-relevant conceptual features in each network, training the classifier on sound features (high vs. low sound words) during sound judgments, and testing on action features (high vs. low action words) during action judgments, and vice versa. We found that cross-decoding was significant above chance in all networks except the limbic network (Figure 8; Table S14).

However, decoding accuracies were higher in the frontoparietal control network than in the visual, somatomotor, salience ventral attention, limbic, and default networks (Table S15). Accuracies were higher in the default than visual and limbic networks; and decoding was more accurate in the dorsal attention than visual network.

Again, the 17-network parcellation showed similar results at a higher granularity (Figure S3).

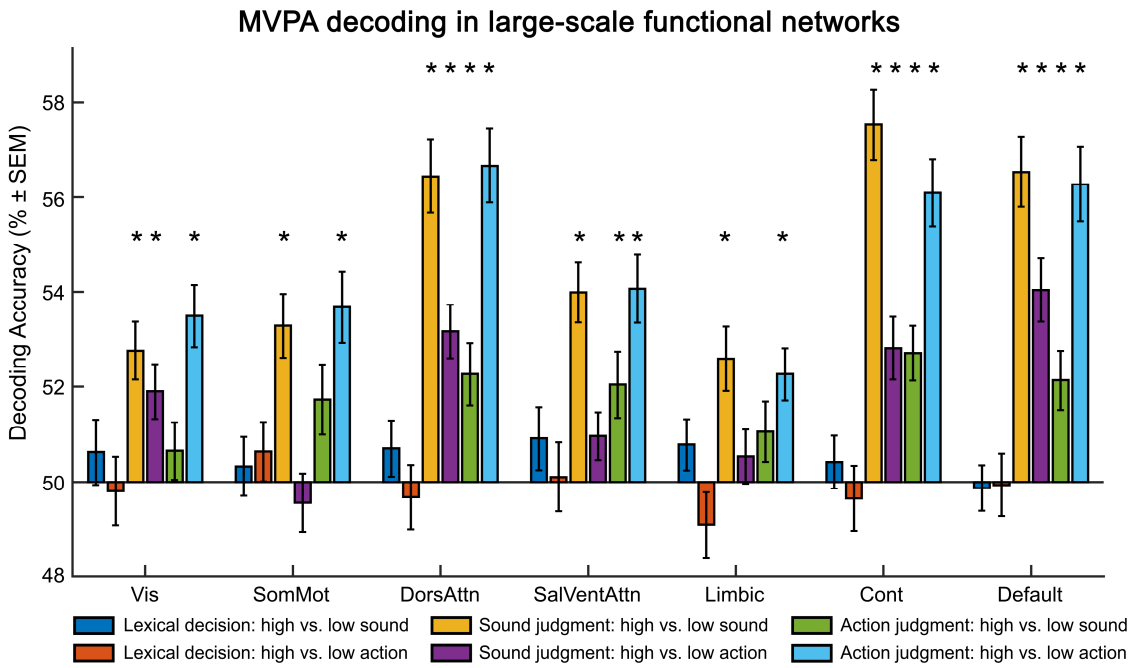

Figure 7. Results of ROI-based MVPA decoding analyses in the 7 resting-state networks by Yeo et al. (2011). A machine-learning classifier was trained on the activation patterns in a given network for 5 out of the 6 blocks, and tested on the remaining block (i.e., leave-one-block-out cross validation). *: $p < 0.05$ (Bonferroni-corrected for the number of networks).

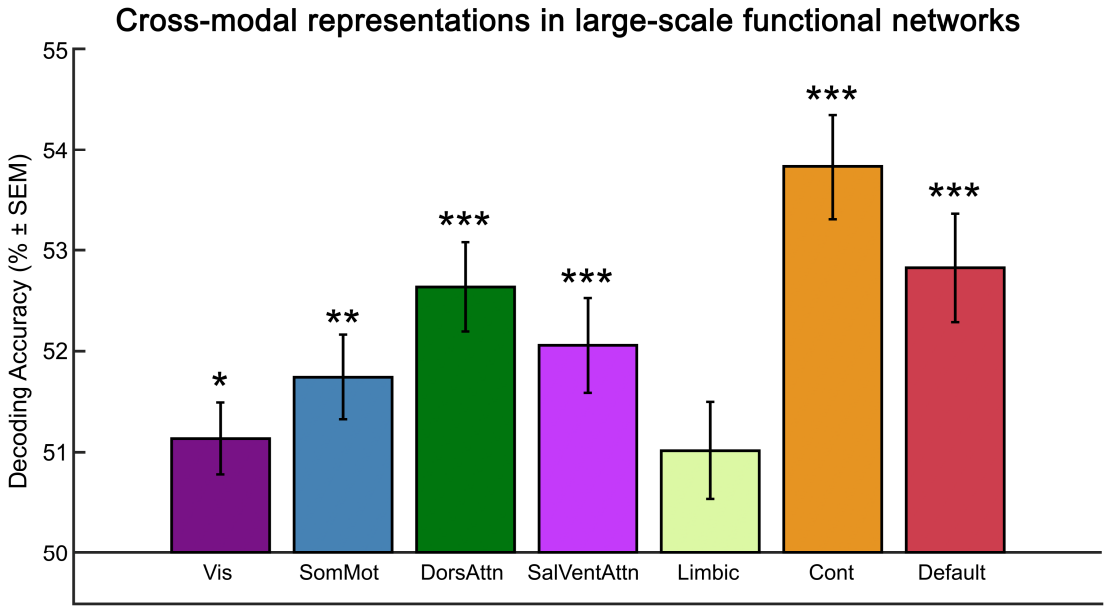

Figure 8. Cross-decoding of task-relevant conceptual features in the 7 resting-state networks by Yeo et al. (2011). The classifier was trained on activation patterns for task-relevant sound features (sound judgments: high vs. low sound words) and tested on task-

relevant action features (action judgments: high vs. low action words), and vice versa. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$ (Bonferroni-corrected for the number of networks).

4. Discussion

This study investigated neural representations of conceptual features in the human brain. Specifically, we asked (1) whether conceptual representations in modality-specific perceptual-motor and multimodal brain regions are modulated by the task, (2) whether conceptual representations in putative multimodal areas are indeed cross-modal, and (3) how the conceptual system relates to the large-scale functional brain networks.

We found that neural representations of conceptual features are strongly modulated by the task. Searchlight MVPA revealed task-dependent modulations of activity patterns for sound and action features of concepts: Both in modality-specific perceptual-motor and multimodal brain regions, activity patterns were most distinctive for sound features during sound judgments, and for action features during action judgments.

Several multimodal areas indeed showed evidence for cross-modal conceptual representations. Specifically, the bilateral IPL/IPS, left PC and left dmPFC enabled cross-decoding of task-relevant conceptual features—from task-relevant sound to action features, and vice versa.

Finally, conceptual feature retrieval mainly involved the default mode network (DMN), frontoparietal control network (FPN), and dorsal attention network (DAN). MVPA searchlight maps for action and sound feature retrieval, as well as cross-modal areas showed extensive spatial overlap with these three networks. Direct MVPA decoding analyses within each network revealed that the DMN, FPN and DAN display the highest decoding accuracies for task-relevant conceptual features, constitute the only networks that could decode task-irrelevant features, and enable cross-decoding between task-relevant sound and action features.

These results suggest that conceptual representations in large-scale functional brain networks are task-dependent and cross-modal. Our findings support theories that assume conceptual processing to rely on a flexible, multi-level neural architecture.

4.1. Task dependency of conceptual representations

Our results indicate that conceptual representations encoded in fine-grained, multi-voxel activity patterns are strongly modulated by the concurrent task. Searchlight MVPA revealed by far the most extensive brain activity for sound and action features when they were task-

relevant (i.e., for sound features during sound judgments, and for action features during action judgments).

These findings extend previous results from univariate neuroimaging analyses showing that the *general involvement* of brain regions in conceptual processing is task-dependent, with the strongest activation for task-relevant conceptual features (Borghesani et al., 2019; Hoenig et al., 2008; Hsu et al., 2011; Kemmerer, 2015; Kiefer and Pulvermüller, 2012; van Dam et al., 2012). For example, we previously found that both modality-specific perceptual-motor and multimodal brain regions are selectively engaged for sound features during sound judgments, and for action features during action judgments (Kuhnke et al., 2021, 2020b).

However, compared to univariate analysis, MVPA revealed more extensive brain activity for task-relevant features in both modality-specific and multimodal areas. Only for MVPA, sound feature retrieval recruited the bilateral auditory association cortex (AAC) (Fernandino et al., 2016a; Kiefer et al., 2008; Trumpp et al., 2013), while action feature retrieval engaged the left premotor cortex (PMC) (Hauk et al., 2004; Kellenbach et al., 2003; Tettamanti et al., 2005; van Elk et al., 2014). These regions were selectively engaged for one feature, indicating that they are modality-specific (Barsalou, 2016; Kiefer and Pulvermüller, 2012). Multimodal convergence zones were more extended for MVPA than univariate analysis in left aIFG, pMTG/ITG and IPL/IPS. Moreover, MVPA selectively revealed additional multimodal areas in left MFG/PreCS, PC/PCC, dmPFC, as well as in right IPL/IPS and aIFG. These results converge with two recent MVPA studies demonstrating multimodal conceptual effects in bilateral IFG, MFG/PreCS, PC/PCC and dmPFC (Fernandino et al., 2022; Tong et al., 2022).

Finally, only MVPA revealed conceptual feature activity in the right cerebral hemisphere. These findings suggest that the right hemisphere is also involved in conceptual processing, but plays a weaker role than the left hemisphere, at least under “normal” conditions in young and healthy human adults. In support of this view, Jung-Beeman (2005) summarized evidence that both the left and right hemispheres are engaged in conceptual-semantic cognition, but the right hemisphere seems to perform coarser computations than the left. This view is also corroborated by a recent large-scale fMRI study (n=172) which revealed conceptual effects in both the left and right IPL, but stronger in the left (Kuhnke, Chapman et al., 2022).

Notably, the task dependency of conceptual representations seems to be *graded*, rather than binary: Whereas no brain region showed significant activity for sound or action features during lexical decisions, we found some activity for sound features during action judgments, and for action features during sound judgments. These results suggest that in contrast to implicit tasks (e.g., lexical decision), explicit conceptual tasks (e.g., sound or action

judgment) can induce task-*irrelevant* feature activation. However, this feature-related activity was restricted to high-level, cross-modal regions (i.e., left IPL, PC/PCC). Modality-specific perceptual-motor regions were selectively engaged when the respective feature was task-relevant (e.g., AAC during sound judgments, PMC during action judgments). These results are in line with the view that the recruitment of modality-specific perceptual-motor areas is particularly task-dependent (Binder and Desai, 2011; Kemmerer, 2015; Kuhnke et al., 2023; Willems and Casasanto, 2011). This view is now supported by several functional neuroimaging studies (Hoenig et al., 2008; Hsu et al., 2011; Kuhnke et al., 2021, 2020b; van Dam et al., 2012).

Overall, our findings support theories that assume conceptual processing to rely on a flexible, multi-level architecture (Binder and Desai, 2011; Fernandino et al., 2016a; Kemmerer, 2015; Kiefer and Harpaintner, 2020; Popp et al., 2019). For instance, we previously proposed that conceptual processing relies on a representational hierarchy from modality-specific perceptual-motor regions to multiple levels of cross-modal convergence zones (Kuhnke et al., 2023, 2021, 2020b). The representation of a concept within this neural hierarchy is not a static, task-independent entity, but it is flexibly shaped to the requirements of the current task or context (Hoenig et al., 2008; Kiefer and Pulvermüller, 2012; Lebois et al., 2015; Yee and Thompson-Schill, 2016). Crucially, our current results indicate that the task dependency of conceptual representations varies between different levels of the neural hierarchy: Conceptual representations in modality-specific perceptual-motor regions seem to be selectively retrieved when they are task-relevant (Binder and Desai, 2011; Kuhnke et al., 2021, 2020b). In contrast, conceptual representations in multimodal convergence zones can also be activated (to some extent) when they are task-irrelevant, at least in explicit conceptual judgment tasks (Fernandino et al., 2016a, 2016b).

4.2. Cross-modal conceptual representations in multimodal convergence zones

We found that multimodal convergence zones in the bilateral IPL/IPS, left PC and left dmPFC allowed for cross-decoding of task-relevant conceptual features: from task-relevant sound to action features, and vice versa. This suggests that these multimodal cortices indeed contain cross-modal representations of task-relevant conceptual information.

Importantly, our results indicate that these cross-modal representations are not “amodal” (i.e., completely invariant to modality-specific features) but “multimodal”, that is, they retain modality-specific information (Kuhnke et al., 2023, 2022, 2020b). Multimodal areas encode action features (high vs. low action words) during action judgments, and sound features (high vs. low sound words) during sound judgments. Crucially, however, these task-relevant features are represented in an abstract fashion across modalities, encoding their presence vs. absence (cf. Binder, 2016). This multimodal view is supported by several

neuroimaging studies (Fernandino et al., 2022, 2016a; Kuhnke et al., 2022, 2020b; Tong et al., 2022). For example, Fernandino et al. (2016a) showed that neural activity in the bilateral IPL, PC and dmPFC correlated with the strength of perceptual-motor associations for all tested modalities (action, sound, shape, color, and motion).

As an alternative explanation, cross-decoding between sound and action features could reflect the concomitant activation of action features during sound feature processing, and vice versa (Reilly et al., 2016). Such "cross-modality spreading" is plausible due to "sound-action coupling"—the phenomenon that many human actions are associated with typical sounds (e.g., knocking on a door; Lemaitre et al., 2018). However, cross-modality spreading is highly unlikely to explain the cross-modal representations identified in our study. If cross-modality spreading was prevalent, we would have expected cross-modal effects in modality-specific perceptual-motor regions. For example, auditory cortex should have been engaged for action feature retrieval, and somatomotor cortex for sound feature retrieval (Lemaitre et al., 2018; Reilly et al., 2016). This was clearly not the case: Cross-modal representations were exclusively found in high-level multimodal hubs distant from modality-specific cortices (Binder and Fernandino, 2015; Margulies et al., 2016).

Notably, evidence for a causal role of multimodal conceptual areas is currently weak. For example, we previously found that transcranial magnetic stimulation (TMS) over left IPL selectively impairs action judgments, but not sound judgments, on written words (Kuhnke et al., 2020a). These findings suggest that left IPL might be specialized for action knowledge retrieval, challenging the view of left IPL as a multimodal conceptual hub (also see Ishibashi et al., 2011; Pobric et al., 2010). Future studies should further test the causal relevance of presumptive multimodal areas for the processing of multiple conceptual features.

4.3. Involvement of large-scale functional networks in conceptual processing

Our results indicate that conceptual processing mainly recruits the large-scale networks of the DMN, FPN and DAN. The searchlight MVPA maps for action and sound feature retrieval, as well as cross-modal representations showed extensive spatial overlap with the DMN, FPN and DAN. In direct network-based decoding analyses, the DMN, FPN and DAN yielded the highest decoding accuracies for task-relevant conceptual features, constituted the only networks that enabled decoding of task-irrelevant features, and showed evidence for cross-modal conceptual representations.

These findings partially support views suggesting a correspondence between the conceptual system—particularly cross-modal convergence zones—and the DMN (Binder et al., 2009, 1999; Fernandino et al., 2016a). However, our results indicate that the DMN is not the only large-scale network engaged in conceptual cognition; conceptual processing also recruits domain-general executive control (FPN) and attention (DAN) networks. Moreover, our

findings suggest that not only the DMN contains cross-modal conceptual representations. While almost all large-scale networks enabled above-chance cross-decoding between task-relevant sound and action features, cross-decoding accuracies were highest in DMN, FPN and DAN. Cross-modal conceptual representations seem to be widely distributed throughout the large-scale networks of the human brain.

Crucially, in all networks including the DMN, FPN and DAN, task-relevant features were associated with higher decoding accuracies than task-irrelevant features. This result further corroborates the task dependency of conceptual feature retrieval (Binder and Desai, 2011; Kemmerer, 2015; Kiefer and Harpaintner, 2020; Kuhnke et al., 2021, 2020b). The task dependency of the FPN and DAN is expected. FPN and DAN strongly overlap with "multiple demand" cortex, which has an established role in cognitive control and flexibility (Assem et al., 2020; Duncan, 2010; Wang et al., 2021). Activation level of these areas positively correlates with cognitive demand across a large variety of tasks (Camilleri et al., 2018; Duncan, 2010; Fedorenko et al., 2013), and their activity patterns can encode task-relevant information (Bracci et al., 2017; Cole et al., 2016; Wang et al., 2021).

The task dependency of the DMN is a more intriguing result. The DMN is traditionally characterized as a "task-negative" network, which is deactivated during attention-demanding tasks as compared to the resting state (Fox et al., 2005; Raichle, 2015). Under the task-negative account, the DMN should not be actively engaged in attention-demanding tasks and should not encode task-relevant information (Wang et al., 2021). Our findings are clearly inconsistent with the task-negative view: The DMN showed significant decoding of sound and action features, with the highest decoding accuracies when these features were task-relevant in explicit, attention-demanding conceptual judgment tasks. In contrast to the task-negative view, our results converge with a growing body of evidence that the DMN is actively engaged in demanding cognitive tasks (Crittenden et al., 2015; Smallwood et al., 2021; Sormaz et al., 2018; Wang et al., 2021). We show that the DMN actively supports task-relevant conceptual feature retrieval. This is in line with the view that DMN deactivation during (non-conceptual) attention-demanding tasks as compared to the "resting state" may indeed *reflect* its involvement in conceptual processing (Binder et al., 2009, 1999; Kuhnke et al., 2022). "Resting" can involve spontaneous thought, autobiographical memory, as well as self-referential and introspective processes (Andrews-Hanna, 2012; Smallwood et al., 2021). Crucially, all of these processes may involve the retrieval of conceptual knowledge (Binder et al., 2009, 1999; Kuhnke et al., 2022). Therefore, the DMN may be "deactivated" during non-conceptual attention-demanding tasks, as compared to rest, since the conceptual processing that occurs during rest is interrupted (Kuhnke et al., 2022; Seghier, 2013). Moreover, the DMN may contribute to conceptual processing via its role in mentalizing (Buckner et al., 2008; Christoff et al., 2016), which could be particularly relevant for the processing of abstract

concepts (Kiefer et al., 2022; Ulrich et al., 2022). Self-referential processes may also play a role for concrete concepts, particularly during explicit conceptual tasks that involve simulating oneself as experiential agent (e.g. sound or action judgment; Barsalou, 1999).

Finally, our findings converge with a recent study showing that task goals during conceptual feature matching can be decoded from activity patterns in DMN, FPN and DAN (Wang et al., 2021). However, in that study, task goals were confounded with stimulus differences, and task-irrelevant information could not be decoded. Our study extends these previous findings by demonstrating task dependency of conceptual representations in DMN, FPN and DAN, even when the stimuli are identical. Moreover, we could show that DMN, FPN and DAN contain task-irrelevant conceptual feature information. This could reflect a graded task dependency, where task-irrelevant features can be activated (albeit less strongly) in explicit conceptual judgment tasks (i.e., sound features during action judgments, and action features during sound judgments). Alternatively, it could reflect the active suppression of task-irrelevant features, which is particularly plausible for the FPN and DAN (Corbetta and Shulman, 2002).

5. Conclusion

In conclusion, we found that (1) conceptual representations in modality-specific perceptual-motor and multimodal brain regions are strongly modulated by the task, (2) conceptual representations in several multimodal convergence zones are indeed cross-modal, and (3) conceptual processing recruits the default mode network (DMN), frontoparietal control network (FPN), and dorsal attention network (DAN). Neural representations in all three of these core networks are enhanced for task-relevant (vs. –irrelevant) conceptual features, and enable cross-decoding between modalities. Overall, these findings suggest that large-scale functional brain networks contribute to conceptual processing in a task-dependent and cross-modal fashion.

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.

Markus Kiefer: Conceptualization, Writing—review and editing.

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

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