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The Neural Representations of Movement across Semantic Categories

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Abstract

Previous evidence from neuropsychological and neuroimaging studies suggests functional specialization for tools and related semantic knowledge in a left frontoparietal network. It is still debated whether these areas are involved in the representation of rudimentary movement-relevant knowledge regardless of semantic domains (animate vs. inanimate) or categories (tools vs. nontool objects). Here, we used fMRI to record brain activity while 13 volunteers performed two semantic judgment tasks on visually presented items from three different categories: animals, tools, and nontool objects. Participants had to judge two distinct semantic features: whether two items typically move in a similar way (e.g., a fan and a windmill move in circular motion) or whether they are usually found in the same environment (e.g., a seesaw and a swing are found in a playground). We investigated differences in overall activation (which areas are involved) as well as representational content (which information is encoded) across semantic features and categories. Results of voxel-wise mass univariate analysis showed that, regardless of semantic category, a dissociation emerges between processing information on prototypical location (involving the anterior temporal cortex and the angular gyrus) and movement (linked to left inferior parietal and frontal activation). Multivoxel pattern correlation analyses confirmed the representational segregation of networks encoding task- and category-related aspects of semantic processing. Taken together, these findings suggest that the left frontoparietal network is recruited to process movement properties of items (including both biological and nonbiological motion) regardless of their semantic category.

INTRODUCTION

Given the constantly changing environment in which we live, it is evolutionary important to be able to understand, and appropriately react to, actions and movements of all things surrounding us. The conceptual knowledge we store of both animate and inanimate entities includes information on various semantic features allowing rapid identification and

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categorization. For instance, in each given setting, we know which items we are likely to encounter and which ones would be at odds with that location (e.g., “in a pond, it is common to find a frog, not a penguin”). Similarly, we store information on how to interact with different items (e.g., “we can manipulate useful tools,” “we should run from dangerous animals”) as well as on how they spontaneously move (e.g., “a rocking chair swings up and down,” “a bird can fly away”). Decades of neuropsychological and neuroimaging investigations have deepened our understanding of the neural substrate of motor–perceptual (e.g., “you need one hand to use chopsticks”) and conceptual (e.g., “chopsticks were first used in China”) semantic features of concrete items (for a recent review, see Borghesani & Piazza, 2017). However, various theoretical perspectives assign different weights to the categorical and featural constraints driving the cortical organization of conceptual knowledge. Some authors have highlighted the role played by domain-specific clusters dedicated to evolutionary-relevant semantic categories such as animals, tools, and conspecific (Caramazza & Shelton, 1998). Others have stressed how sensory–motor and functional features are differentially correlated, respectively, with animals (it is vital to rapidly recognize one from the other) and tools (it is critical to correctly manipulate them; Tyler, Moss, Durrant-Peatfield, & Levy, 2000; Warrington & Shallice, 1984). It remains to be established the extent to which task demands would modulate the relevance of a given semantic feature (e.g., “how does it move?”) differentially across semantic domains (animate vs. inanimate) and categories (tools vs. nontool objects). Would a category-independent representation of movement-related information emerge if the retrieval of those features is required by the task at hand? And, which cortical regions would support it?

Functional imaging studies involving picture naming or word reading have shown that, compared with animals, tools are associated with greater activation of a left frontoparietal network (Chao, Weisberg, & Martin, 2002; Chao & Martin, 2000; Okada et al., 2000). The same network responds when participants are asked to retrieve the actions (or movements) associated with tools (Canessa et al., 2008; Boronat et al., 2005; Kellenbach, Brett, & Patterson, 2003). A growing body of converging evidence suggests that this left-lateralized network is optimally organized to represent knowledge associated with tool use (for a meta-analysis, see Gallivan & Culham, 2015, and Lewis, 2006), likely because of cytoarchitectonic and connectivity constraints as it appears to develop even in the absence of direct sensorimotor experience (Vannuscorps, Wurm, Striem-Amit, & Caramazza, 2018). Recent evidence suggests that the dorsal frontoparietal portion encodes action-related representations, whereas the ventral occipito-temporal component encodes category-related information (Bracci, Cavina-Pratesi, Connolly, & Ietswaart, 2016). Coherently, neuropsychological studies showed that focal lesions to the left inferior parietal areas cause limb apraxia, that is, an impairment in production and recognition of actions and pantomimes (Buxbaum, Kyle, Grossman, & Coslett, 2007; Sirigu et al., 1995; De Renzi, Faglioni, Lodesani, & Vecchi, 1983; Heilman, Rothi, & Valenstein, 1982; Geschwind, 1975). Moreover, a dissociation between anterior temporo-parietal regions and more posterior dorso-parietal ones has been observed: The former appears to be associated with conceptual aspects; and the latter, with action-related ones (Martin et al., 2016). Hence, both functional neuroimaging and lesion studies highlight the role of the frontoparietal action network in processing action and movement information, while suggesting a dissociation

between (anterior) ventral and (posterior) dorsal paths, preferentially involved in conceptual and action-related information, respectively (Bracci et al., 2016; Martin et al., 2016). However, most of the empirical efforts were restricted to the use of tools as stimuli, likely because the skillful manipulation of other semantic categories is more arbitrary in nature. Yet, movement properties are semantic features of a broader range of categories, such as animals and nontool objects.

Interestingly, making inferences on the unfolding of physical events appears to engage a similar frontoparietal network, irrespective of the stimuli used (Fischer, Mikhael, Tenenbaum, & Kanwisher, 2016). Moreover, there is a growing body of evidence indicating supramodal action representations in lateral occipito-temporal and inferior parietal cortices that generalize across stimuli and task (e.g., observation vs. execution vs. imagery; Wurm & Lingnau, 2015). Similarly, the left inferior parietal lobule (IPL) has been found to represent actions independently from object identity, stimuli format, and task performed (Chen, Garcea, Jacobs, & Mahon, 2018). These findings raise the hypothesis that this frontoparietal network encodes the neural representations of action- and movement-related information needed to appropriately interpret the physical elements of the environment and plan/execute appropriate action(s). However, to our knowledge, no study has addressed the task-specific sensitivity of the frontoparietal action system to biological and nonbiological motion when such movement is not directly perceived yet can be retrieved accessing stored semantic representations.

In this study, we used fMRI and a semantic decision task on pictorial stimuli to investigate the neural correlates of specific semantic features across categories. Healthy participants were shown pairs of static images representing animals, tools, or large nontool manmade objects and were asked to make forced-choice decisions based on movement patterns (do they move the same way?) or encyclopedic semantic knowledge (are they found in the same environment?). We performed both mass univariate and multivariate information-based searchlight statistical analyses. We hypothesized that featurespecific (action vs. encyclopedic) activations would be observed for all object categories, possibly accompanied by category-specific interactions because of the relative relevance of each feature for each category.

METHODS

Participants

Thirteen right-handed, native Italian-speaking volunteers took part in the study (four men and nine women; mean age = 27 years \pm 7.37, range = 19–47 years). All participants had normal or corrected vision, and none reported a history of head injury or other neurological problems. All participants gave written informed consent for their participation in the study. The experimental procedures were approved by the ethics committee of the University of Trento.

Stimuli and Tasks

The task involved a semantic judgment on pairs of visually presented object pictures (Figure 1). We used a 3×2 full factorial design, resulting in six conditions. The first factor was the semantic category of the presented items: (a) animals, including domestic and foreign ones (e.g., dog and giraffe; hereafter, animals); (b) tools, defined as objects whose movement depends, from initialization to completion, on the manipulation by human hands (e.g., hammer and pencil; hereafter, tools); and (c) large nontool manmade objects, that is, objects that move on the basis of intrinsic mechanisms (e.g., car and helicopter; hereafter, nontools). In this latter case, the initialization of the movement may depend on the interaction with humans, but it is then autonomously maintained, like the spinning of a washing machine or the swinging of a pendulum. The second factor was the semantic judgment that participants were required to perform on each pair of pictures (i.e., the same picture pairs were used in both tasks). The first task required access to encyclopedic semantic knowledge: Participants were asked to decide whether two items are typically found in the same environment or geographical habitat. For example, pen and telephone are found in the office, and duck and frog are found in a pond. Participants were instructed to think about the human environment for manmade objects (e.g., workshop, office, kitchen, and garden) and the geographical habitat (e.g., desert or forest) for animals. The second task required access to movement-related semantic knowledge: Participants were asked to consider whether two stimuli moved—actively or passively—in a similar way. For example, knives and saws both require similar linear back-and-forth movements, seagulls and toucans both flap their wings, and washing machines and cement mixers both rotate. Therefore, the six resulting conditions will be referred to as “animals-place” (Ap), “animals-movement” (Am), “tools-place” (Tp), “tools-movement” (Tm), “nontools-place” (Np), “nontools-movement” (Nm). Participants were instructed and familiarized with both tasks before the scanning session using a separate set of stimuli. All pairs of stimuli were selected as to belong to the same semantic category while being orthogonal to the prototypical movement and place features. For instance, toucans and seagulls share the same movement but are different in terms of prototypical environment, whereas pairs such as pen and telephone or swing and merry-go-round share the typical location but are different in terms of movement.

Stimuli Standardization

To validate the final set of stimulus pairs necessary for the fMRI experiment, a behavioral normative study was conducted on a separate group of 40 age-matched participants (16 men and 24 women; mean age = 26 years \pm 4.53, range = 20–40 years). Static naturalistic images of animals ($n = 146$), tools ($n = 132$), and nontools ($n = 149$) were selected from the Internet and converted to grayscale pictures while completely removing the background, as to avoid cueing of the semantic attributes of interest (place and movement). We then assembled pairs of animals ($n = 40$), tools ($n = 40$), and nontools ($n = 40$), so that one of the relevant semantic features was congruent (movement or place) whereas the other feature was not. For each picture pair, participants had to rate whether the two items are typically found in the same place and whether they typically move (or are moved) in the same way. For each semantic category, we selected 20 picture pairs judged by at least 70% of participants to be typically found in the same place and by less than 40% of participants to move in the same way. Similarly, we selected 20 picture pairs judged by at least 70% of participants to move

in the same way and by less than 40% to be found in the same place. Thus, in the final set of 40 pairs per category, half of the trials were expected to elicit the “same place” response; whereas the other half, the “same movement” response. The final set of stimuli is listed in the Appendix.

To control for low-level psychophysical features of the stimuli, participants were also required to rate, for each picture pair, the visual similarity between pictures (Likert scale from 1 to 5: 1 = *low visual similarity*, 5 = *high visual similarity*). Moreover, for each individual picture, participants had to judge familiarity (Likert scale from 1 to 5: 1 = *low familiarity*, 5 = *high familiarity*) and visual complexity (Likert scale from 1 to 5: 1 = *low visual complexity*, 5 = *high visual complexity*). We then averaged familiarity ratings and visual complexity ratings across each pair of pictures. We run three 2 (Feature shared) \times 3 (Categories) ANOVAs comparing the six conditions in terms of their average familiarity, visual similarity, and visual complexity ratings. Post hoc multiple comparisons were performed using Tukey’s honestly significant difference with a family-wise error rate of $p = .05$. Concerning familiarity ratings (Figure 2A; descriptive statistics in Supplementary Table 2A¹), there was a significant main effect of Category, $F(2) = 6.85$, $p < .05$, no significant main effect of Feature shared, $F(2) = 0.7$, $p < .39$, and a significant interaction, $F(2) = 3.55$, $p < .05$. These effects were driven by significant differences between animals and nontools, and tools and nontools, in the absence of a significant difference between animals and tools. As for visual complexity (Figure 2C; descriptive statistics in Supplementary Table 2A), there was only a significant main effect of Category, $F(2) = 46.84$, $p < .001$, with all pairwise categorical comparisons being significant [main effect Feature shared: $F(2) = 0.83$, $p > 3$; interaction: $F(2) = 0.32$, $p > 7$]. Finally, regarding visual similarity (Figure 2B; descriptive statistics in Supplementary Table 2A), there was a significant main effect of Category, $F(2) = 6.77$, $p < .001$, and Feature shared, $F(2) = 86.91$, $p < .001$, as well as a significant interaction, $F(2) = 3.83$, $p < .05$. These effects were driven by a significant difference between tools and nontools (in the absence of differences between animals and tools and between animals and nontools). Given the observed differences, these ratings were included in the fMRI analyses as explanatory variables (EVs).

fMRI Experimental Design

Participants underwent four scanning runs. Each run consisted of the presentation of two blocks of five trials for each of the six experimental conditions: that is, animals, tools, and nontools, judged for movement (Am, Tm, Nm) and place (Ap, Tp, Np). It should be noted that, within category, the same picture pairs were used (e.g., the same images are used in Am and Ap). The order of the conditions was counterbalanced across blocks and participants. In total, for each condition, 40 trials were presented, with only half of them being congruent with respect to the relevant semantic feature. Participants were instructed to press a key with their right index finger if the stimuli were congruent for the dimension of interest (e.g., movement) and to press a key with their left index finger if otherwise. They were instructed to respond as quickly as possible and to provide a response even if unsure.

¹Supplementary material for this paper can be retrieved from DOI: [10.17605/OSF.IO/FKT8C](https://doi.org/10.17605/OSF.IO/FKT8C).

One second before the start of each block, written instructions were given to remind the participant of the semantic feature to be evaluated (i.e., place or movement). In each trial, the grayscale pairs were presented simultaneously on a white background for 3.5 sec. Intertrial intervals were jittered intervals between 2 and 7 sec. A black fixation cross was presented in the center of a white screen for the duration of these intervals as well as before (20 sec) and after (16 sec) the first and last trials of each run.

Stimuli were back-projected onto a screen with a liquid-crystal projector at a frame rate of 60 Hz and a screen resolution of $1,280 \times 1,024$ pixels. Participants viewed the stimuli binocularly via an adjustable mirror mounted on the head coil. The task was programmed using the software ASF (Schwarzbach, 2011), based on the MATLAB Psychtoolbox-3 for Windows (Brainard, 1997).

Acquisition and Analysis of Behavioral Data

Participants' responses were collected with fMRI-compatible button boxes (Lumina LU400-PAIR). The first RT was recorded. Accuracy and mean RT were calculated for each participant and condition and then compared using a two-way repeated-measures ANOVA.

Neuroimaging Data Acquisition

All participants were screened by a neurologist to assess MRI compatibility, then trained with the experimental task, and familiarized with the MRI environment. The scanning session consisted of one structural scan (approximately 6 min) and four functional scanning runs of approximately 10 min each. Neuroimaging data were acquired using a 4-T Bruker MedSpec Biospin MR scanner and a birdcage transmit, eight-channel receive head radiofrequency coil. The functional runs were acquired with an EPI protocol, optimized for the acquisition of signal in the anterior temporal lobes (Gesierich et al., 2012). In particular, 318 volumes were acquired with 43 axial slices oriented approximately -20° relative to the AC-PC plane (approximately parallel to the longitudinal axis of the temporal lobes) and in interleaved order: slice thickness = 2 mm with a 0.3-mm gap, field of view = 192×192 mm, matrix = 64×64 , repetition time/echo time = 2000/21 msec, and flip angle = 75° . A point spread function scan was acquired before the functional run for distortion correction (Zaitsev, Hennig, & Speck, 2004; Zeng & Constable, 2002). Full-brain coverage was not possible with the optimized EPI protocol. Approximately the upper 2 cm of the brain were not included, whereas the main areas of interest were covered, including the temporal, inferior parietal, and occipital as well as most of the frontal lobes (see Supplementary Figure 1). Structural images were acquired for coregistration, using a 3-D magnetization prepared rapid acquisition gradient echo sequence with echo time/repetition time/inversion time = 4.18/2700/1020 msec, flip angle = 7° , voxel size = $1 \times 1 \times 1$ mm³, and Generalized Autocalibrating Partially Parallel Acquisition acceleration factor of 2.

Image Preprocessing

Functional data were distortion-corrected using the point spread function method (Zaitsev et al., 2004; Zeng & Constable, 2002). The first five volumes of each run were discarded to allow T₁ equilibrium to be established. Further preprocessing was performed with SPM5 (www.fil.ion.ucl.ac.uk/spm/software/spm5), including slice time correction and motion

correction. The mean realigned functional image was coregistered with the structural image using a rigid body transformation. Structural images were segmented, bias corrected, and spatially normalized to Montreal Neurological Institute (MNI) space using a unified segmentation procedure (Ashburner & Friston, 2005). Functional images were normalized to MNI space, using the same parameters, and spatially smoothed with a Gaussian kernel of 8-mm FWHM.

fMRI Univariate Analyses

Effects at the participant level were estimated by fitting a general linear model for each voxel using SPM5. The four functional runs for each participant were concatenated. The design matrix consisted of one EV per experimental condition and run. The EVs were created by convolving a box-car function (corresponding in duration to the stimulus presentation) with a canonical hemodynamic response function. To control for differences in visual complexity and familiarity of the items, we created one additional EV in an analog way, which modeled the events of these six conditions. This EV was then modulated parametrically by the familiarity and visual complexity ratings obtained during the standardization procedure. For each run, six additional regressors were included, corresponding to the head motion parameters estimated during the realignment step, as well as one variable encoding the mean. Model parameters were estimated using restricted maximum likelihood, an autoregressive AR(1) model to correct for nonsphericity arising from serial correlations. The data and model were highpass filtered with a cutoff frequency of 1/128 Hz.

Contrast images calculated at the single participant level were entered in a random effects analysis. This second level of analysis was conducted using the flexible factorial design implemented in SPM5. Average RTs were calculated for each participant and condition and entered as a covariate.

First, we aimed at identifying brain areas in which there was a main effect of Semantic category (animals vs. tools vs. nontools, regardless of task) and a main effect of Task (movement vs. place, independently from semantic category). Then, we investigated the interaction between Semantic category and Task, looking for areas where the effect of Task was heightened for specific categories. Contrasts were calculated at the single voxel level, correcting for false discovery rate (FDR) at $p < .05$, with a cluster extent threshold of 100 voxels.

Second, based on a priori hypotheses, whole-brain analyses were complemented by an ROI in the left IPL. We recalculated certain contrasts using the MarsBar ROI toolbox (marsbar.sourceforge.net) in a sphere of 10-mm radius centered at MNI coordinates: $-61, -25, 37$. The center of the sphere was calculated as a mean across coordinates found in three representative studies comparing tools against living things (Devlin et al., 2002), animals (Noppeney, Price, Penny, & Friston, 2005), and nontool manmade objects (Mahon et al., 2007). We hypothesized that the left IPL would be automatically activated by tools regardless of task, whereas for animals and nontools, this region would be significantly activated only when the task forced specific processing of the movement feature, that is, a Task \times Category interaction.

Third, to visualize the size of cognitive effects on the BOLD signal, the percent signal change was plotted in two activation clusters revealed by the contrast of movement > place and place > movement respectively. We selected the two main cortical peaks for each contrast and calculated the average percent signal change across all voxels within a sphere of 10-mm radius around the peak voxel.

SPMs were displayed as overlays on the single-subject T1 map provided with MRIcron (www.mricro.com).

fMRI Multivariate Analyses

We then performed correlation-based multivoxel pattern correlation analyses (Haxby et al., 2001) to investigate the representational content, that is, how the distributed pattern of activation differs in response to the different tasks as well as semantic domains and categories (Davis & Poldrack, 2013). On the basis of the six experimental conditions, four predicted similarity matrices can be modeled (Figure 3). Two matrices depict semantic effects: one for semantic domain (higher pattern similarity if the pairs of stimuli are both animate or both inanimate) and one for semantic category (higher pattern similarity if the pairs of stimuli are both animals, tools, or nontools). The other two matrices depict tasks effects: one for location (higher pattern similarity if the pairs of stimuli were both judged for place) and one for movement (higher pattern similarity if the pairs of stimuli were both judged for movement).

Representational similarity analysis was performed using a spherical whole-brain searchlight approach (Kriegeskorte, Goebel, & Bandettini, 2006). For each participant, a sphere of 8-mm radius was centered in each voxel, and voxel-wise correlations (by means of Pearson's correlation) were computed between the six contrast maps (corresponding to the six experimental conditions, i.e., Am, Tm, Nm, Ap, Tp, and Np) generated with the first-level GLM implemented in SPM. The resulting neural similarity matrices depict how similar the different conditions are in terms of distributed pattern of activity. Values were Fisher r -to- z transformed, and partial correlation was then used to compute the correlation between the neural matrix and each of the predicted ones while controlling for the others (Borghesani et al., 2016; Clarke & Tyler, 2014). For each participant, we thus obtained four maps depicting the multivariate effect of (1) semantic domain: animate versus inanimate, (2) semantic category: animals versus tools versus nontools, and task focusing on (3) location or (4) movement. These maps were smoothed (Gaussian kernel of 6-mm FWHM) and then entered into four separate group-level random effects models in SPM. All multivariate analyses were implemented with custom Python scripts relying on Nilearn (nilearn.github.io/), Numpy (www.numpy.org/), and Scipy (www.scipy.org/scipylib).

RESULTS

Behavioral Results

RTs (descriptive statistics are shown in Figure 4A and reported in Supplementary Table 2B) were significantly different across object categories, $F(2) = 11.825$, $p = .0003$, and tasks, $F(2) = 6.685$, $p = .0239$. The interaction between both factors was also significant: Task \times

Category, $F(2) = 7.198$, $p = .0036$. RTs were thus entered as covariates in the statistical analyses of functional images. No significant differences were found for response accuracy (descriptive statistics are shown in Figure 4B and reported in Supplementary Table 2B, movement animals).

fMRI Results

Main Effect of Semantic Feature—Statistical maps of the comparison between the task requiring access to movement-related versus environment-related semantic knowledge are shown in Figure 5A, and details are reported in Table 1. The movement task elicited a higher BOLD response than the place task in the bilateral supramarginal gyrus (SMG) and intraparietal sulcus (IPS), the bilateral opercular part of the inferior frontal gyrus, the bilateral inferior temporal gyrus (ITG), the right superior parietal gyrus, and the left triangular part of the inferior frontal gyrus. It should be noted that the IPL ROI is included in the left parietal cluster emerging from this analysis. Conversely, the place task was associated with higher levels of activation in the left retrosplenial cortex, the left middle occipital gyrus (MOG)/angular gyrus (AG), the left middle temporal gyrus (MTG), and the left fusiform gyrus (FG).

Main Effect of Semantic Category—Activations revealed by all pairwise comparisons of the three semantic categories are shown as statistical maps in Figure 6, and details are listed in Table 1. The animals' conditions elicited a higher BOLD response than the tools' conditions in the bilateral lateral FG, bilateral inferior occipital gyrus (IOG), right MTG, left MOG, and right precuneus. Conversely, tools produced higher activations in the bilateral medial FG. Similarly, contrasting animals against nontools revealed higher activations for nontools' trials in the bilateral medial FG and bilateral MOG, whereas animals' trials elicited a higher BOLD response in the bilateral IOG, left MOG, bilateral lateral FG, right MTG, and precuneus. Finally, in comparison with tools, the nontools' conditions were associated with a higher activation in the bilateral medial FG, right calcarine sulcus, and right MTG. No area showed a significantly higher BOLD response for tools than for nontools.

Whole-brain analyses were followed by an ROI investigation, looking for category-selective effects in IPL, where previous studies had found consistent selectivity for tools (Mahon et al., 2007; Noppeney et al., 2005; Devlin et al., 2002). Once restricted to this ROI, analyses revealed the hypothesized preference for tools: tools > animals, $t(12) = 5.55$, $p < .007$, and tools > nontools, $t(12) = 5.02$; $p = .04$.

Interaction between Semantic Category and Semantic Feature—We fail to detect any significant interaction between semantic categories and tasks. To avoid missing nonsignificant tendencies and limit the chances of false negatives, interaction contrast maps were explored, thresholded at $p < .001$ uncorrected. Even at this lenient threshold, no differences were detected. Figure 5B visualizes the percent signal change in two representative clusters revealed by the contrast of movement > place (left SMG, MNI coordinates: $-60, -36, 36$) and place > movement (left AG, MNI coordinates: $-42, -75, 30$).

The two main effects are clearly appreciable, whereas no effect of semantic category (nor any sign of its interaction with the task-related effects) can be detected.

Multivariate Analyses of the Representational Content—We assessed the correlation between distributed patterns of activity and each of the sources of information (e.g., semantic domain) while controlling for the others (e.g., semantic category, place and movement features). This means that the results indicate the amount of residual domain-, category-, or task-related information present in a given area once all other effects have been accounted for. Significant effects of semantic domain (animate vs. inanimate) and semantic category (animals vs. tools vs. nontools) were found in partially overlapping clusters in the FG and the IOG, respectively (Figure 7 and Table 2). A significant effect of place information was detected in the AG: Irrespective of categorical information, patterns of activation were more similar for pairs of stimuli both judged with respect of their prototypical location. Finally, significant effects for movement information were found in a frontoparietal network encompassing SMG, IPS, and the bilateral opercular part of the inferior frontal gyrus (Figure 7 and Table 2). Here, patterns of activation appeared more similar for pairs of stimuli that were both judged with respect to their prototypical movement and irrespective of the semantic category (and domain) they belonged to.

DISCUSSION

In this study, we investigated the neural correlate of two semantic features across three different semantic categories. We observed, for both animate and inanimate objects, a dissociation between retrieval of movement-related information (associated with left frontoparietal activations) and encyclopedic semantic knowledge (recruiting the left MTG and AG). We failed to detect any sign of an interaction between semantic features and semantic categories. Moreover, multivariate analyses confirmed the representational dichotomy between feature- and category-related information. We thus provide evidence that the left parietal cortex is recruited to process biological motion of animals as well as nonbiological motion of both tools and large manmade objects—a result with important theoretical implications as discussed below.

Category-independent Processing of Movement-related Information

Compared to judgments about items' prototypical location, retrieving movement-related semantic information was associated with enhanced activations in a network of regions including dorsal parietal (SMG and IPS), inferior frontal, and posterior temporal regions. These activations were bilateral yet strongly left lateralized. Multivariate analyses further qualify this result by indicating that the pattern of activity in a very similar network (with the notable exception of occipito-temporal cortex) encodes information on the semantic feature targeted by the task (i.e., movement), even when controlling for semantic category and domain.

Similar activation patterns have been observed in studies comparing activations for tools versus other categories of objects (animals, faces, and houses), suggesting the existence of a left-lateralized frontoparietal network selective for tools (e.g., Chao & Martin, 2000). These findings have been interpreted in light of the fact that tools are manipulable, movement-

related objects. Consistently, this network anchored on the dorsal parietal region has been activated in imaging studies on action execution, observation, simulation, and imitation (Iacoboni et al., 1999, 2005; Buccino et al., 2001, 2004; Grèzes & Decety, 2000). Moreover, the same regions have been linked to the processing of hand gestures (Hermsdörfer et al., 2001) as well as whole-body movements (Downing, Peelen, Wiggett, & Tew, 2006). Taken together, these studies suggest that inferior dorsal parietal and connected inferior frontal regions are involved in representing movement/action independently of the effector and even in the absence of manipulable objects. We found additional movement-specific activation in a cluster of areas in posterior MTG and ITG, a region consistently associated with human action semantics in a variety of tasks (for a review, see Noppeney, 2008). For example, activation in the posterior MTG has been found during the observation of actions (Perani et al., 2001; Rizzolatti et al., 1996) and static pictures implying motion (Senior et al., 2000) as well as during the simulation of self-performed actions (Ruby & Decety, 2001) and the generation of action-related semantic information when prompted with items' pictures or written names (Phillips, Noppeney, Humphreys, & Price, 2002; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995).

Our study aimed at directly testing whether semantic category modulates the recruitment of the left frontoparietal action network. We hypothesized that tools would show the greatest activation of this network compared with animals and nontools. Instead, we failed to find a significant interaction: Retrieving movement-related semantic information similarly recruits the left frontoparietal action network irrespective of stimuli semantic category. Previous reports of preferential activation for tools compared with living items could thus be a byproduct of the different weights that specific semantic categories assign to movement-related versus perceptual semantic features. Action patterns are the most salient features of tools, therefore explaining why we might automatically retrieve movement-related information even when the task does not explicitly require it (Mahon et al., 2007; Chao & Martin, 2000; Okada et al., 2000; Epstein & Kanwisher, 1998).

Taken together, our findings indicate that, regardless of stimuli semantic category, the same left frontoparietal network is recruited to process movement-related semantic information. It could thus be speculated that this network stores the representations of movement patterns associated with tools (e.g., linear back-and-forth movements for “saw”) as well as with biological motion of animals (e.g., wings flapping for “seagull”) and intrinsic mechanical motion of nontool objects (e.g., rotating motion for “washing machine”). It would follow that patients with lesions to IPS who manifest ideomotor apraxia (Buxbaum, 2001) would also perform poorly in tasks requiring retrieval of movement properties of animals and nontool objects, while being overall spared (across categories) in an orthogonal task (e.g., naming; Rosci, Chiesa, Laiacona, & Capitani, 2003). Our results should hence inform task and stimuli selection for future clinical evaluations of and interventions with apraxic patients.

Our results are in line with previous evidence suggesting that the neural representations stored in this frontoparietal network, and in particular, in the IPL, allow not only action planning and execution but also a more general (and abstract) understanding of our surroundings. For instance, Fischer and colleagues have shown similar frontoparietal

activation in participants engaged in causal reasoning tasks (Fischer et al., 2016). It should be noted that the visuospatial inferential reasoning elicited by Fischer's task leads to a bilateral activation, whereas our design, requiring semantic access to movement-related information, leads to left-lateralized activation. Moreover, the left IPL has been linked to the representation of object function, suggesting that it plays a role in understanding not only how items move and can be moved but also what they can be used for (Leshinskaya & Caramazza, 2015).

Category-independent Processing of Encyclopedic Knowledge

Relative to judgments about item movement, retrieving semantic information on items' prototypical place was associated with enhanced activation in a left-lateralized network including the AG and the anterior temporal lobe. However, the discrepancy between univariate and multivariate results suggests that, once accounted for all other sources of similarity, only the pattern of activity in AG encodes information on the semantic feature targeted by the task (i.e., place).

One previous functional imaging study, which compared judgments about the typical location of objects versus their typical color, found similar activations in the temporo-occipito-parietal junction and in the posterior cingulate cortex (Mummery, Patterson, Hodges, & Price, 1998). Furthermore, similar medial FG and retrosplenial cortex activations are often reported in studies presenting scenes and buildings as stimuli (Nasr et al., 2011; Sugiura, Shah, Zilles, & Fink, 2005; Gorno-Tempini & Price, 2001; Epstein & Kanwisher, 1998). The original study linked scene-selective activity to the parahippocampal gyrus (hence the name of parahippocampal place area; Epstein & Kanwisher, 1998), yet more consistent selectivity for scene is centered on the medial FG, with average coordinates closer to the ones we report (for a meta-analysis, see Nasr et al., 2011). Activation patterns similar to the ones we observed, including areas in the TPJ, the MTG, and the retrosplenial cortex, have been reported in a variety of semantic tasks (for a meta-analysis, see Binder, Desai, Graves, & Conant, 2009). Examples from these studies include reading written names or naming pictures of semantically associated object pairs (e.g., robin–nest, bell–whistle; Mechelli, Josephs, Lambon Ralph, McClelland, & Price, 2007), retrieving person-specific semantics during the presentation of famous faces (Gesierich et al., 2012), and retrieving semantic information associated with real words during a lexical decision task on words and nonwords (Binder et al., 2003).

Our study design allowed us to test whether semantic category modulates the recruitment of the left-lateralized ATL–AG network. We found similar activations in these regions for judgments on the prototypical location of animals (e.g., frogs are usually close to a pond), tools (e.g., keyboards can be found on office desks), and nontool objects (e.g., swings belong to playgrounds). Thus, processing encyclopedic knowledge on item location appears to rely on this network irrespective of stimuli category. This result converges with decades of findings in patients with the semantic variant of primary progressive aphasia, who present with a deep conceptual loss affecting all semantic categories (Gorno-Tempini et al., 2011; Hodges & Patterson, 2007). Particularly relevant here, patients with the semantic variant of primary progressive aphasia show impaired performance on tasks requiring to evaluate

items' typical environmental context (e.g., a horse on a field, on a desert, or in a shopping center; Garrard & Carroll, 2006).

Taken together, these findings suggest that the left ATL–AG network is involved in storing and retrieving conceptual features that are detached from (or require merging of) physical properties of the items (Borghesani & Piazza, 2017; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017).

Task-independent Organization of the Occipito-temporal Cortex

An implicit feature of our stimuli, orthogonal to the two tasks performed, was the semantic category they belong to. Overall, our results are in line with the previously described organization of the occipito-temporal cortex (Konkle & Caramazza, 2013). Both our univariate and multivariate analyses allowed dissociation of the representations of animals, small manipulable tools, and large nontool objects.

Contrasting univariate activations for animals versus tools, we replicated previous findings: Animals activated more lateral regions of the FG, whereas tools activated more medial regions (Mahon et al., 2007; Rogers et al., 2006; Chao et al., 2002; Chao, Haxby, & Martin, 1999). In addition, animals elicited stronger activations in the MOG and MTG, extending into the STS. At the whole-brain level, we did not find tool-selective activation in the IPL. However, ROI analysis confirmed a preferential activation for tools over animals in a region associated with tool-selective effects in previous studies (Mahon et al., 2007; Noppeney et al., 2005; Devlin et al., 2002). In addition, we found heightened bilateral activations for animals between the IOG and ITG, which is similar in location to the so-called extrastriate body area. Previous evidence links this area to the representation of human bodies (Peelen & Downing, 2005; Downing, Jiang, Shuman, & Kanwisher, 2001). Therefore, one possible interpretation is that similar neuronal circuits are involved in the representation of human and animal bodies. Indeed, they share features such as bilateral symmetry; segmentation in the head, abdomen, and limbs; and the degree of freedom in which the different body parts can move. Crucially, this area did not show task-specific effects, which is consistent with the idea that the extrastriate body area is involved in the representation of static structure, rather than dynamic aspects of the human form (Downing et al., 2006).

Overall, similar clusters emerged when activation profiles elicited by animals were compared with both tools and nontools. Differences between tools and nontools were instead limited to two clusters (bilateral medial portion of the FG and bilateral dorsal MOG), where nontools exhibit higher activation than tools. It should be noted that, in our experiment, semantic categories and domains are orthogonal to the main task (same movement or same place) performed by the participants. In other words, although semantic category and domain are implied by the stimuli pairs used, no direct attention is drawn upon them—and attention has been shown to strongly modulate neural representations (Çukur, Nishimoto, Huth, & Gallant, 2013). It is thus fair to assume that, in this setting, the distinction between living versus nonliving items is stronger than the one between tools and nontools.

Multivariate analyses corroborated these findings indicating encoding of domain- and category-specific information in the distributed pattern of activity of posterior occipito-

temporal areas irrespective of the task performed by the participants. Crucially, we used partial correlation to assess the unique contribution of the similarity in terms of semantic domain while controlling for that of semantic category (and vice versa). The results indicate that, once the similarity in terms of semantic domain is accounted for, the neural similarity driven by belonging to the same semantic category is confined to a restricted portion of the visual cortex. This is overall not surprising given the ongoing discussion on the role played by low-level visual properties on the categorical effects detected with static pictorial stimuli. One theoretical interpretation of these and similar neuropsychological (e.g., Caramazza & Shelton, 1998) and neuroimaging (e.g., Konkle & Caramazza, 2013) findings is that concepts are represented in the occipito-temporal cortex according to two nested properties: the semantic domain they belong to (animate vs. inanimate) and the kind of actions one can perform with them (living items vs. small manipulable tools vs. large nontool objects and navigable scenes). A growing body of research indicates that this functional specificity emerges even in the absence of direct sensorimotor experience (Striem-Amit, Vannuscorps, & Caramazza, 2017; Peelen et al., 2013) and cannot be fully accounted for by differences in shape or texture between living and nonliving items (Proklova, Kaiser, & Peelen, 2016). Unsurprisingly, given that we did not control our stimuli for real-world size, we failed to detect a tripartite organization, while being able to replicate the dissociation between semantic domains. Although the contribution of low- and high-level visual features to category-specific effects is still highly debated (Bracci, Ritchie, & de Beeck, 2017; Peelen & Downing, 2017), our findings expand previous observations highlighting how these effects can be detected during two different, orthogonal, semantic judgment tasks.

Dissociating the Dorsal and Ventral Components of the Action Network

The results of our multivoxel pattern correlation searchlight analyses suggest a representational segregation within the action network: A dorsal, frontoparietal component encodes the semantic features targeted by the task, whereas a ventral, occipito-temporal one encodes the semantic domain and category implied by the stimuli. We detect category-independent information of task requests in IPS and task-independent encoding of category information in both lateral and ventral occipito-temporal cortex (LOTc and VOTc, respectively). These results are consistent with a study comparing pattern of activations across four different semantic categories (bodies, hands, tools, and nontool objects) during an orthogonal 1-back repetition detection task (Bracci et al., 2016). Notwithstanding the overlap in terms of univariate activation, the multivariate analyses performed by Bracci and colleagues qualified the contribution of specific areas within the classical action network. IPS appeared to carry functional information (stronger similarity if items share the association with fine movements, i.e., tools and hands); whereas VOTc, the categorical one (stronger similarity if items belong to the same semantic domain, i.e., animate vs. inanimate). In LOTc, a significant effect of both function and category was found, suggesting that this area lies at the interface between the computations performed by the parietal and occipito-temporal cortices. Corroborating evidence stems from the recent evidence that ventral areas represent tools' properties irrespective of the task being performed, whereas dorsal areas encode only task-relevant properties (Bracci, Daniels, & Op de Beeck, 2017).

Recent studies have called attention to the dynamic interplay between the different nodes of the action network. For instance, psychophysiological interaction analysis and dynamic causal modeling findings show that semantic category (i.e., “toolness”) and perceptual features (i.e., elongation) differentially modulate the connectivity between ventral and dorsal streams (Chen, Snow, Culham, & Goodale, 2018). In particular, they suggest that information about perceptual features necessary for action can be resolved in the dorsal stream, whereas analyses of semantic feature necessary for object recognition depend on the ventral stream. Similarly, functional connectivity between parietal and temporo-occipital areas involved in tool processing appears to be modulated by the task performed by the participants. Whereas pantomiming requires interactions among regions that process perceptual features and motor-relevant information (i.e., the frontoparietal network), picture matching relies on the interplay of high-level visual and semantic processes (i.e., VOTC and LOTC; Garcea, Chen, Vargas, Narayan, & Mahon, 2018).

Altogether, these findings highlight the role played by frontal and inferior parietal areas in the multiple-demand system (Duncan, 2010) as well as their crucial, dynamic, involvement in retrieval of action/movement-related semantic information.

Limitations and Future Perspectives

Our results speak of category-independent recruitment of the left frontoparietal network during a task explicitly tapping into movement-related semantic information (vs. encyclopedic knowledge). The degree to which other tasks would lead to category-specific effects within this region calls for further investigations. Overall, given the variety of tasks (and stimuli) used in previous studies, it is difficult to disentangle task-general processing (e.g., retrieving the concept of “hammer”) from task-specific processing (e.g., naming the picture of a hammer or manipulating a hammer). A recent meta-analysis suggests that task-general processing recruits the left IPL (BA 40) and ventral premotor cortex, whereas task-specific activations are linked with the superior parietal lobule, the dorsal premotor cortex, and the occipito-temporal cortex (Ishibashi, Pobric, Saito, & Lambon Ralph, 2016). Hence, future studies should aim at extending our results by comparing different tasks and stimuli to test for potential interactions. Of particular interest would be the comparison, across semantic categories, of the areas recruited to process semantic of movement (as done here), implied movement (as done, for instance, in Kourtzi & Kanwisher, 2000), and the perception of actual movements.

We fail to detect a significant interaction between semantic categories and tasks. One issue with such negative finding is that one cannot exclude the possibility that a small effect was missed because of a lack of power. In particular, our sample size could be considered relatively small for the complex 2×3 design. Future replication of this study should aim to include more participants and to overall heighten the statistical power to detect (potential) interaction effects we might have missed.

Finally, although the EPI sequence we used has been optimized for the acquisition of fMRI signal in the ATL, we cannot exclude lower signal-to-noise ratio in this region (as compared with parietal areas), given its known susceptibility to signal dropout and distortion artifacts (Visser, Jefferies, & Lambon Ralph, 2010; Devlin et al., 2000). Converging evidence from

neuropsychology and noninvasive brain stimulation will help overcome this drawback while elucidating the specific contribution of different areas within the networks examined here.

Conclusion

A long-standing debate in cognitive neuroscience is whether the cortical representation of semantic knowledge is organized according to semantic categories (e.g., animals, tools, nontool objects; Caramazza & Shelton, 1998) or semantic features (e.g., how things move, where things are found, how perceptually similar things are; Tyler et al., 2000). For instance, the functional specialization for tools versus living items observed in left frontoparietal areas could be interpreted as the effect of a preferential activation for a specific semantic category (i.e., tools > any other items) or for a specific semantic feature (i.e., movement pattern). By combining univariate activation-based and multivariate information-based analyses, we provide empirical evidence that retrieval of movement-related semantic information recruits the same left frontoparietal action network independently of stimuli category. This finding suggests that the observed preferential activation of this network for tools is secondary to its computational role: supporting the visuomotor integration processes necessary to retrieve movement-related semantic information.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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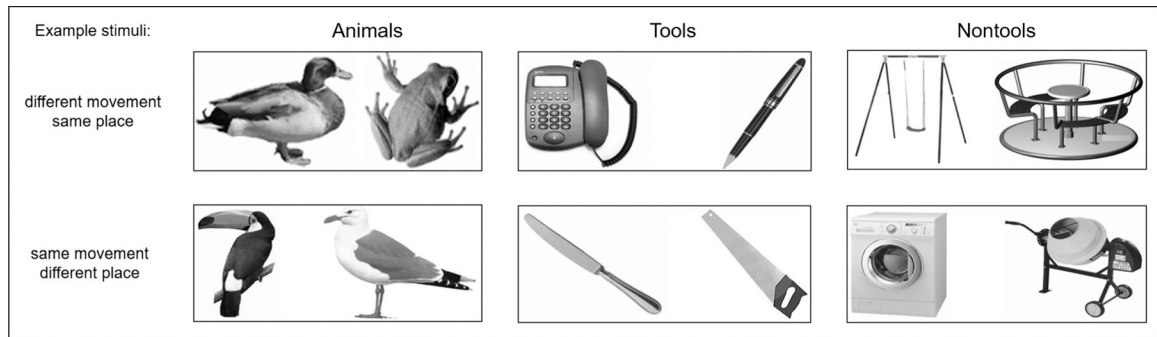


Figure 1.

Experimental stimuli. For each category (animals, tools, and nontools), half of the picture pairs used are typically found in the same place yet do not move in the same way (examples in the first row), whereas the other half are found in different places yet move in a similar way (second row). The full set of stimuli is listed in Supplementary Table 1.

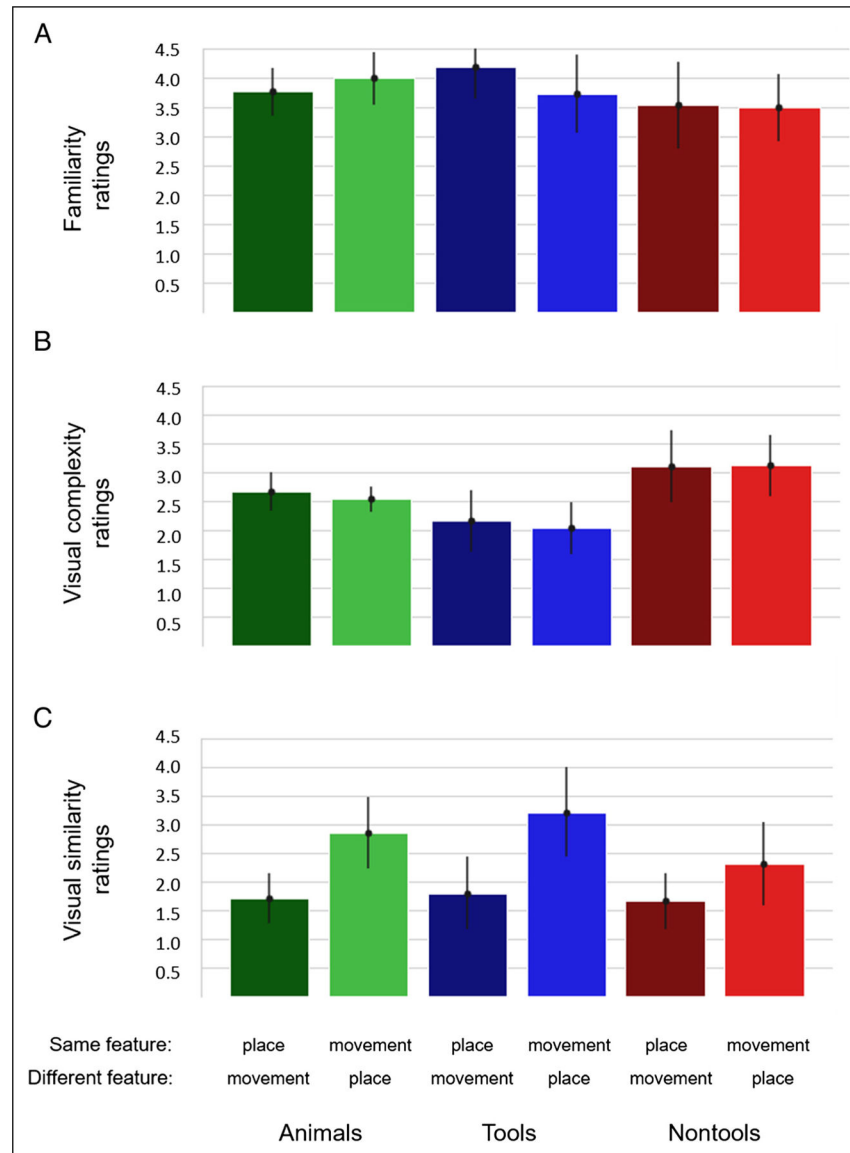


Figure 2. Low-level psychophysical features of the stimuli. Mean and standard deviation are shown for (A) familiarity, (B) visual complexity, and (C) visual similarity ratings collected during stimuli standardization. All descriptive statistics are reported in Supplementary Table 2A.

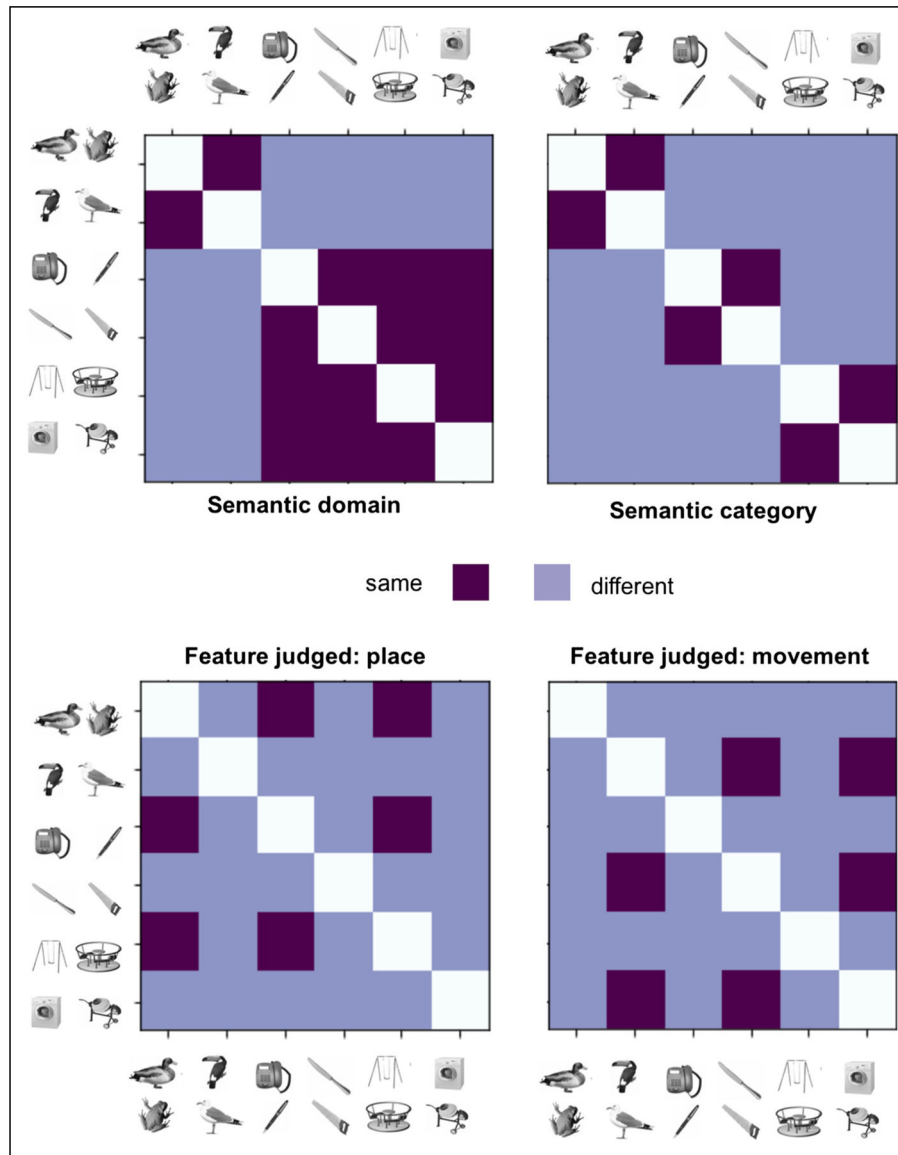


Figure 3. Predicted matrices modeling the representational similarities across experimental conditions. The semantic domain matrix indicates whether two pairs of stimuli are both animate (or inanimate) or not (top left). Similarly, the semantic category matrix highlights which pairs of stimuli belong to the same category (i.e., animals vs. tools vs. nontools, top right). Finally, the place (bottom left) and movement (bottom right) matrices indicate whether the pairs of stimuli were judged on the same semantic feature (place or movement, respectively) or not.

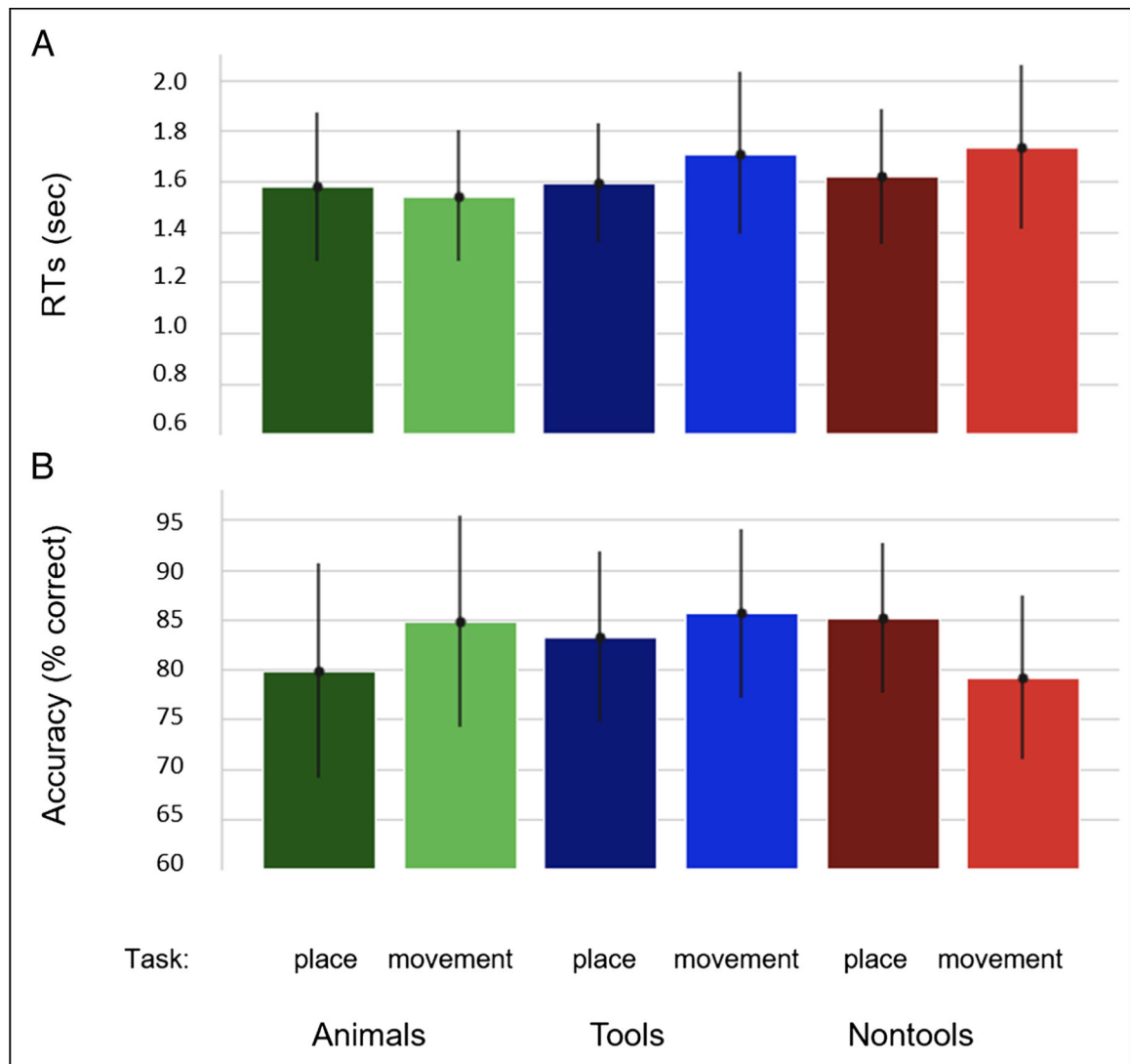


Figure 4. Behavioral results during the scanning session. Mean and standard deviation are shown for (A) accuracy and (B) RT in the six experimental conditions. All descriptive statistics are reported in Supplementary Table 2B.

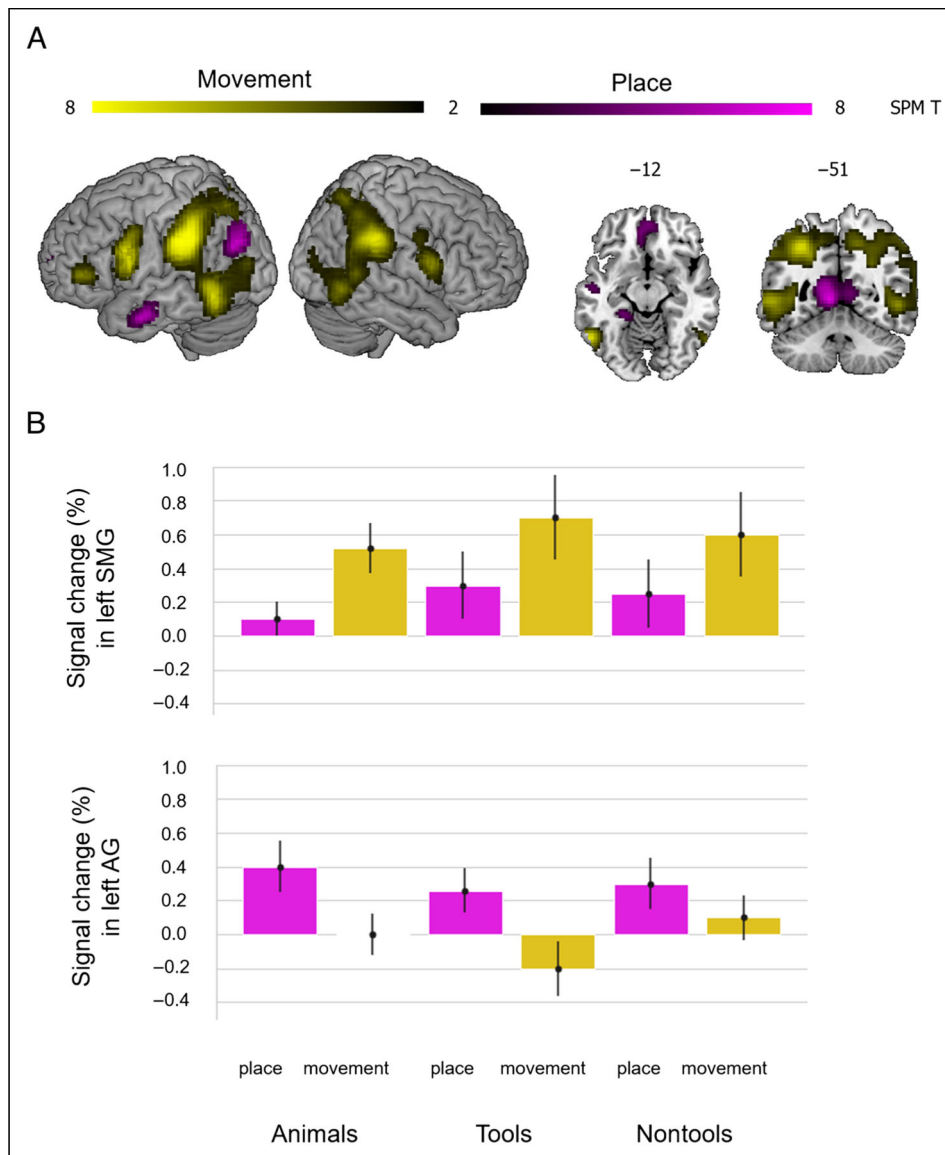


Figure 5. Whole-brain univariate effect of task. (A) Main effect of task: movement versus place. Renderings of the left and right hemispheres and one axial and coronal slice are shown for each contrast. Plotted clusters are thresholded at $p < .05$, FDR corrected, with a cluster extent threshold of 100 voxels. (B) Percent signal change is shown for the two main clusters defined by the contrast Movement > Place (left SMG) and Place > Movement (left AG).

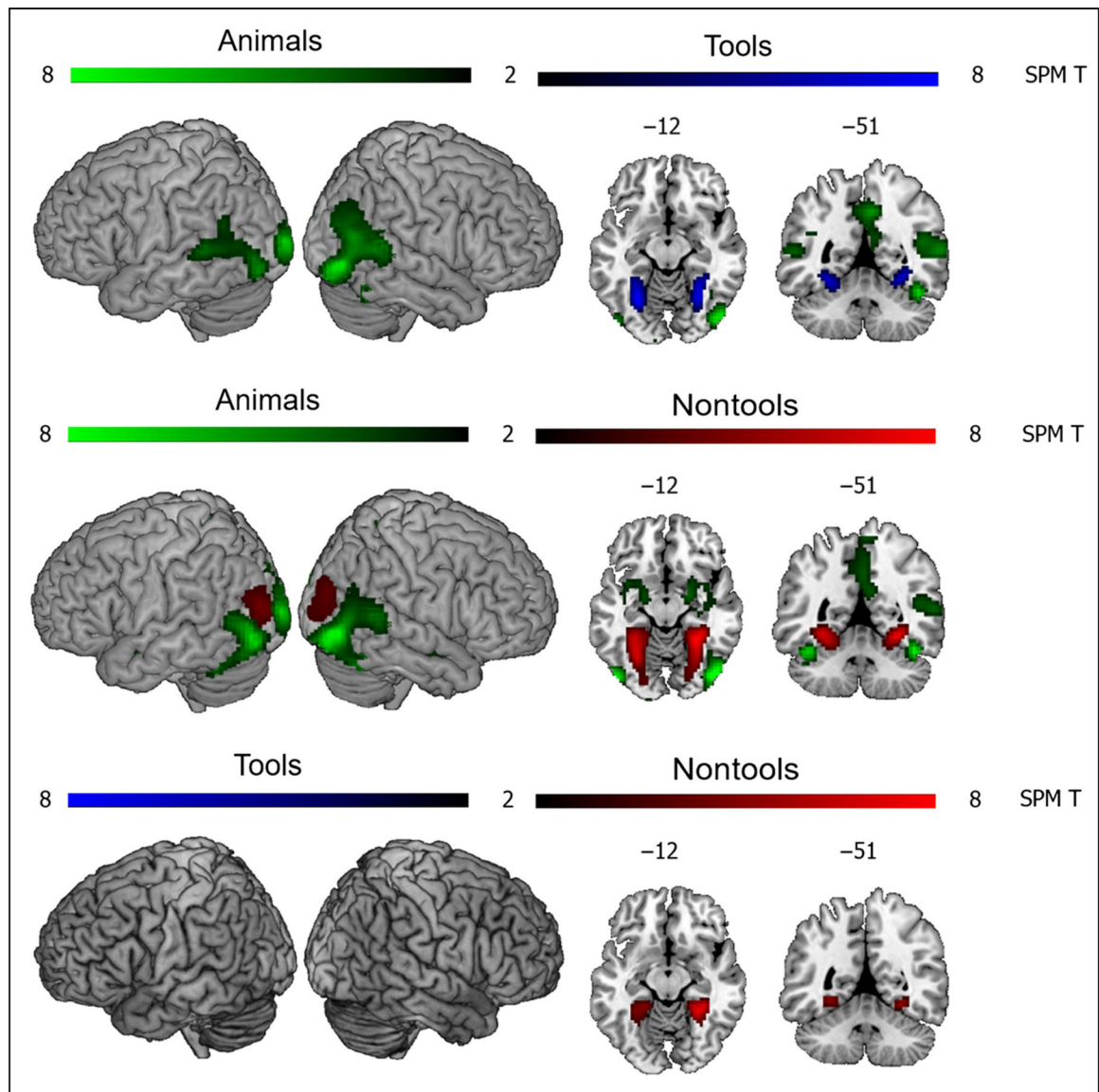


Figure 6.

Whole-brain univariate effect of semantic category. Main effect of stimuli category: animals versus tools (first row), animals versus nontools (second row), and tools versus nontools (third row). Plotted clusters are thresholded at $p < .05$, FDR corrected, with a cluster extent threshold of 100 voxels.

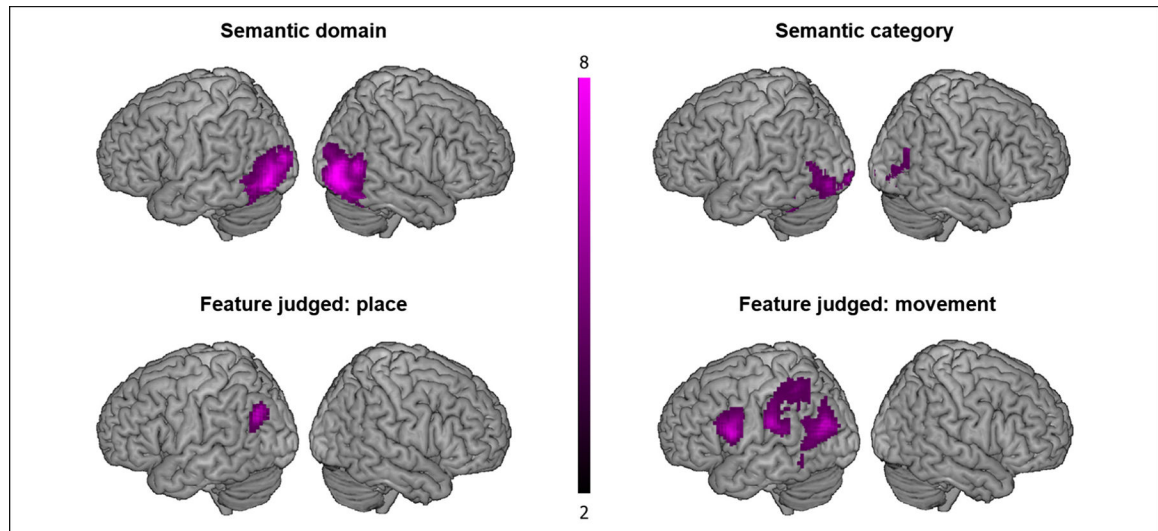


Figure 7. Results of the multivoxel pattern correlation searchlight analyses. Rendering of the left-hemisphere searchlight analysis was performed to look for areas where the distributed pattern of activity reveals effects of semantic domain (animate vs. inanimate, top left), semantic category (animals vs. tools vs. nontools, top right), and prototypical place (bottom left) or movement (bottom right). Plotted clusters are thresholded at $p < .05$, FDR corrected, with a cluster extent threshold of 100 voxels.

Table 1.

Whole-Brain Univariate Effects of Semantic Category and Task

Contrast	Brain Area	MINI Coordinates						N Voxels	p (FDR)	Max T
		x	y	z	x	y	z			
Tools > Animals	Left fusiform	-27	-63	-12	198	<.001	8.32			
	Right fusiform	30	-60	-9	163	<.001	7.31			
	Right inferior occipital	45	-75	-6	987	<.001	10.41			
Animals > Tools	Left middle occipital	-21	-99	6	218	<.001	7.56			
	Right inferior occipital	42	-51	-21	103	<.001	6.74			
	Left inferior occipital	-45	-81	-6	372	<.001	6.01			
	Right precuneus	6	-51	42	369	<.001	5.38			
Tools > Nontools	No significant effects									
Nontools > Tools	Right fusiform	27	-45	-12	224	<.001	7.28			
	Left fusiform	-27	-33	-21	171	<.001	5.25			
Nontools > Animals	Right fusiform	27	-48	-12	523	<.001	13.55			
	Left lingual	-27	-60	-9	708	<.001	12.46			
	Right middle occipital	36	-81	21	228	<.001	5.6			
Animals > Nontools	Right inferior occipital	45	-75	-6	917	<.001	11.60			
	Left inferior occipital	-45	-78	-6	419	<.001	8.15			
	Left middle occipital	-18	-99	6	1,128	<.001	7.60			
	Right anterior temporal	30	-3	-27	273	<.05	4.54			
	Left anterior temporal	-21	-3	-15	218	<.05	4.49			
Movement > Place	Left supramarginal	-60	-36	36	4,448	<.001	9.95			
	Left precentral	-48	6	24	443	<.001	8.63			
	Right inferior frontal	48	12	18	258	<.001	6.35			
Place > Movement	Left inferior frontal	-45	42	6	116	<.001	5.48			
	Left posterior cingulate	-9	-54	6	498	<.001	7.26			
	Left AG	-42	-75	30	157	<.001	7.13			
	Left middle temporal	-54	-3	-24	108	<.001	6.24			
Frontopolar	0	51	-9	322	<.05	4.46				

Table 2.

Results of the Multivoxel Pattern Correlation Searchlight

Contrast	Brain Area	MINI Coordinates			N Voxels	p (FDR)	Max T
		X	y	z			
Semantic category	Left FG	-21	-90	9	2,455	<.001	5.65
	Right FG	36	-60	-6	3,494	<.001	5.55
Semantic cluster	Left inferior occipital	-12	-96	-12	1,953	<.001	4.90
	Right inferior occipital	36	-57	-15	481	<.001	4.99
Place	AG	-48	-69	30	345	.014	4.67
Movement	SMG	-36	-75	21	2,032	<.001	4.91
	Inferior frontal gyrus	-51	6	18	654	<.001	4.57