

## Abstract categories of functions in anterior parietal lobe



Anna Leshinskaya\*, Alfonso Caramazza

Harvard University, United States

### ARTICLE INFO

#### Article history:

Received 10 July 2014

Received in revised form

2 December 2014

Accepted 9 January 2015

Available online 12 January 2015

#### Keywords:

Semantic knowledge

Abstract concepts

Object functions

Actions

Inferior Parietal Lobule

Fmri

### ABSTRACT

Knowledge of function is critical for selecting objects to meet action goals, even when the affordances of those objects are not mechanical—for instance, both a painting and a vase can decorate a room. To identify neural representations of such abstract function concepts, we asked participants in an fMRI scanner to view a variety of objects and evaluate their utility to each of four goals (two Decoration goals: dress up for a night out and decorate a house, and two Protection goals: protect your body from the cold and keep objects dry in a flooded basement). These task conditions differed in the kind of functional evaluation participants had to perform over objects, but did not vary in the objects themselves. We performed a searchlight multivariate pattern analysis to identify cortical representations in which neural patterns were more similar for the pairs of similar-goal than dissimilar-goal task conditions (Decorate vs. Protect). We report such effects in anterior inferior parietal lobe (aIPL) close to regions typically reported for processing tool-related actions, and thought to be important for representing how they are manipulated. However, the current study design fully controlled for manipulation similarity, which predicted orthogonal relationships among the conditions. We conclude that the aIPL likely has nearby, but distinct, representations of both manipulation and function knowledge, and thereby may have a broader role in understanding how objects can be used, representing not just physical affordances but also abstract functional criteria such as esthetic value or purpose categories such as *decorate*. This pattern of localization has implications for how semantic knowledge is organized in the brain.

© 2015 Elsevier Ltd. All rights reserved.

### 1. Introduction

The semantic system is the part of memory responsible for generalized knowledge about the world—distinct from episodic memories, and from representations specific for processing input from a particular sensory channel. Concepts enable us to have thoughts “about the same thing” (Rey, 1983) whether that thing is seen, heard, or talked about through language; to have thoughts about things never seen at all (*desire, causality*); and about things whose sensory qualities are myriad and varied (*beauty, protection*). To get a handle on semantics experimentally, it may be best to approach it through its unique signature—its abstraction away from episodic and sensory particulars—by using concepts that do not refer to sensory events or qualities: non-sensory concepts.<sup>1</sup> In this experiment, we aimed to do so through the special case of function concepts.

\* Corresponding author.

E-mail address: [anna.leshinskaya@gmail.com](mailto:anna.leshinskaya@gmail.com) (A. Leshinskaya).

<sup>1</sup> We grant that there is no clear dividing line between ‘sensory’ and ‘non-sensory’ types of concepts, but rather a continuum with respect to how much generalization across sensory particulars a concept denotes. The concept ‘red’ refers to particular wavelengths of light but, of course, spans others. We chose concepts at a certain level of such abstraction.

The centrality and flexibility of the semantic system does not mean that it is unorganized at the level of brain structure. To the contrary, the study of how semantic memory is implemented in the brain has shown that it has neurally separable components that each have a privileged role in representing a particular kind of content, including not just domains of things such as animate or inanimate (Blundo et al., 2006; Caramazza and Shelton, 1998; Hillis and Caramazza, 1991; Laiacina et al., 1997; Lambon-Ralph et al., 1998; Warrington and Shallice, 1984)) but also, attribute types, such as color (Luzzatti and Davidoff, 1994; Miceli et al., 2001) and visual form (Vandenbulcke et al., 2006). What are the general principles behind these attribute-based divisions, and how are the components localized topographically with respect to each other and other cognitive systems?

fMRI has been used to observe spatially differential responses to thinking about, reading about, looking at or otherwise retrieving distinct kinds of attributes, including motion, manipulation, color, shape, sound and taste (Chao et al., 1999; Goldberg et al., 2006; Kable et al., 2005, 2002; Kellenbach et al., 2001; Martin et al., 1995; Phillips et al., 2002; Simmons et al., 2005). These observations have led to the proposal that much of semantics is organized by attribute type, and that these attribute types correspond to the sensory/perceptual types that they refer to—that semantic divisions follow perceptual divisions (Martin, 2007;

Patterson et al., 2007; Thompson-Schill, 2003). The further observation is that these attribute-selective areas are overlapping with or anatomically adjacent to their respective perceptual areas, supporting the idea that the general localization principles for semantic components is also based on localization principles for perceptual systems (Martin and Chao, 2001; Thompson-Schill, 2003).

However, this model offers no clear account of where non-sensory attributes should be represented—that is, attributes which do not refer to any particular sensory information, and thus have no particular associated modality. One possibility is that all content with no modality is represented in a common area, but evidence from work on non-sensory concepts speaks against such a hypothesis, given the heterogeneity of regions observed both within and across experiments for non-sensory concepts relative to concrete ones (Binder et al. 2005; Bright et al., 2007; Cappa et al., 1998; Goldberg et al., 2007; Noppeney and Price, 2002; Rodríguez-Ferreiro et al., 2011; Skipper and Olson, 2013). Instead, we expect that distinct kinds of non-sensory concepts are represented in distinct neural regions, and, for this reason, should be studied not as one kind, but each in turn. Here, we carry out a directed investigation of one such kind (function concepts) with the hope that investigating the way in which particular non-sensory contents are neurally localized, we can gain deeper understanding of the broad organizational principles of semantic knowledge.

Furthermore, sensory attribute-selective responses might not reflect the operation of the semantic system at all. Are the observed effects at the semantic level of representation or due to their associated sensory memories? To the extent that a concept is reliably associated with particular sensory information (for instance, the color yellow with banana), that associated sensory information could be activated regardless of whether banana is read as a word, seen as a picture, or tasted. In other words, cross-modal access by itself does not guarantee that a representation is semantic, because modality-specific information can be associatively retrieved from multiple input modalities. Thus, previously reported attribute effects might be at any level of representation, anywhere from sensory associations to semantics. These challenges are difficult to overcome when studying concrete concepts, because they are reliably associated with sensory representations. This suggests that concepts of non-sensory attributes may be a better window into semantic knowledge.

Non-sensory attributes are neither rare nor peripheral in our conceptual system. Indeed, much of what we know about objects, people, and actions is not describable in terms of specific sensory properties. Although we certainly represent what tools look like and how they are manipulated, one of the main things we know about tools—and other artifacts—is what they are *for*; that is, what outcomes they are designed to achieve (Futó et al., 2010; Garcea and Mahon, 2012; Gutheil et al., 2004; Kelemen and Carey, 2007; Lombrozo, 2009; Träuble and Pauen, 2007, 2011; Tyler and Moss, 1997). Such outcomes can be concrete (e.g., a comb can create neat hair) but many are abstract (e.g., a comb can make one look more beautiful; a book can be used to learn things). Functions at this level can be accomplished by many different objects, each with distinct manners of manipulation and sensory effects on the world (lipstick, a suit, a bracelet can all serve to make one look beautiful in very distinct ways). Being able to represent function concepts this abstractly—that is, beyond specific sensory outcomes—allows us to flexibly select tools to meet action goals, and understand language, wherein action concepts often denote general aims, not body movements (e.g., *learning*, *decorating*).

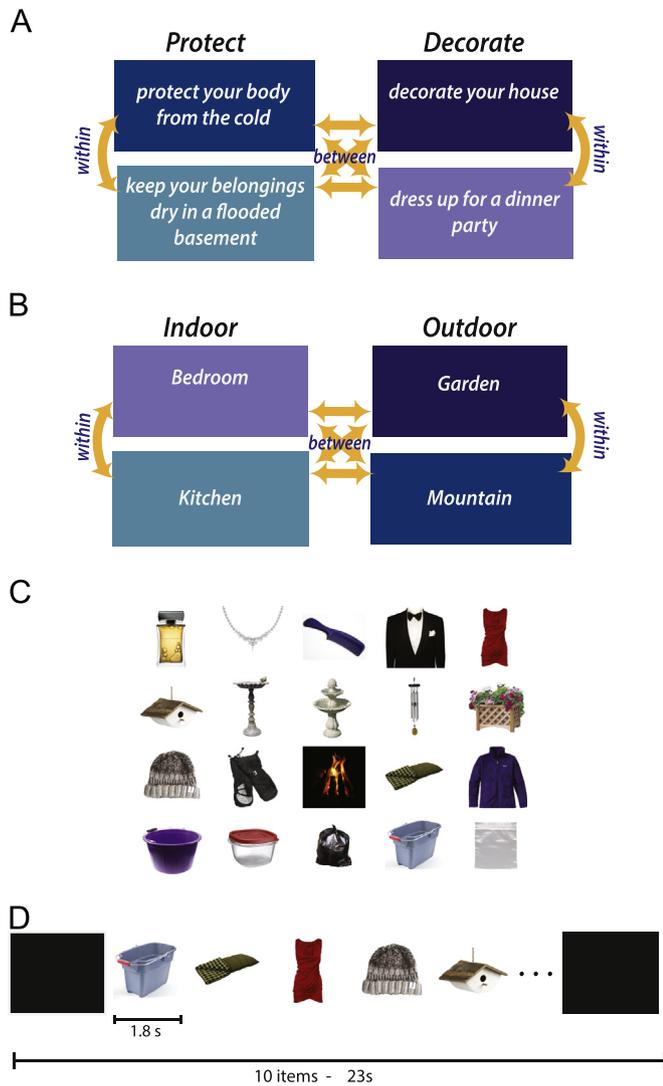
Attempts to describe neural representations of functions have been met with several methodological challenges, however. fMRI experiments contrasting the retrieval of function and

manipulation knowledge have found no regions responding more to function than to manipulation retrieval, despite significant effects of the reverse contrast (Boronat et al., 2005; Kellenbach et al., 2003). This could be because retrieving manipulation knowledge may *require* retrieving function. Can one think about how one moves a hammer without imagining that one is pounding a nail? Yet, one can retrieve that hammers are used for pounding nails without representing the details of one's body movement. Thus, the manipulation condition may simply have activated both kinds of information, and function-related activations were thus canceled out in the contrast. Other studies concerning function have typically emphasized context of use, such as kitchen vs. garage, which might correlate with function, but is not function per se (Canessa et al., 2008; Peelen and Caramazza, 2012). It thus remains unclear where in the brain function attributes are represented. And yet, the answer to this localization question could be instrumental to our understanding of the organization of the brain's semantic system.

In the present experiment, we took an approach to localizing function concepts that did not require a direct contrast between function and manipulation tasks. Instead, we asked participants to attend to function and used multi-voxel pattern analysis (MVPA) information-mapping (Mur et al., 2009) to find regions that contained information about categories of functions. According to representational similarity logic (Haxby et al., 2001; Kriegeskorte et al., 2007), a neural representation of function concepts should show similar patterns during the retrieval of similar functions, but relatively different patterns during the retrieval of different functions. We used four particular functions as conditions in the experiment (see Fig. 1), which we designed to belong to two broader categories: *protect* (Protect Body and Protect Objects) and *decorate* (Decorate Self and Decorate House). Participants thought about each function in turn during an object-relevance judgment task, but the objects remained the same through all conditions. In a searchlight analysis, we looked for neighborhoods of voxels whose patterns were more correlated for within-category conditions than for between-category conditions, as illustrated in Fig. 1. Importantly, conditions in the same function categories did not have similar body movement or context properties, relative to conditions in different function categories (as explained in Section 2).

It should be noted here that our aim is to identify one case of non-sensory content, and it is of less concern that it is specifically of function as opposed to other conceptual properties. There are two ambiguities we leave open: whether the functions are canonical and whether they are distinct from action goals.

A canonical function is the intended purpose of an object and not just any purpose it can serve to achieve (Bloom, 1996; Kelemen and Carey, 2007); the present design does not distinguish these. In fact, like most neuroimaging experiments on attribute knowledge, ours is designed only to find a signature of the attribute itself—the concepts *decorate* and *protect*—but not whether and how their representation relates to objects they might belong to (e.g., the knowledge *that* an umbrella has a protection function). However, we take one step towards this aim by additionally looking for neural representations that distinguish function-relevant from function-irrelevant objects, according to the function being considered. Lastly, because function concepts denote the achievement of a particular outcome, they are indistinguishable in this research from representations of action goals (outcomes achieved by actions, whether using objects or not). These conceptual issues will be more deeply addressed in Section 4.



**Fig. 1.** (A) The conditions in the Function task, and their predicted similarity relationships according to the categories *decorate* and *protect*. (B) The conditions in the Context task, and their predicted similarity relationships according to the categories *indoor* and *outdoor*. (C) One exemplar of each object type used in the experiment, arranged by rows into their condition-relevant sets, which are, from top to bottom, Dress Up/Bedroom, Decorate House/Garden, Protect Body/Mountain, Protect Objects/Kitchen. (D) Example of the block structure, common to all conditions. A task cue was followed by 10 objects, each presented for 1.8 s and ended with an evaluation question about the preceding object set.

## 2. Methods

### 2.1. Participants

Eighteen right-handed, neurologically healthy English-speaking participants (17 native speakers, 1 non-native but fluent; 8 female, mean age 25.6 years) took part in the fMRI experiment. For behavioral ratings of the stimuli, 75 participants were recruited online through Amazon Mechanical Turk (mean age 36 years). All participants provided informed consent either in writing or electronically. Procedures were approved by the institutional review board at Harvard University.

### 2.2. fMRI experimental procedure

The main experimental task (Function Task), performed during fMRI scanning, involved four kinds of function-based judgments over a common set of objects presented as images

(see Section 2.3). The four task conditions were: 1) Protect your body from the cold (Protect Body); 2) Keep your belongings dry in a flooded basement (Protect Objects); 3) Decorate your house (Decorate House); and 4) Help you and your date be well dressed for a dinner party (Dress Up). Tasks were presented in short, intermixed, 23-s blocks. Participants were cued to the task condition at the start of each block with a written instruction screen (1.6 s, with a 0–100 ms jitter before the block continued). They then saw a series of 10 objects, presented sequentially for 1.8 s each. The block concluded with a response screen, asking participants to rate on a 1–4 scale how well the function could be accomplished by the set of objects just presented; they responded using a button-box in their right hand. The structure of the block is illustrated in Fig. 1 C. This task design required participants to keep each function in mind for the duration of the block, while minimizing the number of explicit responses, reducing the chance of a response confound in the task design.

The objects that appeared in each block were chosen from a pool of 20, each with 3 exemplars (see Section 2.3). Fourteen 10-item series were created, one per block; these were reused for each condition, albeit with the order of the objects shuffled within the block. The series were constructed such that each of the 20 objects appeared exactly 7 times through the experiment, creating 140 trials (over 14 blocks) per condition.

Interleaved with the Function Task was a control task (Context Task) which asked participants to think about the context in which the (same) presented objects could be found. Instead of a function, participants were cued to think about one of four contexts: Kitchen, Bedroom, Mountain, or Garage. After viewing the 10 objects, they were asked to rate to what extent that set of objects would belong in the cued context. In every other aspect, the Context Task was identical to the Function Task.

Blocks from each task were presented in intermixed order, creating 8 conditions (or, block types) overall. The order of task blocks was sequenced randomly and arranged into 7 runs, such that each condition occurred exactly twice in each run (allowing runs to be modular); each run had 16 blocks of 23 s each, and lasted 5.9 min. Participants also performed two other tasks, which were reported as part of another experiment (Leshinskaya and Caramazza, 2014).

Before starting the scan, participants were given a 5.9 min practice (equal to 1 run) on a laptop computer. During the scan, the stimuli were viewed through a mirror attached to the head-coil, which was positioned to reflect the contents of a computer screen projected behind the bore of the scanner. MATLAB (The MathWorks Inc., 2009) and its Psychtoolbox extensions (Brainard, 1997) were used to control stimulus presentation and collect responses from the button box.

### 2.3. Stimuli and behavioral ratings

Twenty objects were chosen such that 5 were suitable, or relevant, for each of the four functions, and, simultaneously, each of the four contexts. As such, the objects were implicitly composed of 4 sets: those relevant for Dressing Up/Bedroom; Decorating House/Garden; Protecting Body/Mountain; and Protecting Objects/Kitchen. One exemplar of each object is shown in Fig. 1 B, arranged so that each row is one set.

These objects were presented in various, intermixed series of 10, with the same series repeated across conditions (as described in Section 2.2). Each series thus contained between 0–4 task-relevant, and 6–10 task-irrelevant trials. The number of relevant objects for each condition across series was equal.

It is important to note that the nature of each function condition (and context condition) was determined by an interaction of the task and the objects, as the task involved thinking about how a

function could be accomplished by the objects given. Thus, the control measures were obtained on task–object combinations (i.e., based on the 4 functions with these particular objects). The primary logic of the controls was to ensure that the two within-function-category pairs (i.e., Decorate Self and Decorate House; and Protect Body and Protect Objects) were not more similar than the between-function-category pairs (all other pairs, as illustrated in Fig. 1A) in any dimension other than function.

### 2.3.1. Control 1: Identity of relevant objects

The aim of this control was to ensure that within-function-category task conditions were not more similar than between-function-category task conditions in terms of the identities of their relevant objects (i.e., so that function similarity is not confounded by overlapping sets of relevant objects). This was accomplished by selecting objects that could primarily serve only one of the four functions, making the relevance relationships orthogonal across function conditions.

To compute relevance measures, behavioral ratings were obtained on an initial set of 40 objects (with 3 exemplars each). Forty-five online participants were shown each of the objects (15 participants per exemplar; 4 excluded for incomplete or overly fast responses) and asked to rate their suitability to each function—e.g., “how useful would it be for decorating a house (inside or outside)?”—and rated it from 0 (very useless) to 10 (very useful). Out of these, 4 sets of 5 objects were chosen, such that the 5 objects in the set had high values predominantly to one function condition (e.g., Decorate House). For each object set, its average relevance to each function is shown in Table 1A. To ensure relevance was not confounded with function similarity, the average absolute differences in relevance were calculated for within-category function pairs (e.g., Protect Objects vs. Protect Body) and for between-category function pairs (e.g., Protect Body vs. Decorate House). For example, for overall relevance, the within value was calculated from the Average row as:  $abs(3.16-3.04+3.16-2.36)/2$  for the within-difference and  $abs(3.16-3.16)+(3.16-2.35)+(3.04-3.16)+(3.04-2.36)+(3.16-3.16)+(3.16-3.04)+(2.36-3.16)+(2/36-3.04)/8$  for the between-difference. The results of the calculations are shown in Table 1B. On all measures, the within-category function pairs were more different in relevance ratings than the between-category function pairs. Because there were so few items, item statistics were not computed; instead, it was numerically ruled out that between-category pairs were more different than within-category pairs. Not shown, because less critical for the present purposes, these controls were also assured for the Context conditions and object sets (i.e., it was not the case that Outdoor contexts [Garden, Mountain] had similar sets of relevant objects than cross-context-category object sets).

Another approach is to measure the correlation between pairs of functions in terms of their relevance ratings across all individual objects; these data are presented in Fig. 2A. These are primarily negative, and also, are more negatively correlated for within-category pairs ( $r=-.36$ ) than between-category pairs ( $r=-.29$ ),

Table 1a

Object set	Average relevance to function			
	Decorate House	Dress Up	Protect Body	Protect Objects
Decorate House	9.22	0.33	0.31	0.67
Dress Up	0.92	9.19	1.83	0.47
Protect Body	1.25	2.33	9.46	1.01
Protect Objects	1.23	.32	1.06	7.28
Average (all sets)	3.16	3.04	3.16	2.36

For each 5-item object set (rows), its average rated relevance or utility to each function (columns) was primarily orthogonal.

Table 1b

Average absolute difference of each object set in terms of relevance to each function			
Within-category	<b>4.44</b>	Between-category	<b>3.86</b>
Average absolute difference of each function in terms of relevance of each object set			
Within-category	<b>4.45</b>	Between-category	<b>4.09</b>
Average absolute difference of overall relevance across all objects of each function			
Within-category	<b>0.46</b>	Between-category	<b>0.37</b>

The within-category conditions did not have more similar values than the between-category conditions. Top row compares object sets to each other, middle row compares functions to each other for each object set individually, and bottom row compares functions in terms of their averages.

demonstrating again that the category structure of conditions did not coincide with object relevance. In summary, the category structure of the function conditions did not coincide with the identity of the objects that could be useful for them.

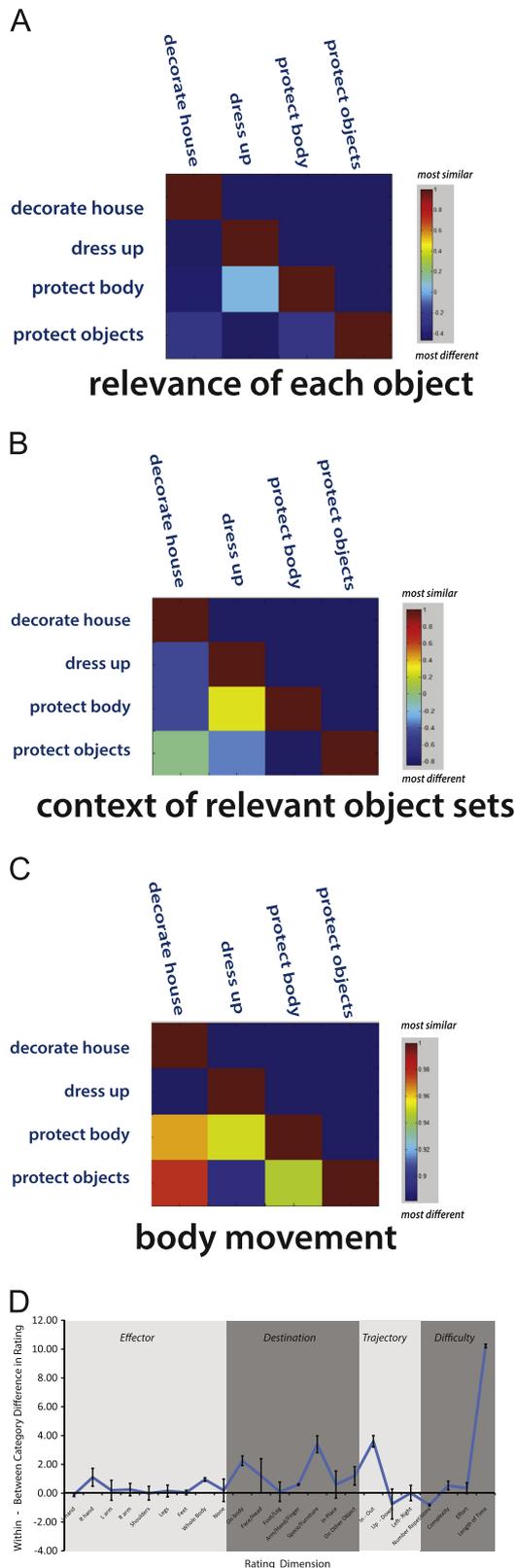
### 2.3.2. Control 2: context similarity

Function category structure (Decorate vs. Protect) and context category structure (Indoor vs. Outdoor) were also orthogonalized. Each object set had a primary relationship with one function and one context, but these were opposing in category relationship with other conditions. For example, the Decorate House objects were also the Garden objects; however, the within-category pair for Function was the Dress Up set, whose context was Bedroom, i.e., Indoor and thus opposite-category. In other words, pairs of conditions that were in the same category for Function were in a different category for Context. This ensured not only that the object sets had opposing category structures, but so did the associated task conditions, because it made Decorate House specifically an Outdoor function in this experiment.

Measures were also obtained for the context-relevance of each object independently of the particular function it is used for. The same participants described in Control 1 rated each object for its typical context (Kitchen, Bedroom, Mountain, and Garden) by answering, e.g., “How often is it found in a kitchen?”, from 0 (not at all) to 10 (frequently). Context ratings were not more similar for within than between-function-category object sets. This is illustrated in Fig. 2B, which displays the correlation of context ratings (i.e., typicality for Kitchen, Bedroom, Mountain, and Garden) between the sets of objects relevant to each function. On average, within-function-category object sets were more negatively correlated in their context ratings ( $r=-.64$ ) than between-function-category object sets ( $r=-.14$ ).

### 2.3.3. Control 3: body movement similarity

To control for body movement similarity, we ensured that objects in the same function category were not more similar to each other than objects in different function categories, in terms of how they would be physically used to perform their functions. Intuitively, it is apparent that the physical use of a fountain to decorate a house is distinct from the physical use of a comb to dress up for a dinner party, and that Dress Up should be most similar to Protect Body, which goes against function similarity. To ensure that that this was indeed the case, another group of behavioral participants ( $n=30$ , 4 excluded for incomplete or overly fast responses) was asked to rate, on a number of dimensions, how they would use each object to achieve its relevant function (e.g., shown a picture of a fountain and asked, *consider this object and how you would use it to decorate your house*). This was followed by



**Fig. 2.** (A) Correlations among each pair of Function conditions in terms of the relevance or utility ratings of each object to each condition. (B) Correlations among each pair of Function conditions in terms of the rated context of their respective object sets. (C) Correlations among each pair of Function conditions in terms of the movement properties (on 23 dimension) of their respective object sets. (D) The within-between function category difference of the ratings on each dimension of movement. Error bars are standard error of the mean as measured across items.

a set of questions including which body parts would be used, at which location the object would end up (e.g., on body, on face, on another object), the direction and motion of body movements involved (e.g., towards body vs. away; down vs. up), the effort exerted, and length of time the movement would take. This created a vector of 23 values, which was averaged within object sets and correlated between all object set pairs, providing a measure of how similar each object-set was to each other object-set. Values were compared for within-category function pairs vs. between-category function pairs, to ensure that function similarity was orthogonal to movement similarity. This was indeed the case. As illustrated in Fig. 2C, object sets with similar functions had similar body movements ( $r = .91$ ) but that this was not greater than the correlation between object sets with different functions, which was in fact higher ( $r = .95$ ). This was also true when considering only effector similarity ( $r = .92$  vs.  $r = .94$ ); only trajectory similarity ( $r = -.92$  vs.  $r = -.01$ ) or only destination similarity ( $r = -.28$  vs.  $r = .30$ ); and values were equal for effort similarity ( $r = .99$  vs.  $r = .99$ ). Fig. 2D shows that these similarity relationships were also apparent in the absolute differences in values across the vector of movement measures (overall: 2.77 point difference within category; 1.67 point difference between category). On almost every individual dimension, the within differences were greater than the between differences. There was a negative or null numerical difference between within-category conditions on every measure of motoricity. Thus, even if participants implicitly imagined themselves physically acting on the objects during their function judgments, these acts of motor imagery could not explain differences in similarity of within- vs. between-category functions.

In summary, the function similarity model was specific to the function dimension: the within-category conditions (e.g., the two Protect functions and the two Decorate functions) differed more in terms of their relevant object identities, the body movements used to accomplish them, the contexts in which they occur, and where their relevant objects would be found, relative to the between category pairs.

#### 2.4. fMRI acquisition parameters

fMRI data was acquired using a Siemens Magnetom TrioTim syngo 3 T scanner at the Center for Brain Science, Harvard University, Cambridge, MA. Anatomical volumes were acquired with T1-weighted MPRAGE sequence, at a  $1 \times 1 \times 1$  mm<sup>3</sup> voxel resolution ( $256 \times 256$  matrix size). Functional data were acquired with an EPI sequence (32-channel coil; TR=2.0 s; TE=28 ms; flip angle 90°). For each volume, 33 interleaved slices were collected, covering the whole brain (oriented at AC-PC-40, 0.6 mm gap; matrix size  $72 \times 72$  cm<sup>2</sup>), which produced a voxel resolution of  $3 \text{mm} \times 3 \text{mm} \times 3 \text{mm}$ . Runs were comprised of 105 volumes each.

#### 2.5. fMRI preprocessing and linear modeling

fMRI data were pre-processed and modeled with AFNI software (Cox, 1996). Slices in each volume were corrected for acquisition timing, using Fourier interpolation (3dTshift). Each volume was then aligned to the 4th volume of the first scan (3dVolReg). In each run, a Fourier high-pass temporal filter (.008 Hz) was applied to remove low-frequency trends (3dDetrend), and image intensities were normalized (scaled to range from 0 to 100). For basic mean contrast analyzes, the data were spatially smoothed with a 6 full-width, half-maximum Gaussian kernel. All of the runs were concatenated, excluding runs in which displacement from the start of the scan exceeded 3 mm. Regressors for each condition (i.e., task block) were created by convolving their time-courses in the experiment with a gamma-modeled hemodynamic response, separately for each participant. These convolved time-courses were

used as predictors in a mixed-effects, least squares linear regression over the signal time-course in each voxel (3dAnova2). The model also included motion derivatives in each of 4 directions and 2 rotations, and excluded volumes with motion outliers. The linear modeling procedure produced a map of beta values for each voxel and each condition, reflecting the slope of the relationship between the voxel's signal and the occurrence of that condition; the corresponding  $t$ -values were also produced, reflecting the statistical significance of these slopes. This analysis also produced maps of the residuals in predicting each voxel's activity. For multiple comparison correction of tests of mean signal differences, the smoothness of these residuals maps was estimated in each participant; the average smoothness value was used in a simulation (3dClustSim) to estimate the size of a cluster (contiguous set of voxels with  $p < .01$ ) expected to occur by chance with  $p < .05$ , given the number of voxels estimated.

## 2.6. Anatomical surface analysis

Anatomical data were processed using the Freesurfer software function recon-all (Fischl et al., 1999), which skull-stripped the volumes and used intensity gradients to segregate white and gray matter and generate inflated cortical surface maps for each individual. Inter-individual alignment was performed over the surfaces. First, functional maps were aligned to each individual's native-space anatomical volume; the inflated surface based on this volume was then registered with other participants' surfaces using the AFNI function Maplcosohedron, and the alignment parameters from the volume to the resampled surface were used to align the functional data. These procedures were implemented using the Surfing Toolbox (available at <http://surfing.sourceforge.net>) and described in more detail elsewhere (Oosterhof et al., 2011, 2010).

## 2.7. Multivariate pattern analysis and searchlight procedure

Within each task (Function and Context), pair-wise relationships between the 4 conditions were categorized as either within-category or between-category, according to the category models illustrated in Fig. 1A. The aim of the multivariate pattern searchlight analysis was to identify sets of voxels whose patterns exhibited more highly correlated patterns of activation for within-category pairs than for the between-category pairs. The following steps were performed within each subject, and are illustrated in Fig. 3. First, neighborhoods of 123 voxels were defined surrounding each surface node, while respecting the curvature of that subjects' cortical surface (using the Surfing Toolbox [Oosterhof et al., 2011]). In contrast to neighborhoods defined volumetrically, this resulted in neighborhoods with a curved cylindrical shape that followed the contours of the sulci and gyri of each individual. Second, within each neighborhood of voxels, all pair-wise correlations among conditions were computed in terms of the activation level ( $t$ -value) of the voxels in that neighborhood; unsmoothed maps were used for this analysis. These correlation values were fisher-corrected to improve normality and enable parametric testing. The pair-wise correlations among within-category and between-category pairs were then respectively averaged and subtracted, yielding a correlation difference value for within vs. between category pair for that neighborhood of voxels. This value was recorded at the center surface node around which the neighborhood was defined. For group-level statistics, the correlation difference value was compared to 0 using a  $t$ -test across subjects, at each node.

The resulting statistical maps were corrected for multiple comparisons using a cluster-size simulation. Error maps for the MVPA searchlight analysis were computed using subject-map residuals from the group mean (obtained by subtracting each

individual's maps from the group maps). The smoothness of each error map was estimated using the Afni function 3DFWHM and averaged. Next, over 1000 iterations, 18 random noise maps were created (equal to the sample size) and smoothed to an equivalent level to the average of the noise maps. At each iteration, these random maps were submitted to a  $t$ -test against 0, and the maximal cluster size in the resulting statistical map (thresholded at  $p < .01$ , one-tailed) was recorded. This produced a distribution of 1000 maximal cluster sizes, reflecting the probability of obtaining a given cluster size by pure chance, given the same number of comparisons and equivalent smoothness. This null distribution was used to assign  $p$ -Values to the searchlight results.

A standard volume-based searchlight analysis was also performed for comparison, using spherical neighborhoods of 123 voxels (equivalent to a sphere with a 9 mm radius), and a similar approach to multiple comparison correction, and yielded indistinguishable results.

## 2.8. Relevance analysis

A linear model was constructed to predict responses to individual trials within a block. Each trial was coded in terms of both its task (e.g., Protect Body) and the set to which the object of that trial belonged (e.g., a Decorate House object). Thus, 32 new conditions were created (one for each combination of the Function tasks and object sets, 16, and each combination of the Context tasks and object sets, also 16). A multivariate pattern searchlight analysis was then performed (as described in Multivariate Pattern Analysis and Searchlight Procedure) to distinguish two types of trials: Relevant-object and Irrelevant-object, across object identity. This was done by comparing the correlation between two types of trial pairs: those of same-relevance where objects were different, and those of different-relevance but where the objects were the same. For example, a trial might be coded as Decorate House–Dress Up, indicating a trial in which a Decorate House object was viewed during a Dress Up task block; it was thus an Irrelevant trial. A same-relevance pair for this trial might be Protect Body–Decorate House, indicating a trial in which a Protect Body object was viewed during a Decorate House block. Although the objects were different, they shared the property of being task-irrelevant. Another same-relevance pair might be Protect Body–Protect Body and Decorate House–Decorate House. Here, the relevance status is also the same (both relevant). The different-relevance pairs included conditions with the same object but different relevance status: e.g., Decorate House–Decorate House and Decorate House–Protect Body. The average correlation among all different-relevance trials was then subtracted from the average correlation among all same-relevance trials, yielding a difference reflecting how much relevance status (relevant vs. irrelevant) could be distinguished. In the same fashion as the other searchlight analyses, the correlation differences at each surface node were then submitted to a group  $t$ -test, and a cluster-wise multiple comparison correction was applied. A similar analysis was performed separately for the Context trials, creating group maps for Function-relevance and Context-relevance.

## 2.9. ROI definition

Several ROIs were defined based on past literature to increase comparability between present findings and past results. A left anterior IPL ROI was defined from coordinates of previously reported adaptation effects to similar reach targets across movement trajectory (Hamilton and Grafton, 2006), at Talairach coordinates  $-57, -48, 8$ . A left middle temporal gyrus (MTG) ROI was defined based on a meta-analysis of action concept retrieval, reported at  $-58, -50, 6$  in MNI space (Watson et al., 2013) but which was

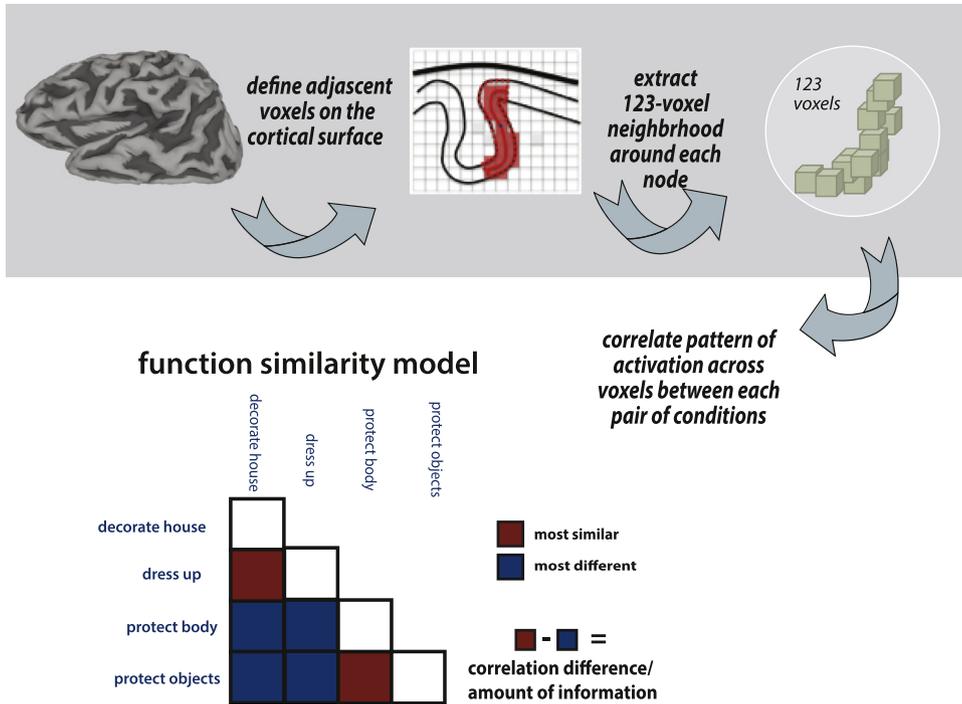


Fig. 3. Surface-based searchlight analysis and model testing procedure.

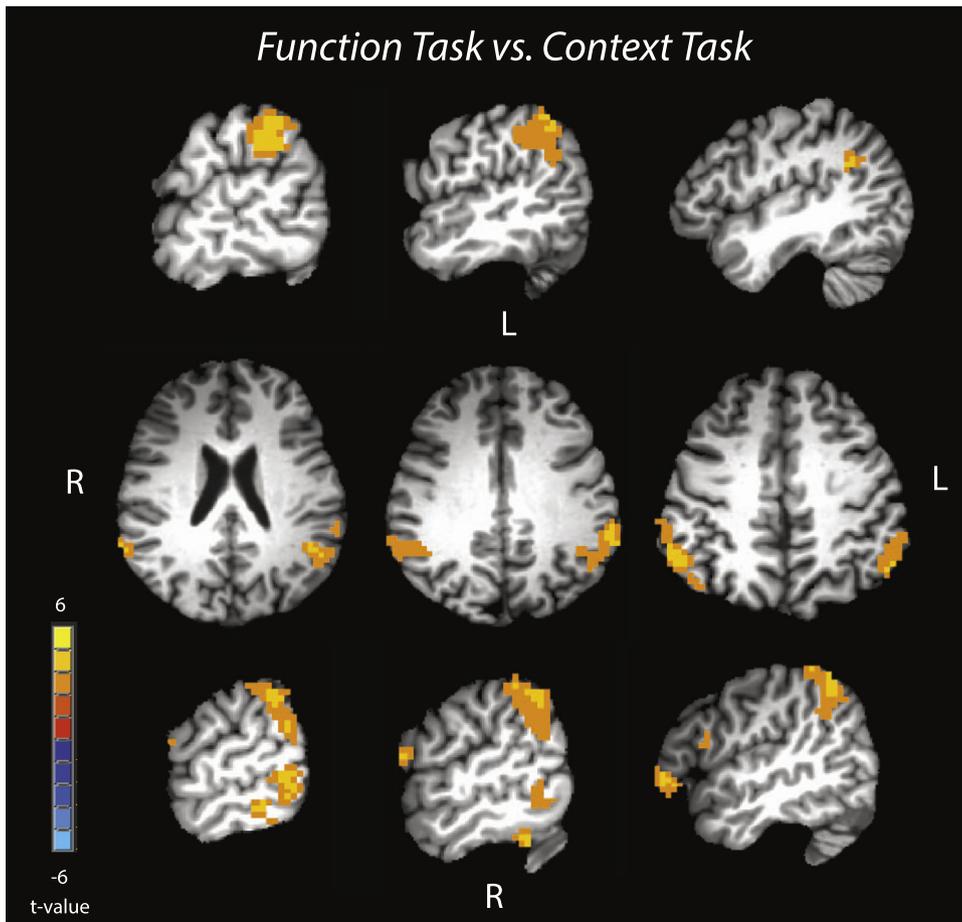


Fig. 4. Results of a univariate contrast of BOLD signal during the Function task vs. Context task, thresholded at  $p < .05$ , corrected for multiple comparisons using a cluster-size threshold of 81 voxels at  $p < .01$  uncorrected.

converted to Talairach coordinates  $-57, -48, 8$  using the Matlab-based function `mni2tal` (available at [http://eeg.sourceforge.net/doc\\_m2html/bioelectromagnetism/mni2tal.html](http://eeg.sourceforge.net/doc_m2html/bioelectromagnetism/mni2tal.html)). An average coordinate for the left retrosplenial cortex ( $-11, 54, 15$ ) was defined from 3 papers contrasting contextual or place-related knowledge retrieval relative to retrieval of other kinds of knowledge (Bar and Aminoff, 2003; Canessa et al., 2008; Fairhall et al., 2013). To maintain relative spatial specificity and also allow enough voxels such that the correlations are relatively stable, a sphere with a 6 mm radius was defined around the center coordinate to create the ROIs.

### 3. Results

#### 3.1. Behavioral responses

Participants responded at the end of each block to indicate the degree to which the set of objects presented in that block would either enable accomplishing a pre-specified function (in the Function task) or would belong in a pre-specified context (in the Context task). The two tasks did not differ in response time (790 msec vs. 773 msec;  $t(17)=1.28, p=.22$ ) or in the response value to the task question ( $t(17)=.046, p=.65$ ). The responses were fast overall, most likely because participants were cued to the task in advance and thus could prepare during the block.

To verify that the within-between category models (Fig. 1 (A) and (B)) were not confounded with behavioral responses, either in reaction time (RT) or response value, responses were analyzed using a within-vs.-between comparison analogous to the MVPA analysis of fMRI data (see Section 2). In short, for each participant, responses were averaged by condition, and the absolute pairwise differences between all condition pairs were computed. The within-category and between-category pairs were respectively averaged and subtracted, creating a within-vs.-between response difference measure for each participant, which was tested against 0 at the group level. For Function task conditions, neither response time, nor response value, differed between the within- vs. between-category condition pairs, implying that these factors were not confounded with the category model (RT difference within-category=120 msec; between-category: 110 msec;  $t(17)=-.50, p=.62$ ; response difference within-category=.39, between-category, .36,  $t(17)=-.77, p=.45$ ). For Context task conditions, response time did not differ between the within- and between-category conditions (both RT differences=120 msec;  $t(17)=-.30, p=.77$ ), but response value was marginally less different within (.44) than between (.58) categories ( $t(17)=1.97, p=.06$ ). This should present a concern when interpreting the Context category searchlight results (but see Section 3.3, Context).

#### 3.2. Mean contrast results: function vs. context task

Fig. 4 shows the results of a mean signal contrast between Function task blocks and Context task blocks overall; Table 2 lists

Table 2

Anatomical label	x	y	z	#Voxels in cluster
Left Inferior Parietal Lobule (BA 40)	-52.5	-46.5	+47.5	221
Right superior parietal lobule (BA 7)	+52.5	-49.5	+47.5	202
Right fusiform gyrus (BA 20)	+61.5	-37.5	-12.5	121
Right inferior frontal gyrus (BA 47)	+58.5	+13.5	+14.5	99

Talairach coordinates, and atlas-derived anatomical labels, of the peak of each significant cluster ( $p < .05$  corrected) that responded more to the Function Task than the Context Task.

the peak coordinates of each significant cluster. Clusters occurred in the left IPL, spanning supramarginal and angular gyri; and in the right hemisphere, spanning both inferior and superior parietal lobules, parts of inferior and middle frontal gyri, and parts of the fusiform and middle temporal gyri. This contrast is not necessarily specific to the retrieval of Function information, as participants could also have engaged in motor imagery during the Function task more than the Context task. However, it is likely that this set of regions includes those that represent function information. No clusters survived a corrected-level threshold of  $p < .05$  in the contrast Context > Function.

#### 3.3. Multivariate searchlight results

**Function.** The aim of the multivariate searchlight analysis was to find regions whose voxel-wise patterns were correlated more within-category than between-category, according to the function category model (Decorate vs. Protect) described in Fig. 1A and Fig. 3. Such a pattern would indicate that this region both generalizes within the category (treats both Decorate House and Dress Up similarly) and distinguishes across category (Decorate vs. Protect).

At each neighborhood of voxels defined on the cortical surface, a  $t$ -test was used to compare each participant's within-vs.-between category correlation difference to 0. This statistical map was then thresholded at  $p < .01$ , the size of each resulting cluster was measured, and a simulated null cluster-size distribution was used to assign a significance value to each cluster. The surviving cluster ( $p=.005$ , corrected) is displayed in Fig. 5. This cluster spanned the anatomical areas of post-central sulcus (PCS), supra-marginal gyrus (SMG), and the anterior intra-parietal sulcus (aIPS), which (as derived from volume-based searchlight data) peaked at Talairach coordinates  $-62, -38, 38$ , and centered on  $-59, -36, 36$ . This cluster partially overlapped with the task-activated clusters in left IPL reported in Table 2 and Fig. 1.

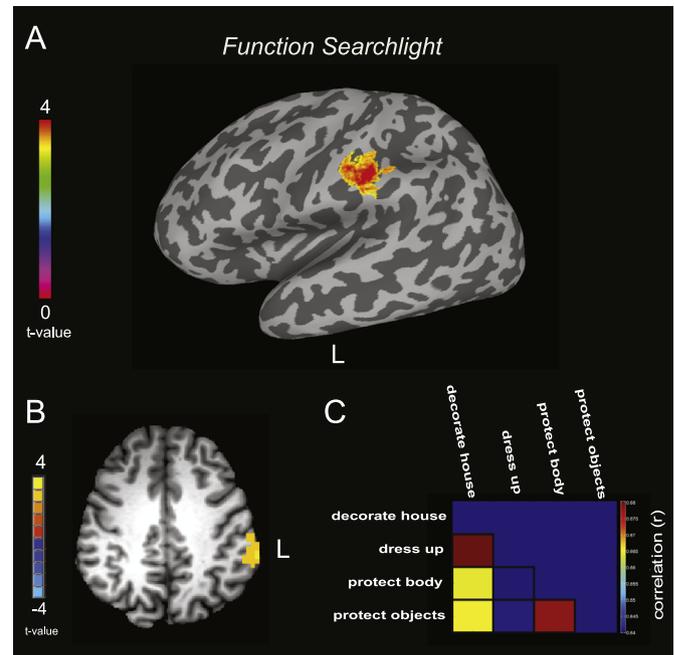


Fig. 5. (A) Significant cluster in the surface-based Function searchlight analysis (anterior IPL, 527 mm<sup>2</sup> at  $p < .01$  uncorrected,  $p=.005$  corrected). (B) Significant cluster in the volume-based Function searchlight analysis (anterior IPL, 106 voxels at  $p < .01$  uncorrected,  $p=.01$  corrected). No other clusters passed a significance threshold of  $p < .05$  corrected. (C) Average pairwise correlations of voxel-wise activation patterns across the conditions, within the cluster shown in A (for illustration only).

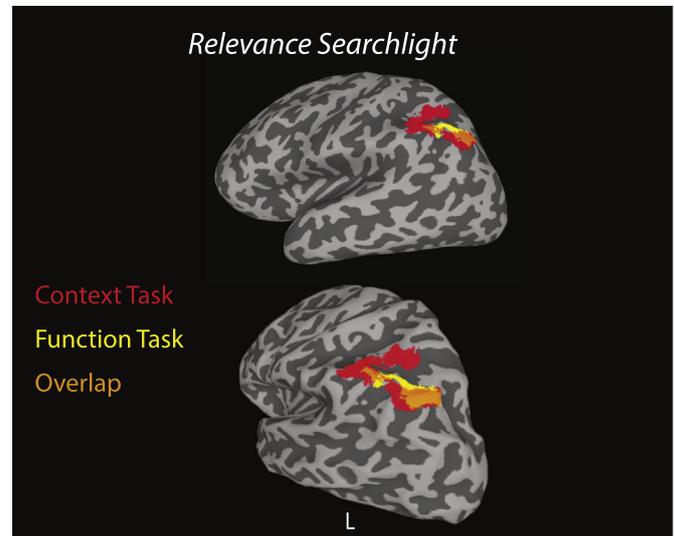
**Context.** The context-category (Outdoor vs. Indoor) searchlight analysis yielded no significant results, similarly to the mean contrast results comparing the Context and Function tasks. One possibility is that the Context task was less engaging, perhaps because context-belonging was a more simple or binary judgment, while the Function task could have engaged more creative reasoning. In an attempt to boost analysis power, context category pattern-analysis was performed within an ROI centered on the left RSC, a region commonly engaged during context judgments. The within vs. between correlation difference was trending, but non-significant ( $t(17) = 1.42, p = .087$ ). Effects of context within the significant cluster identified in the function searchlight were also not significant ( $t(17) = -.86, p = .80$ ).

#### 3.4. Function representations in literature-based ROIs

ROI analyses were also performed to establish a tentative link to previously reported findings. Of course, an important caveat is that shared standardized coordinates across studies do not imply that there is individual or even group-level correspondence of neuroanatomical location of two sets of effects. However, positive ROI effects are suggestive of such a possibility. Towards this end, coordinates from a closely related experiment were used, where adaptation effects were reported for a common reach target (physical goal) across differences in reach direction, at  $-52 -32 44$  (Hamilton and Grafton, 2006). Within-category correlations were significantly larger than between-category correlations in this area;  $t(17) = 2.8, p = .006$ . Function category effects were also tested in a region commonly active during the viewing of actions or reading of action names, the posterior middle temporal gyrus, as described in a recent meta-analysis (Watson et al., 2013), at the Talairach coordinates  $-57 -48 8$ . This result was not significant:  $t(17) = .03, p = .49$ .

#### 3.5. Relevance analysis

The results so far speak to the neural representation of function categories, but not to the objects that are being evaluated with respect to them. It is possible either that the same or a different region than the aIPL encodes information about which object is relevant or useful to a function. To address this question, another multivariate searchlight analysis was performed to look for regions that distinguish task-relevant from task-irrelevant trials—for instance, registering the difference between seeing a fountain when performing the Decorate House task and the same fountain when performing a Protect Body task, but considering a fountain during the Decorate House task as relatively similar to a fleece during a Protect Body task, because they are both relevant in their contexts. Importantly, this fully controls for object identity. (See Section 2.8 for more details on the analysis approach). This analysis was performed separately for Function and for Context conditions, and results from both are displayed on a single surface in Fig. 6. Significant clusters for both effects were found only along the superior IPS, posterior to the region reported for representing function categories themselves. This suggests that the categorization or maintenance of an object as relevant or irrelevant for a specific purpose may be subserved primarily by a region outside of that which represents function categories, and that the relevance categorization process is performed in an attribute- and domain-general fashion. This is consistent with the previously described role of IPS in maintaining flexible categories in service of task-related goals (Freedman and Miller, 2008; Swaminathan and Freedman, 2012).



**Fig. 6.** Significant clusters ( $p < .05$  corrected) in the relevance searchlight analysis, for the Context task in red, the Function task in yellow, and their overlap in orange.

## 4. Discussion

We asked participants to hold in mind four different functions, as they contemplated how various objects could be used to achieve them. Using an information-mapping MVPA approach, we identified a cluster of voxels in the anterior IPL that exhibited a pattern of activation across the four functions such that they were grouped into two abstract categories: *decorate* and *protect*. Below we discuss the best way to describe the content of these representations in aIPL, and the implications that might follow from their localization.

### 4.1. Content of the representations in aIPL

Having carefully selected the four functions and measured how they would be accomplished by their relevant objects, we ensured that the similarity of within-category conditions was based on purpose—an abstractly defined state in the world they are directed towards—and not on any dimension of non-interest (context, body movement), which predicted orthogonal similarity relationships among the conditions. The commonality between dressing up for a night out and decorating a house, and its distinction from keeping oneself warm and protecting objects, is a purely conceptual one, and rests on the meaning of *decorate*: to make more beautiful. This meaning is not reducible to any particular sensory state in the world, nor any particular means of achieving it. The former is true because *beauty* has no particular sensory definition, neither in general, nor in particular, with the kinds of decoration enabled by the set of objects included in our experiments (e.g., perfume, a tuxedo, a fountain, and a flower box). The latter is true because *decorate* is not a category of body movements, again neither in the particulars of this experiment, because body movement was more similar across the two categories than within; nor in general, because it is not by virtue of a type of body movement than an action counts as *decorating*; it is rather by virtue of being directed to making something beautiful—a type of outcome. The same argument extends to *protect*, particularly when this spans such distinct acts as warming one's body and shielding objects from water. These concepts may be specifically functions—i.e., are particular to outcomes enabled by objects—or may also encompass the goals of actions more broadly; but are, in either case, purposes.

One subtly different explanation to function or purpose should be considered, however. Although the objects presented in each

condition were the same, and no particular physical property of the relevant objects correlated with the distinction *decorate* and *protect*, it is still possible that the effects are driven by object property criteria, such as esthetic quality for *decorate* or being waterproof for *protect*, which participants likely held in mind while evaluating the objects. In other words, rather than the concepts *decorate* and *protect*, our design may have uncovered a representation of the concepts *beauty* and *impermeability*. These are not functions per se, but rather function-enabling properties. This alternative is distinct, but nonetheless equally non-sensory, as these properties, too, are not types of body movements or specific sensory qualities. They are either broad generalizations of visual qualities, or, more likely, complex relationships between object and effect; in this case, the creation of esthetic pleasure or the prevention of passing of water.

In sum, the representations we ascribe to this portion of aIPL are of abstract (i.e., non-sensory) categories of functions, purposes, or function-enabling properties. Whatever their precise content, we argue that these representations are conceptual by virtue of two properties: generality and independence from any sensory particulars. Indeed, in this study, the categories we investigated were both general and not reducible to sensory/motor details, inviting the conclusion that their representations in aIPL are part of semantic, and not sensory/motor, memory. This finding has a number of implications regarding the representations in the anterior inferior parietal lobe and the principles of organization of the brain's semantic system.

#### 4.2. Implications for the representational properties of anterior inferior parietal lobe

The presence of such representations within anterior IPL extends and re-characterizes past accounts of this area, both in general and specific terms. In general terms, the anterior IPL—which includes the supramarginal gyrus (SMG) and the anterior portion of the intraparietal sulcus (aIPS)—is considered by many researchers as exclusively motor or visuospatial, supporting processes of manual tool use and physical action execution, as opposed to conceptual. This perspective is evident in interpretations of effects in this vicinity as indexing the operation of a 'motor' system, whether such effects are elicited by the presentation of action videos or words (e.g., see reviews by Van Overwalle and Baetens, 2009; Watson et al., 2013) or images or names of tools (Chao and Martin, 2000; Mahon et al., 2007). The present findings challenge the notion that aIPL can be exclusively described as representing manipulation knowledge, and instead suggest that its repertoire must be expanded to include non-motoric, non-sensory, conceptual information—jumping off from similar hypotheses raised previously about this area (Johnson-Frey, 2004; Tunik et al., 2007).

Importantly, our interpretation is not precluded by past findings, as there is more than one interpretation available of reported tool /action effects. Tools (e.g., a hammer) or actions (e.g., hammering) might evoke at least three types of knowledge: modality-specific, motoric representations; conceptual knowledge of body movement/manipulation; and conceptual knowledge of what the tool/action is for. Activations driven by tools (relative to animals, to static tools, to hands, etc.<sup>2</sup>) could thus be either conceptual or motoric, and while they are often interpreted as low-level or

sensory, their high-level confounds cannot be ruled out. In sum, areas thought to be motoric by virtue of past evidence may in fact be conceptual, and if so, may be about either manipulation or function or both. These ambiguities cannot be resolved without directly testing for conceptual-level content.

All of this said, it is no doubt misguided to consider the anterior IPL in general terms as a homogeneous, unitary system. A more plausible account, which we argue for here, is that it contains neurally separable components for representing function and manipulation. Some effects reported in this area probably do reflect manipulation knowledge, whether conceptual or motoric, and are thus cognitively distinct from those we report here, which concern specifically function knowledge. These kinds of contents are likely represented in distinct neural areas. Neuropsychological research on apraxia has shown that function and manipulation knowledge have distinct neural substrates (Buxbaum et al., 2000; Ochipa et al., 1992; Sirigu et al., 1991; see also Goldenberg (2009); Koski et al. (2002); Ochipa et al. (1989); Wheaton and Hallett (2007)). There is thus little reason to expect manipulation and function to have the same neural substrate, making it likely that reported effects of manipulation and function within IPL occur in distinct subparts. The functional heterogeneity of IPL in general has not escaped attention (Binkofski and Buxbaum, 2013; Cabeza et al., 2012; Caspers et al., 2013; Humphreys and Lambon Ralph, 2014; Hutchinson et al., 2014), and efforts to provide any unifying framework for the many cognitive processes linked to this broad region (including spatial, attentional, and numerical tasks, for instance) prove difficult. Even within the domain of tool-related activations, diverse effects appear in spatially segregated parts of aIPL, as shown in the same group of subjects (e.g., Gallivan et al., 2013; Valyear et al., 2007).

The principles and precise locations of these aIPL subdivisions, however, are not well understood – partly due to the lack of within-subject comparison of the locations of many of the components in question. It is worth noting that a large set of experiments consistently reports tool-related effects around the Talairach coordinates  $-40, -40, 40$ , closer to the aIPS portion of aIPL (Chao and Martin, 2000; Lestou et al., 2008; Mahon et al., 2007; Valyear et al., 2007, 2012; Valyear and Culham, 2010; Vingerhoets et al., 2011), which coincides with many reported action observation and/or execution effects (meta-analysis in Caspers et al., 2010; and for example, Dinstein et al., 2007). This is spatially distinct from the present effect, whose peak was more lateral ( $-60, -38, 38$ ) and closer to SMG. Tool/action experiments also often find SMG, either alone or along with the more medial aIPS, including for effects of novel tool use training (Weisberg et al., 2007), names of tools vs. non-tool objects in blind individuals (Mahon et al., 2010), meaningful vs. non-meaningful actions (Newman-Norlund et al., 2010), and tool action compared to hand action videos (Peeters et al., 2009, 2013). Of particular relevance, this more lateral part of aIPL (as confirmed by direct overlap or ROI analysis) exhibits repetition suppression to a common target of a reaching motion, across kinematics/movement direction (Hamilton and Grafton, 2006, 2008), and allows cross-effector and cross-modal classification of various concrete actions, such as tilting vs. lifting, opening vs. closing, or getting vs. pushing away (Jastorff et al., 2010; Oosterhof et al., 2012; Oosterhof et al., 2010; Wurm and Lingnau, 2014). These previously reported data already suggest that the lateral portion of aIPL represents not hand or body movement, but the end-point or outcome of an action. However, without an extension to non-concrete outcomes as in the present study, these previous results could have been explained in sensory terms as representations of physical events, concrete objects, or their physical states resulting from an action. Our findings thus push further the account that aIPL, at least in its lateral aspect near SMG, computes conceptual representations of outcomes/purposes.

<sup>2</sup> In fact, without a thorough understanding of the functional properties of tools, it is unclear whether even the contrast manipulable > non-manipulable objects isolates manipulation knowledge specifically, because, perhaps, manipulable objects—such as hammers—may also have more specific and thus less variable functions relative to arbitrarily manipulable objects such as houses and books (Mahon et al., 2007).

Whether the difference between the more lateral and more medial aspects of aIPL is systematic and meaningful has yet to be established. Nonetheless, a plausible account of the anterior IPL, based on this brief review, is that it contains various types of representations, including those concerning manipulation (whether conceptual or motoric) and those concerning function/purpose. Representations in this area seem to be accessible from multiple input modalities, but as discussed in the Introduction, this is not enough to establish that they are conceptual. Our result, showing sensitivity to a kind of content that does not coincide with any motoric or sensory quality, is evidence for a conceptual account.

#### 4.3. Implications for the organizational principles of semantic knowledge

The broader question arising from this finding is: why do function/purpose representations land where they do, and more precisely, why is function represented near manipulation in aIPL? This spatial arrangement is not likely accidental. But it is also not predicted by existing accounts of the neural organization of attribute knowledge. An account of organization should explain in general, on what basis is content within the semantic system divided, and by what principles is it localized in cortex? Some accounts of semantic organization propose that concepts are localized according to the sensory/motor modality with which they are associated, such that, for instance, conceptual knowledge referring to properties typically perceived by vision, should be stored together and near visual-perceptual processing areas (Martin, 2007; Patterson et al., 2007; Thompson-Schill, 2003).

As argued above, the functional properties we describe in this experiment do not denote or correlate with body movement or manipulation properties. Although the manipulation and function of particular objects can correlate, they are also independent enough to be dissociated, as in the present experiment. Furthermore, the function of an object is not more related to its manipulation than it is to its shape. Nor is it the case that function is simply a more generalized version of manipulation, because these attribute types specify different dimensions of similarity. For example, an abstract category of manipulation might include a large variety of object-based actions, all involving squeezing with the hand (e.g., using a garlic press and a stapler), but these do not pick out a category of functions. The function *attaching*, on the other hand, even if comprised of many particular object uses (stapling, gluing, hammering), binds together events on the basis of their intended outcomes, and not the body movements involved. In sum, function and manipulations categories are each formed on a different basis, which do not share a common sensory channel.

Indeed, if there were any ‘modality’ to assign to functions, it would be the same as that of other abstract concepts. But it does not appear that function is represented in a common location with other abstract content, because content-general abstract knowledge activates entirely different, albeit variable, regions (Binder et al., 2005; Bright et al., 2007; Cappa et al., 1998; Goldberg et al., 2007; Noppeney and Price, 2002; Rodríguez-Ferreiro et al., 2011; Skipper and Olson, 2013), and, furthermore, other specific kinds of abstract contents have been reported elsewhere (Breining and Rapp, 2011; Koster-Hale et al., 2013; Mitchell et al., 2009; Skerry and Saxe, in press; Zahn et al., 2007). In sum, of the abstract representations tested, aIPL appears to respond only to functions.

The clearest and simplest account, therefore, is that function and manipulation are represented together in aIPL because they serve related roles in cognition: in selecting and using artifacts to achieve goals. We begin actions with broadly defined goals—*protect, learn, communicate*—before selecting the right objects to accomplish them, and before planning the specific body movements or manipulations to undertake. Selecting tools for action requires

reference to their functions at this general level, while actually using them requires manipulation (though many can continue to accomplish their roles without our intervention: e.g., a fountain can decorate a garden without our involvement). Function and manipulation thus participate in a shared stream of processing, that for using tools, despite being about different kinds of sensory-motor qualities (if any).

In sum, the pattern of results we have reported is not accounted for by a framework in which conceptual knowledge is organized strictly by sensory-motor modality, or even by a concrete/abstract distinction. We suggest instead that attribute knowledge is organized and localized in the brain by virtue of the computations it serves. This is simultaneously broader and more precise than a sensory/motor account. It is broader because it can subsume organization by modality; yet it is more precise because of its clearer articulation of why certain contents should be related, because it can explain the organization of non-sensory content, and because it requires the formulation of theories of information exchange and of how computational demands constrain neural localization, such as the connectivity hypothesis of domain-specificity (Mahon and Caramazza, 2008, 2011). It thus has the possibility of explaining the organization of other kinds of abstract concepts, a topic for future research.

#### 4.4. Ambiguities and caveats: functions or purposes?

If not all of abstract knowledge, what is the scope of the representations in aIPL? Our data leave open the question of whether its representations are specific to functions (purposes that belong to artifacts) or are broader, perhaps including the purposes of actions. On the one hand, *protect* and *decorate* are the same concepts, regardless if achieved with tools or with the body. Furthermore, some neuropsychological findings have been used to propose the existence of a common system for artifact and action knowledge, specifically on the basis that they are both purposeful (Pillon and D’Honinckthun, 2011; Vannuscorps and Pillon, 2011). On the other hand, the SMG (at our coordinates) appears to be selective for representing tool-enacted relative to hand-enacted actions, keeping the action constant (e.g., grasping; Gallivan et al., 2013; Peeters et al., 2009, 2013). Lastly, attending to the purpose of an action appears to activate a more posterior part of IPL, near the angular gyrus, relative to attending to how that action is accomplished, which activates anterior IPL (Hesse et al., 2009; Nicholson et al., 2013; Spunt and Lieberman, 2012; Spunt et al., 2011a, 2011b). This implies that action goals may be processed more posteriorly than functions. This distinction may be because, relative to an action goal, an object is effectively a means: for one to protect oneself from the rain, one can do so by using an object with that function. This broader understanding of functions as an abstract instance of *how-knowledge* is another way of understanding their broader commonality with manipulation.

Finally, one might ask whether the representations described in aIPL really capture what is meant by ‘function’, which should be expected to capture not only concepts of functions such as *protect* and *decorate*, but also represent their links to objects—the knowledge that an umbrella can protect from the rain, but a necklace cannot. While the main results of our analysis do not speak to this representational property, our findings do serve to identify a neural locus where one can further test these more elaborate representational capacities.

#### 4.5. Overall conclusion

How conceptual knowledge is distributed through the brain has been a central question in the cognitive neuroscience of semantic memory. Prior findings have suggested that such

organization is principled, but the exact nature of these principles is open to further inquiry. To make progress on this question, one must distinguish semantic from sensory memory systems, and should not assume too readily that the organizational principles of one are mirrored in the other. By using categories that are both general and not systematically co-extensive with sensory properties, we have been able to ascribe a conceptual role to a portion of the anterior parietal cortex, a role that is relatively specific in content. While we can only speculate about the exact reasons this content is found here—adjacent to other, more concrete tool use knowledge—we have argued that it is there not by virtue of being about a given sensory/motor modality of information, but because both kinds of knowledge serve the computations required for using tools. This suggests a principle of organization of the semantic system that diverges from that of sensory-motor systems.

## Acknowledgements

This work was supported by the Natural Sciences and Engineering Council of Canada and the Norman Anderson Fund at Harvard University (to A.L.). We thank Stefano Anzellotti for help with fMRI design optimization, Talia Konkle for helping design the kinematic measurements, Cheng Li for assistance with data collection, and Nick Oosterhof for guidance with the surface searchlight analysis.

## References

- Bar, M., Aminoff, E., 2003. Cortical analysis of visual context. *Neuron* 38 (2), 347–358.
- Binder, J.R., Westbury, C.F., McKiernan, K.A., Possing, E.T., Medler, D.A., 2005. Distinct brain systems for processing concrete and abstract concepts. *J. Cogn. Neurosci.* 17 (6), 905–917.
- Binkofski, F., Buxbaum, L.J., 2013. Two action systems in the human brain. *Brain Lang.* 127 (2), 222–229. <http://dx.doi.org/10.1016/j.bandl.2012.07.007>.
- Bloom, P., 1996. Intention, history, and artifact concepts. *Cognition* 60, 1–29.
- Blundo, C., Ricci, M., Miller, L., 2006. Category-specific knowledge deficit for animals in a patient with herpes simplex encephalitis. *Cogn. Neuropsychol.* 23 (8), 1248–1268. <http://dx.doi.org/10.1080/02643290600896449>.
- Boronat, C.B., Buxbaum, L.J., Coslett, H.B., Tang, K., Saffran, E.M., Kimberg, D.Y., Detre, J.A., 2005. Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. *Cogn. Brain Res.* 23, 361–373.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10 (4), 433–436.
- Breining, B., Rapp, B., 2011. Neural distinctions between categories of abstract and concrete words: a multi-voxel pattern analysis. In Proceedings of the Poster presented at the Third Annual Neurobiology of Language Meeting, November 10–11, 2011, Annapolis, MD, USA.
- Bright, P., Moss, H.E., Longe, O., Stamatakis, E.A., Tyler, L.K., 2007. Conceptual structure modulates anteromedial temporal involvement in processing verbally presented object properties. *Cereb. Cortex* 17, 1066–1073.
- Buxbaum, L.J., Veramontil, T., Schwartz, M.F., 2000. Function and manipulation tool knowledge in apraxia: knowing “what for” but not “how”. *Neurocase* 6 (2), 83–97. <http://dx.doi.org/10.1080/13554790008402763>.
- Cabeza, R., Ciaramelli, E., Moscovitch, M., 2012. Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. *Trends Cogn. Sci.* 16 (6), 338–352. <http://dx.doi.org/10.1016/j.tics.2012.04.008>.
- Canessa, N., Borgo, F., Cappa, S.F., Perani, D., Falini, A., Buccino, G., Shallice, T., 2008. The different neural correlates of action and functional knowledge in semantic memory: an fMRI study. *Cereb. Cortex* 18 (4), 740–751. <http://dx.doi.org/10.1093/cercor/bhm110>.
- Cappa, S.F., Perani, D., Schnur, T., Tettamanti, M., Fazio, F., 1998. The effects of semantic category and knowledge type on lexical-semantic access: a PET study. *NeuroImage* 8 (4), 350–359. <http://dx.doi.org/10.1006/nimg.1998.0368>.
- Caramazza, A., Shelton, J.R., 1998. Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *J. Cogn. Neurosci.* 10 (1), 1–34.
- Caspers, S., Schleicher, A., Bacha-Trams, M., Palomero-Gallagher, N., Amunts, K., Zilles, K., 2013. Organization of the human inferior parietal lobe based on receptor architectonics. *Cereb. Cortex* 23 (3), 615–628. <http://dx.doi.org/10.1093/cercor/bhs048>.
- Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage* 50 (3), 1148–1167. <http://dx.doi.org/10.1016/j.neuroimage.2009.12.112>.
- Chao, L.L., Haxby, J.V., Martin, A., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat. Neurosci.* 2 (10), 913–919.
- Chao, L.L., Martin, A., 2000. Representation of manipulable man-made objects in the dorsal stream. *NeuroImage* 12 (4), 478–484. <http://dx.doi.org/10.1006/nimg.2000.0635>.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.: Int. J.* 29 (3), 162–173.
- Dinstein, I., Hasson, U., Rubin, N., Heeger, D.J., 2007. Brain areas selective for both observed and executed movements. *J. Neurophysiol.* 98 (3), 1415–1427. <http://dx.doi.org/10.1152/jn.00238.2007>.
- Fairhall, S., Anzellotti, S., Ubaldi, S., Caramazza, A., 2013. Person- and place-selective neural substrates for entity-specific semantic access. *Cereb. Cortex* 24 (7), 1687–1696. <http://dx.doi.org/10.1093/cercor/bht093>.
- Fischl, B., Sereno, M.I., Tootell, R.B., Dale, A.M., 1999. High-resolution intersubject averaging and a coordinate system for the cortical surface. *Hum. Brain Mapp.* 8 (4), 272–284.
- Freedman, D.J., Miller, E.K., 2008. Neural mechanisms of visual categorization: insights from neurophysiology. *Neurosci. Biobehav. Rev.* 32 (2), 311–329. <http://dx.doi.org/10.1016/j.neubiorev.2007.07.011>.
- Futó, J., Téglás, E., Csibra, G., Gergely, G., 2010. Communicative function demonstration induces kind-based artifact representation in preverbal infants. *Cognition* 117 (1), 1–8. <http://dx.doi.org/10.1016/j.cognition.2010.06.003>.
- Gallivan, J.P., McLean, D.A., Flanagan, J.R., Culham, J.C., 2013. Where one hand meets the other: limb-specific and action-dependent movement plans decoded from preparatory signals in single human frontoparietal brain areas. *J. Neurosci.* 33 (5), 1991–2008. <http://dx.doi.org/10.1523/JNEUROSCI.0541-12.2013>.
- Gallivan, J.P., McLean, D.A., Valyear, K.F., Culham, J.C., 2013. Decoding the neural mechanisms of human tool use. *eLife* 2. <http://dx.doi.org/10.7554/eLife.00425> (e00425–e00425).
- Garcea, F.E., Mahon, B.Z., 2012. What is in a tool concept? Dissociating manipulation knowledge from function knowledge. *Mem. Cogn.* 40 (8), 1303–1313. <http://dx.doi.org/10.3758/s13421-012-0236-y>.
- Goldberg, R.F., Perfetti, C.A., Fiez, J.A., Schneider, W., 2007. Selective retrieval of abstract semantic knowledge in left prefrontal cortex. *J. Neurosci.* 27 (14), 3790–3798.
- Goldberg, R.F., Perfetti, C.A., Schneider, W., 2006. Perceptual knowledge retrieval activates sensory brain regions. *J. Neurosci.* 26 (18), 4917–4921. <http://dx.doi.org/10.1523/JNEUROSCI.5389-05.2006>.
- Goldenberg, G., 2009. Apraxia and the parietal lobes. *Neuropsychologia* 47 (6), 1449–1459. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.07.014>.
- Gutheil, G., Bloom, P., Valderrama, N., Freedman, R., 2004. The role of historical intuitions in children's and adults' naming of artifact. *Cognition* 91 (1), 23–42. [http://dx.doi.org/10.1016/S0010-0277\(03\)00165-3](http://dx.doi.org/10.1016/S0010-0277(03)00165-3).
- Hamilton, A.F.D.C., Grafton, S.T., 2006. Goal representation in human anterior intraparietal sulcus. *J. Neurosci.* 26 (4), 1133–1137. <http://dx.doi.org/10.1523/JNEUROSCI.4551-05.2006>.
- Hamilton, A.F.D.C., Grafton, S.T., 2008. Action outcomes are represented in human inferior frontoparietal cortex. *Cereb. Cortex* 18 (5), 1160–1168. <http://dx.doi.org/10.1093/cercor/bhm150>.
- Haxby, J.V., Gobbini, M.L., Furey, M.L., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430.
- Hesse, M.D., Sparing, R., Fink, G.R., 2009. End or means—the “what” and “how” of observed intentional actions. *J. Cogn. Neurosci.* 21 (4), 776–790. <http://dx.doi.org/10.1162/jocn.2009.21058>.
- Hillis, A.E., Caramazza, A., 1991. Category-specific naming and comprehension impairment: a double dissociation. *Brain: J. Neurol.* 114 (Pt 5), 2081–2094.
- Humphreys, G.F., Lambon Ralph, M.A., 2014. Fusion and fission of cognitive functions in the human parietal cortex. *Cereb. Cortex*, Sept 9 2014 (epub). <http://dx.doi.org/10.1093/cercor/bhu198>.
- Hutchinson, J.B., Uncapher, M.R., Weiner, K.S., Bressler, D.W., Silver, M. a, Preston, A.R., Wagner, A.D., 2014. Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cereb. Cortex* 24 (1), 49–66. <http://dx.doi.org/10.1093/cercor/bhs278>.
- Jastorff, J., Begliomini, C., Fabbri-Destro, M., Rizzolatti, G., Orban, G.A., 2010. Coding observed motor acts: different organizational principles in the parietal and premotor cortex of humans. *J. Neurophysiol.* 104 (1), 128–140. <http://dx.doi.org/10.1152/jn.00254.2010>.
- Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. *Trends Cogn. Sci.* 8 (2), 71–78. <http://dx.doi.org/10.1016/j.tics.2003.12.002>.
- Kable, J.W., Kan, I.P., Wilson, A., Thompson-Schill, S.L., Chatterjee, A., 2005. Conceptual representations of action in the lateral temporal cortex. *J. Cogn. Neurosci.* 17 (12), 1855–1870. <http://dx.doi.org/10.1162/089892905775008625>.
- Kable, J.W., Lease-Spellmeyer, J., Chatterjee, A., 2002. Neural substrates of action event knowledge. *J. Cogn. Neurosci.* 14 (5), 795–805. <http://dx.doi.org/10.1162/08989290260138681>.
- Kelemen, D., Carey, S., 2007. The essence of artifacts: developing the design stance. In: Laurence, S., Margolis, E. (Eds.), *Creations of the Mind: Artifacts and their representation*. Oxford University Press, Oxford, pp. 415–449.
- Kellenbach, M.L., Brett, M., Patterson, K., 2001. Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cogn. Affect. Behav. Neurosci.* 1 (3), 207–221.
- Kellenbach, M.L., Brett, M., Patterson, K., 2003. Actions speak louder than functions: the importance of manipulability and action in tool representation. *J. Cogn. Neurosci.* 15 (1), 30–46.
- Koski, L., Iacoboni, M., Mazziotta, J.C., 2002. Deconstructing apraxia: understanding

- disorders of intentional movement after stroke. *Curr. Opin. Neurol.* 15 (1), 71–77.
- Koster-Hale, J., Saxe, R., Dungan, J., Young, L.L., 2013. Decoding moral judgments from neural representations of intentions. *Proc. Natl. Acad. Sci. USA* 110 (14), 8437–8439. <http://dx.doi.org/10.1073/pnas.1207992110/DCSupplemental>. [www.pnas.org/cgi/doi/10.1073/pnas.1207992110](http://www.pnas.org/cgi/doi/10.1073/pnas.1207992110).
- Kriegeskorte, N., Formisano, E., Sorger, B., Goebel, R., 2007. Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proc. Natl. Acad. Sci. USA* 104, 20600–20605.
- Laiacona, M., Capitani, E., Barbarotto, R., Foundation, S.M., Hospital, S.P., 1997. Semantic category dissociations: a longitudinal study of two cases. *Cortex* 33 (4), 441–461.
- Lambon-Ralph, M.A., Howard, D., Nightingale, G., Ellis, A., 1998. Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? evidence from a category-specific double dissociation. *Neurocase* 4 (4), 311–338. <http://dx.doi.org/10.1080/13554799808410630>.
- Leshinskaya, A., Caramazza, A., 2014. Nonmotor aspects of action concepts. *J. Cogn. Neurosci.* 26 (12), 2863–2879.
- Lestou, V., Pollick, F.E., Kourtzi, Z., 2008. Neural substrates for action understanding at different description levels in the human brain. *J. Cogn. Neurosci.* 20 (2), 324–341. <http://dx.doi.org/10.1162/jocn.2008.20021>.
- Lombrozo, T., 2009. Explanation and categorization: how “why?” informs “what”. *Cognition* 110 (2), 248–253. <http://dx.doi.org/10.1016/j.cognition.2008.10.007>.
- Luzzatti, C., Davidoff, J., 1994. Impaired retrieval of object-colour knowledge with preserved colour naming. *Neuropsychologia* 32 (8), 933–950.
- Mahon, B.Z., Caramazza, A., 2008. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol. (Paris)* 102, 59–70. <http://dx.doi.org/10.1016/j.jphysparis.2008.03.004>.
- Mahon, B.Z., Caramazza, A., 2011. What drives the organization of object knowledge in the brain? *Trends Cogn. Sci.* 15 (3), 97–103. <http://dx.doi.org/10.1016/j.tics.2011.01.004>.
- Mahon, B.Z., Milleville, S.C., Negri, G. a. L., Rumiat, R.I., Caramazza, A., Martin, A., 2007. Action-related properties shape object representations in the ventral stream. *Neuron* 55 (3), 507–520. <http://dx.doi.org/10.1016/j.neuron.2007.07.011>.
- Mahon, B.Z., Schwarzbach, J., Caramazza, A., 2010. The representation of tools in left parietal cortex is independent of visual experience. *Psychol. Sci.* 21 (6), 764–771. <http://dx.doi.org/10.1177/0956797610370754>.
- Martin, A., 2007. The representation of object concepts in the brain. *Annu. Rev. Psychol.* 58, 25–45. <http://dx.doi.org/10.1146/annurev.psych.57.102904.190143>.
- Martin, A., Chao, L.L., 2001. Semantic memory and the brain: structure and process. *Curr. Opin. Neurobiol.* 11, 194–201.
- Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L.G., Lalonde, F.M., Ungerleider, L.G., 1995. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270 (5233), 102–105.
- Miceli, G., Fouch, E., Capasso, R., Shelton, J.R., Tomaiuolo, F., Caramazza, A., 2001. The dissociation of color from form and function knowledge. *Nat. Neurosci.* 4 (6), 662–667. <http://dx.doi.org/10.1038/88497>.
- Mitchell, J.P., Ames, D.L., Jenkins, A.C., Banaji, M.R., 2009. Neural correlates of stereotype application. *J. Cogn. Neurosci.* 21 (3), 594–604. <http://dx.doi.org/10.1162/jocn.2009.21033>.
- Mur, M., Bandettini, P.A., Kriegeskorte, N., 2009. Revealing representational content with pattern-information fMRI: an introductory guide. *Soc. Cogn. Affect. Neurosci.* 4, 101–109.
- Newman-Norlund, R., van Schie, H.T., van Hoek, M.E.C., Cuijpers, R.H., Bekkering, H., 2010. The role of inferior frontal and parietal areas in differentiating meaningful and meaningless object-directed actions. *Brain Res.* 1315, 63–74. <http://dx.doi.org/10.1016/j.brainres.2009.11.065>.
- Nicholson, T., Roser, M., Bach, P., 2013. Action goal understanding is primarily driven by object, not motor, information. In: Proceedings of the Poster presented at the Rovereto Workshop on Concepts, Actions and Objects, 23–28 May 2013.
- Noppeney, U., Price, C.J., 2002. Retrieval of visual, auditory, and abstract semantics. *NeuroImage* 15 (4), 917–926. <http://dx.doi.org/10.1006/nimg.2001.1016>.
- Ochipa, C., Rothi, L.J.G., Heilman, K.M., 1989. Ideational apraxia: a deficit in tool selection and use. *Ann. Neurol.* 25, 190–193.
- Ochipa, C., Rothi, L.J.G., Heilman, K.M., 1992. Conceptual apraxia in alzheimer's. *Brain* 115, 1061–1071.
- Oosterhof, N.N., Tipper, S.P., Downing, P.E., 2012. Viewpoint (In)dependence of action representations: an MVPA study. *J. Cogn. Neurosci.* 24 (4), 975–989. [http://dx.doi.org/10.1162/jocn\\_a\\_00195](http://dx.doi.org/10.1162/jocn_a_00195).
- Oosterhof, N.N., Wiestler, T., Downing, P.E., Diedrichsen, J., 2011. A comparison of volume-based and surface-based multi-voxel pattern analysis. *NeuroImage* 56 (2), 593–600. <http://dx.doi.org/10.1016/j.neuroimage.2010.04.270>.
- Oosterhof, N.N., Wiggett, A.J., Diedrichsen, J., Tipper, S.P., Downing, P.E., 2010. Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *J. Neurophysiol.* 104 (2), 1077–1089. <http://dx.doi.org/10.1152/jn.00326.2010>.
- Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8 (December), 976–989. <http://dx.doi.org/10.1038/nrn2277>.
- Peelen, M.V., Caramazza, A., 2012. Conceptual object representations in human anterior temporal cortex. *J. Neurosci.* 32 (45), 15728–15736. <http://dx.doi.org/10.1523/JNEUROSCI.1953-12.2012>.
- Peeters, R., Rizzolatti, G., Orban, G.A., 2013. Functional properties of the left parietal tool use region. *NeuroImage* 78, 83–93. <http://dx.doi.org/10.1016/j.neuroimage.2013.04.023>.
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2009. The representation of tool use in humans and monkeys: common and uniquely human features. *J. Neurosci.* 29 (37), 11523–11539. <http://dx.doi.org/10.1523/JNEUROSCI.2040-09.2009>.
- Phillips, J.A., Noppeney, U., Humphreys, G.W., Price, C.J., 2002. Can segregation within the semantic system account for category-specific deficits? *Brain: J. Neurol.* 125, 2067–2080.
- Pillon, A., D'Honin, P., 2011. A common processing system for the concepts of artifacts and actions? Evidence from a case of a disproportionate conceptual impairment for living things. *Cogn. Neuropsychol.* 28 (1), 37–41.
- Rey, G., 1983. Concepts and stereotypes. *Cognition* 15, 237–262.
- Rodríguez-Ferreiro, J., Gennari, S.P., Davies, R., Cuetos, F., 2011. Neural correlates of abstract verb processing. *J. Cogn. Neurosci.* 23 (1), 106–118. <http://dx.doi.org/10.1162/jocn.2010.21414>.
- Simmons, W.K., Martin, A., Barsalou, L.W., 2005. Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cereb. Cortex* 15 (10), 1602–1608. <http://dx.doi.org/10.1093/cercor/bhi038>.
- Sirigu, A., Duhamel, J.-R., Poncet, M., 1991. The role of sensorimotor experience in object recognition. *Brain* 114 (6), 2555–2573. <http://dx.doi.org/10.1093/brain/114.6.2555>.
- Skerry, A.E., Saxe, R., 2014. A common neural code for perceived and inferred emotion. *J. Neurosci.* 34 (48), 15997–16008. <http://dx.doi.org/10.1523/JNEUROSCI.14676-14.2014>.
- Skipper, L.M., Olson, I.R., 2013. Connectivity of cortical networks supporting social and nonsocial, abstract and concrete conceptual knowledge. In: Proceedings of the Poster Presented at the Annual Meeting of the Society for Cognitive Neuroscience, 13–16 April 2013. San Francisco. 10.1093/cercor/bht025.
- Spunt, R.P., Lieberman, M.D., 2012. Dissociating modality-specific and supramodal neural systems for action understanding. *J. Neurosci.* 32 (10), 3575–3583. <http://dx.doi.org/10.1523/JNEUROSCI.5715-11.2012>.
- Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011a. Dissociable neural systems support retrieval of how and why action knowledge. *J. Cogn. Neurosci.* 23 (1), 63–74. <http://dx.doi.org/10.1177/0956797610386618>.
- Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011b. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. *J. Cogn. Neurosci.* 23 (1), 63–74. <http://dx.doi.org/10.1162/jocn.2010.21446>.
- Swaminathan, S.K., Freedman, D.J., 2012. Preferential encoding of visual categories in parietal cortex compared with prefrontal cortex. *Nat. Neurosci.* 15 (2), 315–320. <http://dx.doi.org/10.1038/nn.3016>.
- The MathWorks Inc, 2009. MATLAB Release 2009b. The MathWorks, Inc, Natick, Massachusetts.
- Thompson-Schill, S.L., 2003. Neuroimaging studies of semantic memory: Inferring “how” from “where”. *Neuropsychologia* 41, 280–292.
- Träuble, B., Pauen, S., 2007. The role of functional information for infant categorization. *Cognition* 105 (2), 362–379. <http://dx.doi.org/10.1016/j.cognition.2006.10.003>.
- Träuble, B., Pauen, S., 2011. Cause or effect: what matters? How 12-month-old infants learn to categorize artifacts. *Br. J. Dev. Psychol.* 29 (Pt 3), 357–374. <http://dx.doi.org/10.1348/026151009X479547>.
- Tunik, E., Rice, N.J., Hamilton, A., Grafton, S.T., 2007. Beyond grasping: representation of action in human anterior intraparietal sulcus. *NeuroImage* 36 (Suppl 2), T77–T86. <http://dx.doi.org/10.1016/j.neuroimage.2007.03.026>.
- Tyler, L.K., Moss, H.E., 1997. Functional properties of concepts: Studies of normal and brain-damaged patients. *Cogn. Neuropsychol.* 14 (4), 511–545.
- Valyear, K.F., Cavina-Pratesi, C., Stiglick, A.J., Culham, J.C., 2007. Does tool-related fMRI activity within the intraparietal sulcus reflect the plan to grasp? *NeuroImage* 36 (Suppl 2), T94–T108. <http://dx.doi.org/10.1016/j.neuroimage.2007.03.031>.
- Valyear, K.F., Culham, J.C., 2010. Observing learned object-specific functional grasps preferentially activates the ventral stream. *J. Cogn. Neurosci.* 22 (5), 970–984.
- Valyear, K.F., Gallivan, J.P., McLean, D. a., Culham, J.C., 2012. fMRI repetition suppression for familiar but not arbitrary actions with tools. *J. Neurosci.* 32 (12), 4247–4259. <http://dx.doi.org/10.1523/JNEUROSCI.5270-11.2012>.
- Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *NeuroImage* 48 (3), 564–584. <http://dx.doi.org/10.1016/j.neuroimage.2009.06.009>.
- Vandenbulcke, M., Peeters, R., Fannes, K., Vandenberghe, R., 2006. Knowledge of visual attributes in the right hemisphere. *Nat. Neurosci.* 9 (7), 964–970. <http://dx.doi.org/10.1038/nn1721>.
- Vannuscorps, G., Pillon, A., 2011. A domain-specific system for representing knowledge of both man-made objects and human actions. Evidence from a case with an association of deficits. *Neuropsychologia* 49 (9), 2321–2341. <http://dx.doi.org/10.1016/j.neuropsychologia.2011.04.006>.
- Vingerhoets, G., Vandekerckhove, E., Honoré, P., Vandemaele, P., Achten, E., 2011. Neural correlates of pantomiming familiar and unfamiliar tools: action semantics versus mechanical problem solving? *Hum. Brain Mapp.* 32 (6), 905–918. <http://dx.doi.org/10.1002/hbm.21078>.
- Warrington, E.K., Shallice, T., 1984. Category-specific semantic impairments. *Brain* 107, 829–854. <http://dx.doi.org/10.1016/j.neuropsychologia.2007.11.018>.
- Watson, C., Cardillo, E., Ianni, G., Chatterjee, A., 2013. Action concepts in the brain: an activation-likelihood estimation meta-analysis. *J. Cogn. Neurosci.* 25 (8), 1191–1205. <http://dx.doi.org/10.1162/jocn>.
- Weisberg, J., van Turenout, M., Martin, A., 2007. A neural system for learning about object function. *Cereb. Cortex* 17 (3), 513–521. <http://dx.doi.org/10.1093/cercor/bhj176>.

- Wheaton, L.A., Hallett, M., 2007. Ideomotor apraxia: a review. *J. Neurol. Sci.* 260 (1–2), 1–10. <http://dx.doi.org/10.1016/j.jns.2007.04.014>.
- Wurm, M.F., Lingnau, A., 2014. Decoding action concepts at different levels of abstraction: an MVPA study. In: Proceedings of the Poster Presented at the Annual Meeting of the Cognitive Neuroscience Society, 5–8 April 2014. Boston, Massachusetts.
- Zahn, R., Moll, J., Krueger, F., Huey, E.D., Garrido, G., Grafman, J., 2007. Social concepts are represented in the superior anterior temporal cortex. *Proc. Natl. Acad. Sci. USA* 104 (15), 6430–6435. <http://dx.doi.org/10.1073/pnas.0607061104>.