

Nonmotor Aspects of Action Concepts

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Abstract

■ Reading an action verb elicits the retrieval of its associated body movements as well as its typical goal—the outcome to which it is directed. Two fMRI experiments are reported in which retrieval of goal attributes was isolated from retrieval of motoric ones by contrasting actions that are either done intentionally (e.g., drink) and thus have associated goal information or by accident (e.g., hiccup). Orthogonally, the actions also varied in their motoricity (e.g., drink vs. imagine). Across both levels of motoricity, goal-directedness influenced the activity of a portion of left posterior inferior parietal lobe (pIPL). These effects were not explicable by the grammatical properties, imageability, or amount of body movement associated with these different types

of verbs. In contrast, motoricity (across levels of goal-directedness) activated primarily the left middle temporal gyrus. Furthermore, pIPL was found to be distinct from the portion of left parietal lobe implicated in theory of mind, as localized in the same participants. This is consistent with the observation that pIPL contains many functionally distinct subregions and that some of these support conceptual knowledge. The present findings illustrate that, in particular, the pIPL is involved in representing attributes of intentional actions, likely their typical goals, but not their associated body movements. This result serves to describe an attribute-selective semantic subsystem for at least one type of nonmotor aspect of action knowledge. ■

INTRODUCTION

The human mind has the special ability to represent attributes and ideas not directly available to the senses. We form categories of objects not only on the basis of how they appear but also on how they came to be (Gutheil, Bloom, Valderrama, & Freedman, 2004; Bloom & Markson, 1998; Keil, Smith, Simons, & Levin, 1998; Gelman & Wellman, 1991) and what they are for (Garcea & Mahon, 2012; Träuble & Pauen, 2007, 2011; Kemler Nelson, Franken, Morris, & Blair, 2000). Such properties seem to matter as much, if not more, than concrete ones (Kelemen & Carey, 2007; Bloom, 1996). In a similar vein, what we know about categories of actions includes not only how our body moves to accomplish them but also to what end they are performed (i.e., their goals). Goal attributes form an essential part of the meaning of many action concepts—for instance, that the concept “to teach” denotes the aim of imparting knowledge. Some goals are concrete, but many are not: Learning, communicating, and having fun are all desired states that occur in interpersonal or mental, rather than physical, space. Neuroscience research on conceptual knowledge has focused largely on observable, concrete properties of objects and action concepts (Binder & Desai, 2011; Beauchamp & Martin, 2007; Martin, 2007; Vigliocco & Vinson, 2007; Martin & Chao, 2001), leaving unresolved the mystery of how we are able to encode such abstract

conceptual attributes as goals and which regions might be involved.¹ The aim of the present experiments is to take a step toward elucidating these questions.

There is already strong indication that some sensory attributes of things are neurally dissociable from their nonobservable attributes. This comes from studies of patients who have lost their knowledge for how objects are typically manipulated, but who maintain an understanding of what they are designed to do, or vice versa (Buxbaum, Veramontil, & Schwartz, 2000; Sirigu, Duhamel, & Poncet, 1991; Ochipa, Rothi, & Heilman, 1989; De Renzi & Lucchelli, 1988). These data also illustrate the remarkable content specificity within the brain’s semantic systems, making it unlikely that all abstract knowledge is stored in a single locus. It seems also likely that, by analogy to the patient findings about function, there are distinct systems for knowledge of how to execute actions and their goals.²

From an fMRI perspective, regions that process non-sensory, intention-related aspects of action knowledge should respond more when there is increased information about intention, given equal amounts of information about body movement. They should also do so equally for concrete, motoric actions as for nonmotoric ones. Although in motoric actions, goals are tightly related to how the body moves (e.g., to kick a ball, one must kick a ball), these factors are separable when including a broader range of actions. Even for many motoric actions, the same goal can be accomplished in many ways (e.g., *make coffee*). Furthermore, in the case of nonmotoric action concepts, achieving the intended outcome is either

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unrelated to particular body movements (e.g., *teach*) or requires no movements at all (e.g., *daydream*). This makes it possible to manipulate the amount of intention information and the amount of motoric information conveyed by an action verb. This is precisely what was done in the present experiments. The factor of intentionality was manipulated by comparing actions typically done with some goals in mind (e.g., *kick*) to ones that are performed by accident and thus specify no goal information (e.g., *slip*), controlling for the amount of body movement. The same manipulation was also constructed using non-motoric verbs (e.g., *teach* vs. *forget*). The effect of increased goal information was measured independently of the amount of motor information in both motor and nonmotor verbs. This should allow the identification of regions that process nonsensory, intention-related aspects of action concepts independently of motoric knowledge.

Previous work on action recognition has, of course, studied goal processing, but most of this work aimed to understand how concrete actions are recognized from visual input, rather than what knowledge we store about action concepts per se. In the most closely related category of studies, action videos were presented and participants were directed to think about either the goal or manner of execution of those actions (Nicholson, Roser, & Bach, 2013; Lingnau & Petris, 2012; Hesse, Sparing, & Fink, 2009; De Lange, Spronk, Willems, Toni, & Bekkering, 2008; Majdandzić et al., 2007; Ruby, Sirigu, & Decety, 2002). In two cases, this was done with verbally described actions, but most were still concrete (Spunt & Lieberman, 2012; Spunt, Satpute, & Lieberman, 2011). The most consistent finding across this set of work is increased signal in the left or bilateral TPJ when attending to goal compared with the manner of execution. However, although the same stimuli were used in the goal and execution conditions, there are a few reasons that these studies do not serve to identify motor-independent goal processing.

For one, almost all of the actions presented were motoric: Their intended outcomes are fairly concrete physical events. The resulting effects might therefore be specific to concrete actions. Furthermore, in studies using action videos, different features of the same actions might be highlighted when attending to goals versus means (for instance, target location of a reach vs. the effector). Lastly, often the goal conditions required participants to explicitly think about why an actor performed a certain action, given some observed or described behavior, and thus posing additional demands on the process of inferring a particular actor's mental states ("mentalizing"), whether from visible or described actions in a particular situation. It is thus difficult to disentangle retrieval of stored, conceptual goal knowledge from the inferential process of mentalizing in these studies. This makes it unsurprising that many of them found activation in regions largely resembling the theory of mind network. This network is commonly localized by having participants read false belief stories, which requires inferences about

mental states, and contrasting those to stories about false photographs or other nonmental representations (Saxe & Kanwisher, 2003). This localizer is targeted primarily to processes of mental state inference rather than semantic knowledge of actions. However, it is possible that some parts of the theory of mind network do represent conceptual knowledge of action intentions, regardless of particular reasoning demands. After all, such semantic knowledge would be useful in understanding false belief scenarios, almost all of which include goal-directed actions.

To isolate conceptual processing of action intentions from mentalizing, the present task made minimal demands on inferring a mental state from observed behavior. Participants simply read names of actions conjugated in the first person (e.g., *I run*) and made judgments about how frequently they (themselves) experienced doing each of these actions. Participants were also given theory of mind localizer scans to assess how the various regions in the typical theory of mind network responded to the goal-directedness of actions. This was done to help clarify the relationship between these regions and semantic knowledge of actions.

METHODS

Experiment 1

fMRI Participants

Fourteen right-handed, neurologically healthy native Italian speakers (3 men; ages 20–27 years, mean age = 23 years) participated in the fMRI experiment. One was excluded for excessive head motion. All participants provided informed consent in writing. Procedures were approved by the institutional review board at both Harvard University and the University of Trento.

Stimuli

Stimuli were names of actions, presented as Italian verbs preceded by a first-person pronoun (e.g., *I pedal*). There were four types of actions: goal-directed motor (+Motor +Goal), goal-directed nonmotor (−Motor+Goal), accidental motor (+Motor−Goal), and accidental nonmotor (−Motor−Goal). Examples (translated to English) are presented in Table 1. Various measures collected for these stimuli are summarized in Table 2. Ratings were obtained from a sample of 10 Italian participants recruited through Amazon Mechanical Turk; as a measure of relative reliability of the measures across items, their responses were correlated with r values of .67, .66, and .72 for imageability, motoricity, and goal-directedness, respectively. Participants were required to have an IP address in Italy and to report in free form when they learned Italian. The instructions did not state that they had to be native speakers to encourage honesty, but the data of participants who were not native speakers were excluded. All participants

Table 1. Examples of Stimuli in Each Condition in Experiment 1

<i>+Motor +Goal</i>	<i>+Motor -Goal</i>	<i>-Motor +Goal</i>	<i>-Motor -Goal</i>
Stamp	Slip	Invent	Detest
Catch	Hiccup	Deceive	Adore
Fasten	Yawn	Falsify	Doubt
Clap	Sneeze	Advise	Underestimate
Chew	Shiver	Sacrifice	Forget
Kick	Fidget	Plan	Rejoice
Wave	Stumble	Teach	Waste

Stimuli in Experiment 2 included some of these and similar others. There were 24 items/condition in Experiment 1 and 20 items/condition in Experiment 2.

were presented with 157 action names and asked to imagine performing or experiencing each of them and to rate the following: how easy was it to imagine (imageability); to what extent they imagined a specific motion of the body (motoricity); and to what extent they imagined themselves having a goal in mind, as opposed to the action being unintentional (goal-directedness). A subset of items was then selected so that goal-directed and non-goal-directed conditions did not differ in imageability or motoricity, within either the motor and nonmotor verbs, and such that the differences in goal-directedness in each comparison were equal. Conditions were also matched on length (in number of letters) and frequency using the database of the Istituto di Linguistica Computazionale, Genova (www.ge.ilc.cnr.it/lessico.php). To minimize task difficulty confounds, three Italian speakers also performed the behavioral task designed for the scan sessions (described below), and items

were chosen to minimize differences in responses and RTs. A final set of 24 items per condition was selected.

Procedure

During scanning, on each trial, participants saw the pronoun and action name in 35-point Helvetica font. Participants responded using a four-button response box to indicate whether this was an action they experienced rarely, frequently, or somewhere in between. They pressed 1 and 2 using the middle and index fingers of their left hand and 3 and 4 using the index and middle fingers of their right hand, respectively. The order of the scale was counterbalanced, so that 1 indicated “frequently” for half of the participants and “rarely” for the others. Each trial lasted 3.5 sec, regardless of response. On control trials, participants saw a fixation cross that changed color; the duration of each color was selected randomly and such that it changed between 0 and 3 times per trial. Participants’ task was to press button 1 each time the fixation cross changed color. This task was chosen as a baseline because it is expected to minimize activation in the resting-state network, which roughly overlaps with the regions expected to be active in the experimental task. This was expected to allow beta values to be in the positive range for the task. MATLAB (The MathWorks Inc., Natick, MA) and its Psychtoolbox extensions (Brainard, 1997) were used to present the stimuli and collect responses.

The order of conditions during scanning (including the fixation task) was optimized for signal detection by being organized into blocks of four trials of the same condition and by ordering the sequence of blocks so that each condition preceded every other condition an equal number of times (i.e., was balanced for 1-back history). The

Table 2. Average Values and *p* values of *t* tests of Various Measures Obtained of the Stimuli in Experiments 1 and 2

	<i>+Motor +Goal</i>	<i>+Motor -Goal</i>	<i>p</i>	<i>-Motor +Goal</i>	<i>-Motor -Goal</i>	<i>p</i>
<i>Experiment 1</i>						
Imageability	2.64	2.55	.35	1.69	1.60	.52
Movement	2.54	2.46	.44	1.31	1.18	.40
Goalness	2.58	0.84	.00	2.46	0.97	.00
Percent transitive argument structure	0.88	0.04	.00	0.88	0.58	.02
<i>Experiment 2</i>						
Imageability	3.65	3.43	.14	2.62	2.51	.40
Movement	2.99	2.66	.14	1.72	1.66	.62
Goalness	3.52	1.97	.00	3.30	2.20	.00
Time	1.78	1.92	.59	2.70	2.31	.15
Percent transitive argument structure	0.60	0.10	.00	0.75	0.75	1

sequence of actual conditions was made distinct for every five participants by rotating which condition had which code in the sequence. The assignment of items to trials within their condition blocks was randomized for each participant. In total, there were 240 trials (48 per condition; two repetitions of each unique verb), grouped into sixty 14-sec blocks (12 per condition). The full sequence was split between two runs, each 7 min long.

Theory of Mind Localizer

The stimuli and presentation scripts were taken directly from the lab website of Rebecca Saxe (www.saxelab.mit.edu) and were as described in Dodell-Feder, Koster-Hale, Bedny, and Saxe (2011). The conditions were comprised of two kinds of stories: those involving out-of-date (false) beliefs and those involving out-of-date physical representations such as photographs or maps. Each story was presented for 10.5 sec, followed by a true-or-false question, presented for 4 sec, during which participants answered “true” with response key 1 or “false” with response key 2. This was followed by a 12-sec fixation block. Ten stories of each condition were presented in randomized order across two runs of 4.6 min. The localizer stimuli were translated from English to Italian by a professional translator at the University of Trento.

fMRI Acquisition Parameters

fMRI data were collected with a 4T Bruker MedSpec MRI scanner at the Center for Mind/Brain Sciences, Trento, Italy. Anatomical volumes were acquired with T1-weighted MP-RAGE sequence, at a $1 \times 1 \times 1$ mm voxel resolution (256×224 matrix size). Functional data were then acquired with an EPI sequence (eight-channel coil; repetition time = 2.0 sec; echo time = 30 msec; flip angle = 73°) using 34 interleaved slices per volume (parallel to AC–PC, 33 mm gap; matrix size 64×64 cm), which covered the full brain and produced a voxel resolution of $3 \text{ mm} \times 3 \text{ mm} \times 3 \text{ mm}$. Magnetic field homogeneity maps were acquired before each run and were used to create distortion-corrected DICOM maps with SIEMENS software at the scanner console.

fMRI Preprocessing and Analysis of Individual Participant Data

fMRI data were analyzed with AFNI (Cox, 1996). Slices in each volume were corrected for acquisition timing using Fourier interpolation. Each volume was then aligned to the fourth volume of the first scan. In each run, a Fourier high-pass temporal filter (0.008 Hz) was applied to remove low-frequency trends, and image intensities were normalized. The data were spatially smoothed with a six FWHM Gaussian kernel, and the runs of each task (Actions or Theory of Mind) were concatenated. Regressors for each condition 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 least squares regression over the signal time-course in each voxel. The model also included motion parameter estimates in each of four directions and two rotations, and in Experiment 2, where this posed a potential confound to the contrast of interest, a regressor for that participant’s RT in each trial regardless of condition also convolved with the hemodynamic response. The regression procedure produced a statistical map for each condition, representing a beta weight and t statistic for each voxel, which indicated the partial correlation between the signal in that voxel over the course of the experiment and the occurrence of that condition and are commonly interpreted as percent BOLD signal change relative to the baseline condition, which was the fixation task here. The anatomical volume was skull-stripped and resampled to match a Talairach template provided by AFNI; the statistical maps were then transformed to this space using the transformation parameters calculated from the resampling process. All analyses were subsequently performed on data in this standardized space. To create surface maps (for visualization), the cortical surface was segmented from the volume using Freesurfer and transformed to SUMA format to project functional data using AFNI.

Mean Contrast Analysis

Group-level general linear modeling analysis was used to test the effects of goal-directedness and motoricity, with a four-way (Motoricity by Goal-directedness) mixed-effects ANOVA for the actions task (items treated as fixed, participants as random) and a two-way mixed-effects ANOVA for the theory of mind task. This produced a set of t values representing, for each voxel, the reliability of each factor across participants. AFNI’s program AlphaSim was used to generate corrected probability values for these t maps, using smoothness estimates derived from maps of residuals from each participant’s regression model, transformed into Talairach space (because this can increase smoothness). The average smoothness values were then used as parameters in AlphaSim, which simulated the probability of voxel clusters of a given size when thresholded at uncorrected $p < .01$ in noise data of the same smoothness. The thresholds obtained are reported in each figure.

Conjunction Analysis

To test for the specific pattern of response of interest—greater response to goal-directed actions in both the motor and nonmotor categories—a within-subject conjunction test was performed. For each participant, two difference maps (+Motor+Goal – +Motor–Goal and –Motor+Goal – -Motor–Goal) were each thresholded at $p < .05$ uncorrected ($t > 2$) and then averaged, creating

individual conjunction maps, showing the average statistic where both maps passed the threshold. A *t* test was applied across the beta maps to determine the reliability of each voxel's response in the group. The resulting maps were then submitted to permutation analysis to determine corrected *p* values for each cluster. In each iteration, the sign of each contrast was flipped with a 50% probability (e.g., flipped the +Motor+Goal – +Motor–Goal difference) for each participant, simulating random assignment of condition labels. The two resulting maps for each participant were then thresholded and averaged exactly as in the correctly labeled analysis, and a *t* test was applied to these maps across participants. A group *t* map was thus created for each of 1000 permutations. Each of these 1000 group *t* maps was itself thresholded at $p < .05$ uncorrected, and the size of the largest cluster obtained was recorded. This created a distribution of maximum cluster sizes expected by chance (i.e., if labels were randomly assigned to conditions). The probability of each observed cluster was then determined by its position in this distribution, assigning a probability of $p < .05$ to those clusters that were larger than the 950th largest cluster in the null distribution, etc.

ROI Selection

For ROI analyses of verb conjunction region, individual conjunction maps were created as above. On the basis of group results, individual ROIs were defined by selecting the cluster nearest to the group region. The aim of this analysis was to characterize the profile of the region found at the group level, so participants who did not show any effects in the region were not included (as they would not have contributed to the group conjunction map, as it was done within subjects). The beta values for each condition in the actions task was then extracted from this region and statistically compared across the group using planned *t* tests. The analysis of motor effects was independent of the ROI definition because this was based on comparisons between goal and non-goal actions. The analysis of interaction effects was not fully independent, but because the aim was to rule out an interaction, the analysis was biased toward the null hypothesis. For theory of mind, ROIs were designed to be as specific as possible to the contrast of interest; thus, the top 50 contiguous voxels in terms of *t* values were selected from the left TPJ of each participant. Beta values from the Actions data were then extracted from this region in each participant and statistically compared using planned *t* tests.

Experiment 2

fMRI Participants

Eighteen right-handed, neurologically healthy English-speaking participants (17 native speakers, 1 non-native; 8 women, mean age = 25.6 years) took part in Experi-

ment 2. All participants provided informed consent in writing. Procedures were approved by the institutional review board at Harvard University.

Stimuli

Stimuli were similar to those of Experiment 1, except that items were in English. Ratings on these stimuli were collected with a different sample of 30 English-speaking participants, recruited through Amazon Mechanical Turk (mean age = 34 years). These participants were asked to imagine performing each of 157 actions (translations of those used in Experiment 1). They were then asked to rate how easy that action is to imagine (imageability); how much body movement they imagine (motoricity); to what extent they imagine themselves having a goal in mind, as opposed to the action being unintentional (goal-directedness); and the amount of time the action takes to complete, from the start of planning to the time its intended outcome is achieved (planning scope). Twenty items per condition were selected from this set to ensure that the conditions were matched on these factors, as summarized in Table 2. Items were matched in length in letters and frequency, as assessed with the COHA database (Davies, 2011). In addition, verbs were classified as intransitive if it would be ungrammatical for the verb to take a direct object (e.g., *he slept the bed*). Unlike in Experiment 1, the +Goal and –Goal items in the nonmotor set were matched for number of intransitive verbs. Because of the greater constraints in Experiment 2, the total number of stimuli was smaller than in Experiment 1. Furthermore, the items were less strongly goal-directed in the –Motor+Goal condition than in the +Motor condition and than in Experiment 1 (as seen in Table 2).

Procedure

In almost every aspect, the task design and stimulus presentation were the same as in Experiment 1. The exception was that each condition block had five items rather than four, creating eight 17.5-sec blocks per condition. This difference was because of the mathematical constraints of having 20 rather than 24 items. There were two runs of 20 blocks, each of which lasted 5.83 min.

fMRI Acquisition Parameters

fMRI data were acquired using a Siemens Magnetom TrioTim syngo 3T scanner at the Center for Brain Science, Harvard University, Cambridge, MA. Anatomical volumes were acquired with T1-weighted MP-RAGE sequence, at a $1 \times 1 \times 1$ mm voxel resolution (256×256 matrix size). Functional data were then acquired with an EPI sequence (32-channel coil; repetition time = 2.0 sec; echo time = 28 msec; flip angle = 90°). For each volume, 33 interleaved

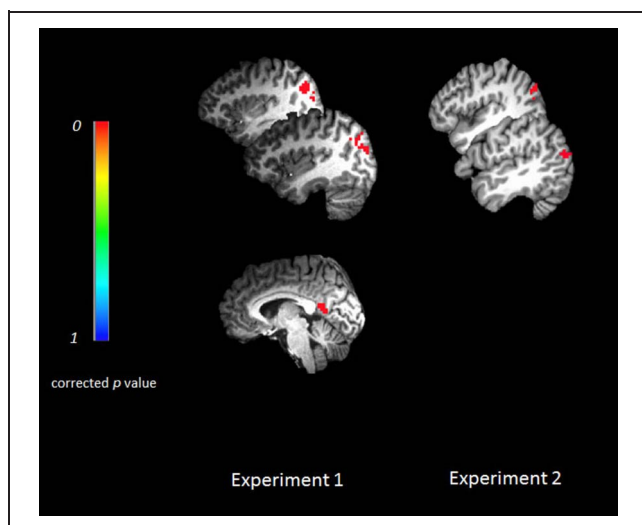


Figure 1. Corrected p values of significant clusters from the conjunction analysis in Experiments 1 and 2; thresholded at $p < .05$.

replicated ($p < .001$). The parietal region observed in Experiment 1 extended more medially and anteriorly than that in Experiment 2; however, this variation was within the scope of variability among individuals. To illustrate this directly, the mean Talairach coordinates of the peaks of individual participants' clusters and their variability are shown in Table 4. There were no significant differences in any dimension of these coordinates (x : $t(14) = 1.7, p = .11$; y : $t(14) = -0.80, p = .44$; or z : $t(14) = -0.65, p = .53$).

Individual Participant Data

As indicated in the conjunction analysis, only one region showed the desired profile of responding to goal-directedness across both motor and nonmotor verbs and replicated across both experiments. As shown in Figure 2, this region was also clearly visible in almost every participant and was the only consistent region to show intentionality effects across motor and nonmotor verbs in individuals.

Mean Contrasts and Interactions

An overall contrast of goal-directed and non-goal-directed actions, using a standard mixed-effects general linear model across participants, was also performed, and results are shown in Figure 3. This analysis revealed similar regions as the conjunction—pIPL and precuneus/posterior cingulate, along with additional areas—because this analysis allows for effects driven by one type of action (motor or nonmotor) more than another. These additional activations (in superior frontal gyrus, parahippocampal gyrus, and anterior cingulate), although responsive to goal-

directedness controlling for motoricity, may be driven by demands made by only one kind of verb (motor or nonmotor)—for instance, perhaps for motoric planning. To confirm this interpretation, an interaction analysis was performed looking for regions that showed a greater intentionality effect within either the motor or nonmotor verbs, relative to the other. Only regions showing a greater goalness effect in the motor verbs than the nonmotor verbs were found; these are displayed in Figure 4. This illustrates that the goal-directedness in superior frontal gyrus in Experiment 1 and precuneus/PCC and parahippocampal gyrus in Experiment 2 was driven primarily by the motor verbs. These regions are thus engaged in information specific to goal-directed, motoric actions only, suggesting that they do not represent goal information generally but may have a more specific role in action knowledge.

Summary

Across two experiments, a region in left pIPL was found to respond more to goal-directed/intentional actions than to accidental ones, for both motor and nonmotor actions. The following analyses probe this region to better understand its response profile.

Response Profile of Parietal Goal-responsive Region

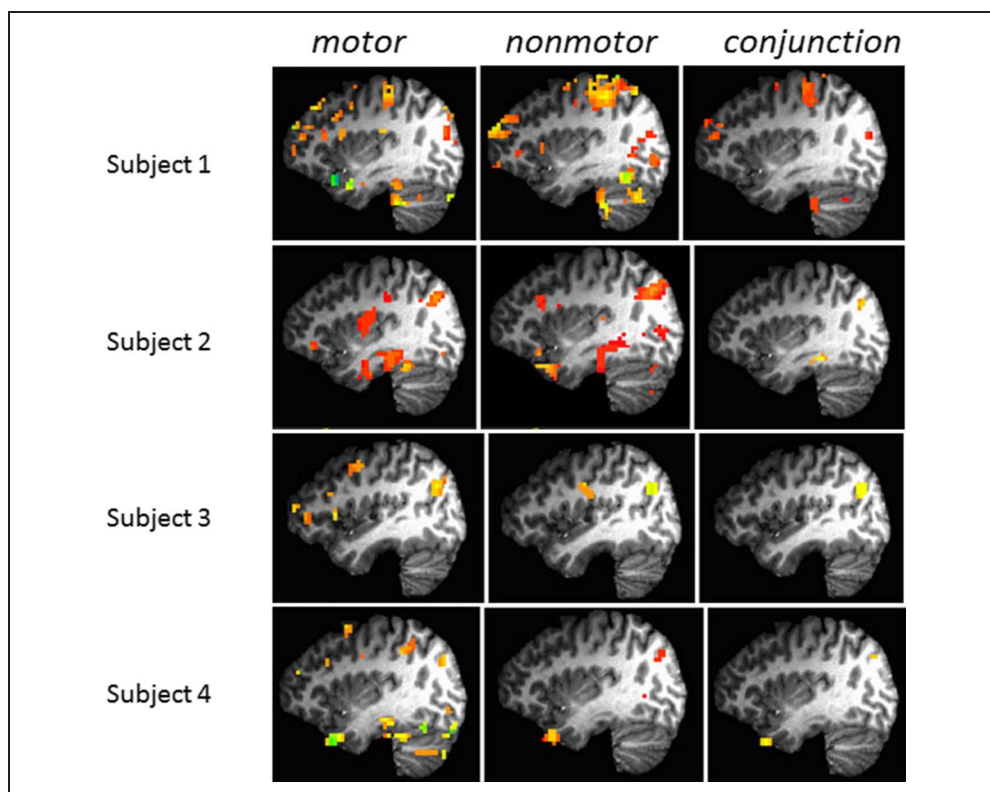
Motoricity

To fully characterize the response profile of the goal-responsive region found in the pIPL, the percent BOLD signal change values for each of the four conditions were extracted within the pIPL conjunction region in individual participants. A contrast of goal versus non-goal would be biased, but a comparison of motor versus nonmotor is

Table 4. Average Coordinates of the Peak of Each Individual Subject's Conjunction Effects in pIPL and Theory of Mind Effects in Left TPJ and Their Standard Deviations

	x	y	z
<i>Goal Conjunction Region, Experiment 1</i>			
Mean	38.7	68.7	25.6
SD	5.5	3.8	7.4
<i>Goal Conjunction Region, Experiment 2</i>			
Mean	45.3	65.9	22.9
SD	9.9	9.7	9.3
<i>Theory of Mind Left TPJ, Experiment 1</i>			
Mean	48.2	55.6	21.0
SD	6.8	5.0	2.0

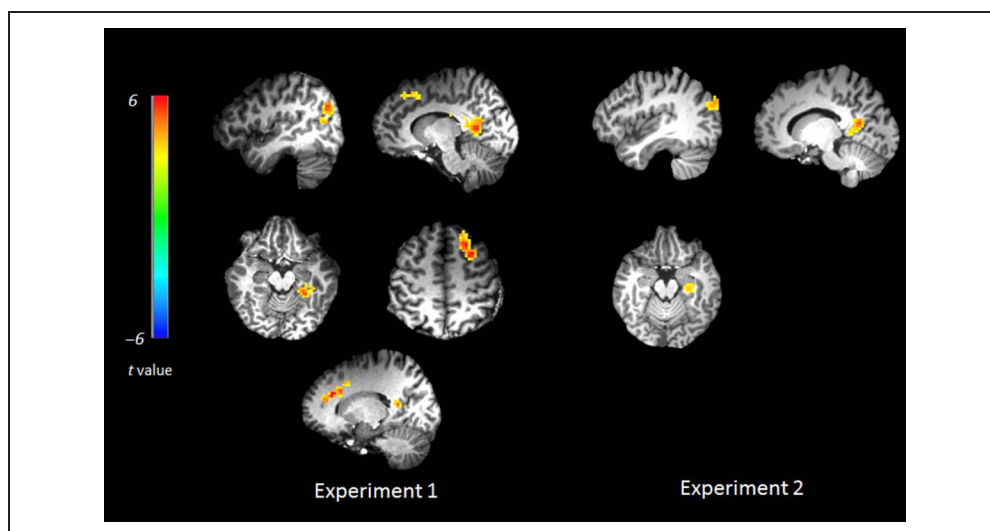
Figure 2. Individual subject statistical maps (uncorrected, various thresholds) for goal > non-goal comparisons within motor and nonmotor verbs separately and their conjunction. This shows the first four participants in Experiment 1. Data are representative of the remaining subjects, except for Subject 1, who had more widespread activation than any other.



fully independent of the data used to define this ROI. This test was used to evaluate the possibility that, in addition to an effect of goal-directedness, this region also responds more to motor than to nonmotor verbs. The ROI approach is the most powerful and direct way to test this question. It is important to note that these ROIs were defined using the same parameters as the conjunction analysis. Thus, participants who did not show conjunction effects in pIPL would not have contributed to the whole-brain results. These ROI data thus speak directly to the nature of the region found at the group level.

As illustrated in Figure 5, BOLD response to all motor actions was not significantly different from the response to all nonmotor actions, in either Experiment 1, $t(8) = 0.50, p = .32$, or Experiment 2, $t(8) = 0.85, p = .21$. The pattern also held at each level of goal-directedness alone. That is, goal-directed motor and nonmotor actions were not significantly different (Experiment 1: $t(8) = 0.33, p = .75$; Experiment 2: $t(8) = 0.89, p = .80$). Non-goal-directed motor and nonmotor actions were also not significantly different (Experiment 1: $t(8) = 0.65, p = .54$; Experiment 2: $t(8) = 0.80, p = .90$).

Figure 3. Group-level contrast between all goal-directed and all non-goal-directed actions; thresholded using a voxel-level threshold of $p < .01$ and cluster size > 52 voxels (Experiment 1) and > 50 voxels (Experiment 2), providing a corrected threshold of $p < .05$.



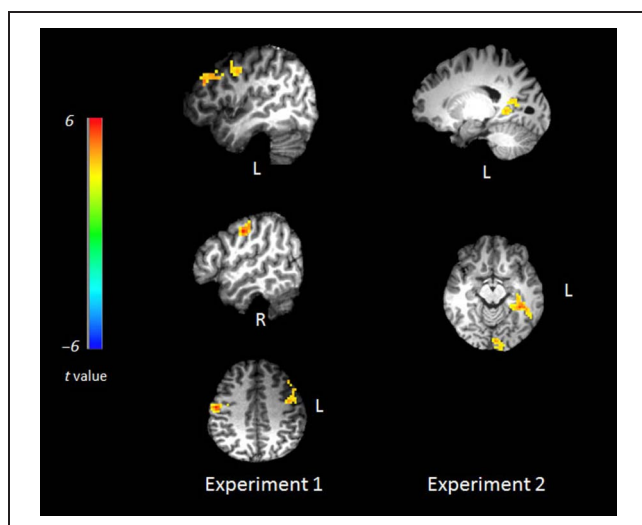


Figure 4. Regions showing an interaction between goal-directedness and motoricity, such that the difference between goal and non-goal actions was greater in the motor than the nonmotor conditions. Results are thresholded at a cluster-corrected level of $p < .05$ by combining a voxel-level threshold of $p < .01$ and cluster extent >50 or 52 voxels, respectively, for Experiments 1 and 2.

The pattern of responses within pIPL across these conditions, in both experiments, illustrates that this region responds when retrieving intention information, but not motor information about actions. The absence of a motoricity effect also confirms that the goal-directedness effects themselves could not have been because of any unmeasured differences in motoricity between goal-directed and non-goal-directed actions, because under any measure, the goal-directed motor verbs (*kick*) are more motoric than nonmotor verbs of either kind (*teach*); if the pIPL were responding to motoricity, it should have shown a difference in such a contrast.

Transitivity

In Experiment 1, goal-directed action verbs were likely to be transitive (be able to take an object, e.g., *kick*), whereas accidental ones were generally not (e.g., *blink*). In Experiment 2, this was controlled within the nonmotor verbs, mostly by including transitive accidental actions (such as *forget*). Thus, to the extent that effects hold independently and equally in the nonmotor intentionality contrast, they are not because of transitivity. There is already indication that the Experiment 2 intentionality effects in pIPL were present in both motor and nonmotor verbs. First, the conjunction analysis already demonstrated that the intentionality effects held in both motor and nonmotor actions. Second, a whole-brain search for interaction effects (greater intentionality effects in motor than nonmotor verbs) found precuneus and parahippocampal cortex, but not pIPL (or any nearby regions). A third way of directly confirming this is to test for interaction effects

in the BOLD response to each condition within the pIPL ROI, as above. This is the most sensitive test. As shown in Figure 5, no such effect was found, $t(8) = -0.31, p = .76$ —that is, the effect of intentionality was equal in the motor and nonmotor contrasts. This set of results makes it unlikely that transitivity was the source of the effects in pIPL. This has implications for how previous reports of transitivity effects in pIPL are interpreted (Den Ouden, Fix, Parrish, & Thompson, 2009; Thompson et al., 2007). Transitive verbs in these studies were more goal-directed than intransitive ones, and the present findings suggest that it was likely goal-directedness that drove activation in pIPL.

What Is the Relationship between Intentionality and Theory of Mind?

Prior fMRI studies of goal knowledge have used action video or description stimuli and have reported regions similar to those observed in studies of theory of mind,

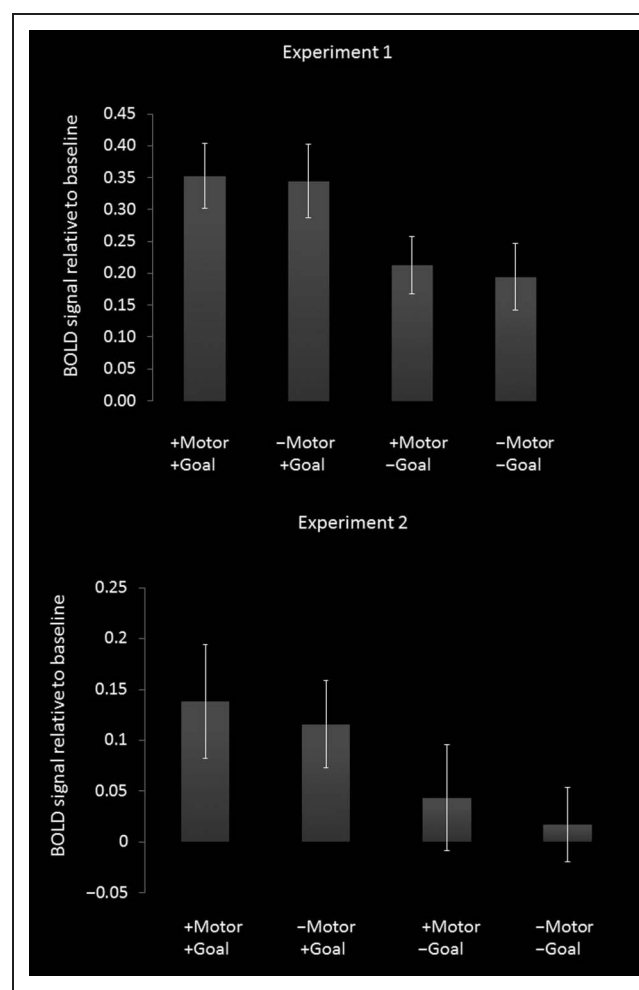


Figure 5. Responses to each action condition within the goal-responsive pIPL region, as defined using a conjunction analysis in individual participants. Statistics of goal-directedness effects are not reported because these are biased; all other effects were nonsignificant.

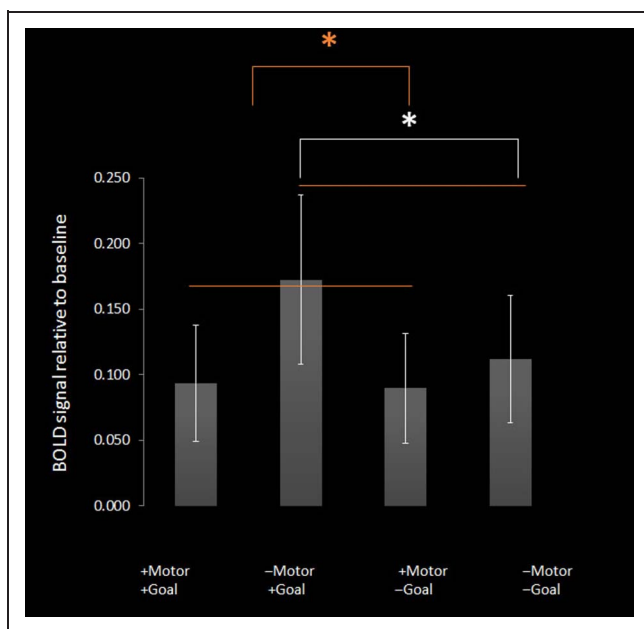
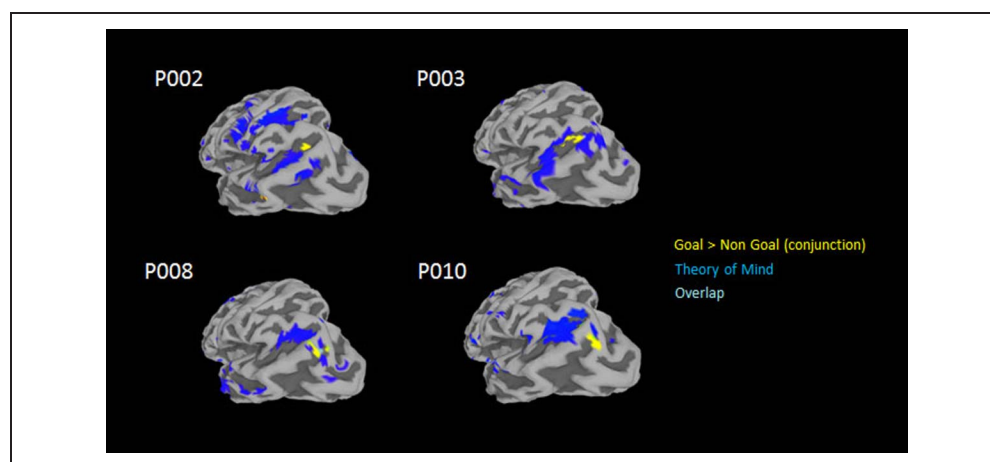


Figure 6. Responses to each action condition within the left TPJ ROI, localized using a theory of mind localizer in each participant.

perhaps because judging actors' intentions naturally involves inferring their mental states (what he or she wants to accomplish). The present paradigm minimized such inference demands because there were no actors to observe. However, a left IPL area was still found to respond to goal-directedness—a region remarkably close to the portion of left IPL in the theory of mind network, commonly referred to as the TPJ (Koster-Hale & Saxe, 2013; Saxe & Kanwisher, 2003). Although the right TPJ appears highly specific to beliefs, the left TPJ may have a broader role (Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Saxe & Wexler, 2005), perhaps including the conceptual knowledge of action intentions. To weigh in on this claim, we tested whether the region observed here to respond to goal-directed actions is the same one that is observed in a commonly used theory of mind task. To

Figure 7. Four representative participants' left-hemisphere cortical surfaces with overlays of theory of mind effects (false belief > false photograph, in blue) and goal conjunction effects (in yellow). Overlaps (which occurred only in subject P008 here) are shown in turquoise. Thresholds were set to $t > 2$ ($p < .05$ uncorrected), except for subject P010, whose threshold was set to $t > 4$ to allow a comparable extent to the other participants.

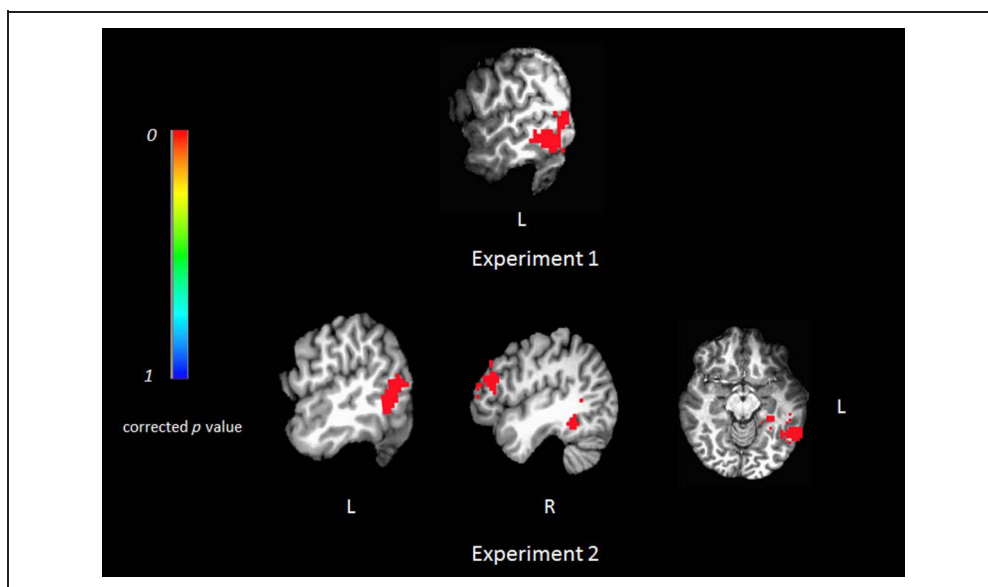


this end, the BOLD signal for each of the action conditions was extracted from individual participant ROIs identified using a theory of mind localizer (Dodell-Feder et al., 2011).

The responses of the left TPJ in individually defined ROIs from the theory-of-mind contrast are displayed in Figure 6. A two-way, repeated-measures ANOVA revealed a main effect of goal-directedness, $F(1, 10) = 6.09$, $p = .033$, and of motoricity, $F(1, 10) = 8.10$, $p = .02$, as well as an interaction, $F(2, 10) = 5.5$, $p = .04$. As visible in Figure 6, the left TPJ responded more to goal-directed actions than accidental actions and more to nonmotor than motor actions. Planned t tests showed that, although there was an effect of goal-directedness within nonmotor verbs in this region, $t(10) = 3.17$, $p = .01$, there was no such effect within the motor verbs, $t(10) = 0.24$, $p = .81$.³ This response profile does not indicate a general responsiveness to action goals in left TPJ and is distinct from that of the pIPL, which responded to goal-directedness equally across motor and nonmotor actions. Indeed, these regions are localized in slightly different, though neighboring, locations in each participant. Figure 7 displays individual participants' activation maps of the theory of mind effects alongside the goal conjunction effects. In every participant, these activations were visibly distinct, with nearly no overlap, at a threshold of $p < .05$ uncorrected that revealed widespread activation in left TPJ. The goal-responsive cluster appeared consistently posterior and/or superior to that for theory of mind.

To test the location differences directly, the Talairach coordinates of the peaks of each participant's left TPJ and pIPL were compared. These values are shown in Table 4; paired-sample t tests revealed significant differences in each dimension (x : $t(7) = 2.96$, $p = .02$; y : $t(7) = 8.10$, $p < .0001$; z : $t(7) = -2.71$, $p = .03$). Correcting for the number of dimensions tested, only the y dimension (posterior to anterior) remained below $p = .05$, confirming that the primary difference was that the goal effects were more posterior than those of theory of mind. To further assess the relationship between pIPL and left TPJ across a

Figure 8. Significant clusters from the motor conjunction analysis, thresholded at $p < .05$.



wider range of tasks and experiments, at least at the group level, the average coordinates for pIPL (Table 4) were checked against aggregate data of 54 studies, as available on neurosynth.org/features/mentalizing. The mentalizing z score at the locations for both experiments was 0, indicating that mentalizing tasks are unlikely to activate these peak coordinates, although this does not rule out that certain theory of mind or social tasks may do so.

Which Regions Show an Effect of Motoricity, Independently of Goal-directedness?

The present design is suitable for looking for regions that respond to motoric verbs more than nonmotoric verbs, independently of their goal-directedness. This analysis would complete the picture of the neural organization of these two kinds of attributes. However, it should be noted that the present design was not optimized to detect selective effects of motoricity for several reasons. One is that motoric verbs were also more concrete. Second, some past work shows that motor imagery effects in premotor areas can be somatotopically organized (Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; though see De Zubicaray, Arciuli, & McMahon, 2013; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). Here, any somatotopically organized effects, real or not, would have been washed out because actions of various effectors were grouped together. Finally, in Experiment 2, goal-directed motor verbs were more goal-directed than goal-directed nonmotor verbs, making it difficult to interpret motoricity effects in this experiment unless using a conjunction approach. With these caveats in mind, two analyses were performed: a motor conjunction analysis in both Experiments and a simple contrast of motor–goal and nonmotor–goal actions in Experiment 1. Figure 8 shows the results of the conjunction analysis, which identi-

fied regions that responded more to motoric actions than nonmotoric ones, at both levels of goal-directedness. Across both experiments, effects were found within posterior temporal regions (perhaps near biomotion-sensitive areas; Beauchamp, Lee, Haxby, & Martin, 2003; Grossman et al., 2000), consistent with past research on action concept retrieval (Hauk, Davis, Kherif, & Pulvermüller, 2008; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). In Experiment 1 and just below threshold in Experiment 2, a portion of lateral superior frontal cortex was also activated. A second analysis looked at the effect of motoricity within the goal-directed verbs in Experiment 1 where these were matched closely for goal-directedness. As shown in Figure 9,

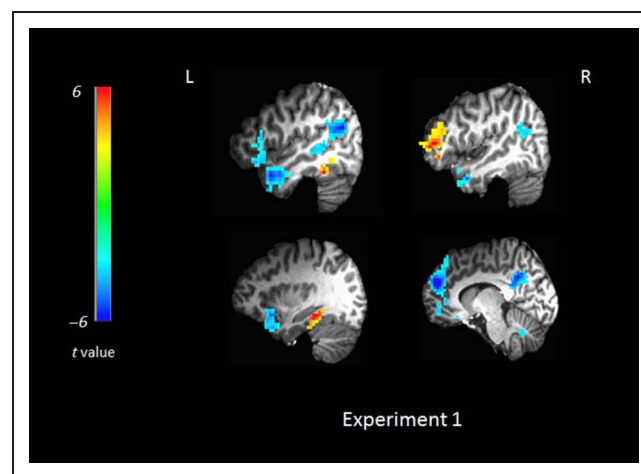


Figure 9. Motoricity effects within the goal-directed actions (+Motor+Goal vs. –Motor+Goal). t Values for nonmotor > motor are shown in the blue scale; t values for motor > nonmotor are shown in the red–yellow scale. Results are thresholded at $p < .05$ corrected for multiple comparisons using a cluster-extent threshold of 52 voxels and a voxel-wise threshold of $p < .01$.

effects were found in a right lateral superior frontal area, perhaps involved in motor planning and consistent with the interaction effects discussed above. Effects were also found in a medial-temporal region near the parahippocampus, perhaps because of the greater concreteness/imageability of the motor verbs. These results are consistent with the findings of a recent meta-analysis of fMRI work on (concrete) action knowledge, which found primarily these two areas (Watson, Cardillo, Ianni, & Chatterjee, 2013). For the reverse contrast, nonmotor, goal-directed actions activated a set of regions resembling the theory of mind network, consistent with the findings in the ROI analysis that the theory of mind network responds most strongly to goal-directed nonmotor verbs than other categories.

Additional Measures

To ensure that goal-directedness effects were not because of the goal-directed items being generally more positively valenced than accidental ones, additional ratings were collected from a separate group of Italian speakers ($n = 20$) on the items used in Experiment 1. Planned t test revealed that the goal-directed items were more positively valenced within the motoric actions, $t(46) = 3.55$, $p < .0001$, and marginally so within the nonmotoric actions, $t(46) = 1.76$, $p = .085$. Thus, these values were entered as a parametric regressor of no interest into the model for the fMRI data in a similar fashion as the latency regressors. The main effects of goal-directedness survived in the pIPL and other regions (Figure 10). There was no significant effect of the valence regressor on BOLD signal, likely because of the generally nonarousing nature of the stimuli and task, although it was marginally present around the right insular cortex at an uncorrected threshold

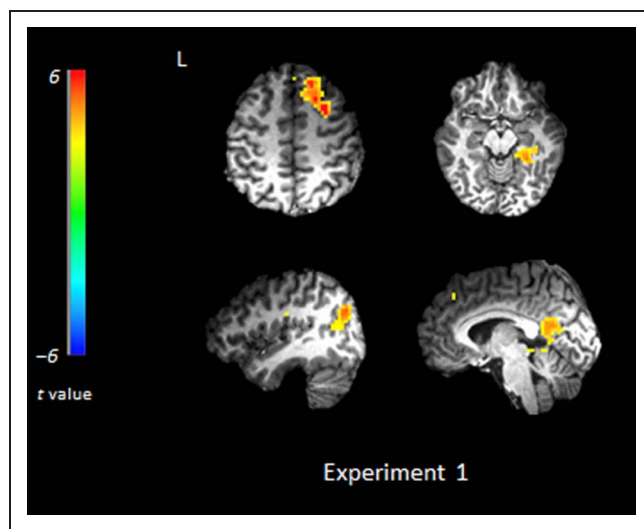


Figure 10. Group-level contrast between all goal-directed and all non-goal-directed actions in Experiment 1, controlling for valence; thresholded using a voxel-level threshold of $p < .01$ and cluster size > 52 voxels, providing a corrected threshold of $p < .05$ for the clusters.

of $p < .05$. Overall, this is consistent with the literature on effects of positive valence, which by and large do not find effects in IPL (Citron, Gray, Critchley, Weekes, & Ferstl, 2014; Denkova, Dolcos, & Dolcos, 2013; Decety & Porges, 2011; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006). One exception (Vigliocco et al., 2014) reported effects of non-neutrality (valence in both directions away from neutral) in a number of areas including parts of IPL. Although non-neutrality differed among motor items, $t(46) = -3.21$, $p < .01$, it was in the opposite direction, with goal-directed items being less valenced overall, and was not significant among the nonmotor items, $t(46) = -0.50$, $p = .62$. In summary, neither positive valence nor non-neutral valence can explain the present findings.

DISCUSSION

During the presentation of action verbs, stronger activation was elicited in posterior parietal cortex by verbs describing intentional actions relative to actions typically done by accident. This was true in the case of motoric actions (e.g., *kick* vs. *stumble*) and equally true in the case of nonmotoric ones (e.g., *teach* vs. *forget*). These effects are not explicable by the grammatical properties, imageability, or amount of body movement associated with these different types of verbs. Indeed, effects of the amount of body movement denoted by the verbs were found in other, distinct areas, such as posterior middle temporal gyrus. We take these findings to suggest that the posterior parietal response is driven by the retrieval of knowledge regarding the kinds of attributes that intentional actions possess: what they are for or what goals they serve to accomplish. This result serves to describe an attribute-selective semantic subsystem for at least one type of nonmotor aspect of action knowledge.

These results help to clarify past findings regarding activations observed for goal-related processing and theory of mind. Prior research has described activation in a similar region when participants were asked to think about the goals of actions depicted in videos or stories (relative to thinking about how the actions are executed); but these studies also often observed activation in right inferior parietal cortex, precuneus cortex, and medial pFC (Nicholson et al., 2013; Lingnau & Petris, 2012; Spunt et al., 2011; Hesse et al., 2009; Majdandzić et al., 2007; Ruby et al., 2002)—closely resembling the set of regions that respond when reasoning about other's mental states compared with nonmental representations (Saxe & Kanwisher, 2003). This is not surprising considering the kinds of demands created by having to interpret action videos of other people. Thus, the findings in these studies could either have been elicited by the retrieval of semantic knowledge about action goals or by the process of attempting to infer actors' mental states ("mentalizing"). The present results help to clarify this issue. Having removed inferential demands by presenting action concepts directly,

goal-related activations were observed only in left parietal cortex (and in Experiment 1, in the precuneus). Furthermore, goal-related and theory-of-mind-related activations in left parietal cortex were dissociated: The left parietal region identified using the theory of mind localizer in the same participants did not show modulation by the goal-directedness of action verbs. Thus, the present results illustrate a functional dissociation within the pIPL between conceptual processing of goal attributes and certain other kinds of operations or contents about mental states or events. The exact nature of content subdivisions within this region and the conditions under which these subsystems are engaged may be a fruitful topic of further research.

Developmental researchers have supplied one analysis of the distinct cognitive components involved in theory of mind and goal understanding. Although understanding beliefs requires distinguishing between mentally represented and actual states of affairs and develops later, understanding a goal needs only to refer to a future possible state of reality toward which an action is a possible means—reference to minds not being specifically necessary (Gergely & Csibra, 2003; Csibra & Gergely, 1998). Csibra and Gergely term this kind of reasoning the “teleological stance” and describe it as a schema that connects an action to a future state of the world and evaluates whether that action can plausibly obtain in the given circumstances.

It is possible that the cognitive role of pIPL is describable as the operation of such a schema. This is difficult to evaluate, however, without distinguishing between two procedures: interpreting actions observed in the world and accessing stored, conceptual knowledge about actions. The former process operates over some observation—the movements of an actor, for instance—and analyzes this input to interpret its meaning. The latter process begins from the other direction—through thought or language, one retrieves directly knowledge about the typical goals of action categories, as in the present experimental task. The pIPL could contribute such stored knowledge to the schemas in the teleological stance. The interpretational process itself, on the other hand, is more likely subserved by the posterior STS or pSTS (Shultz, Lee, Pelphrey, & McCarthy, 2011; De Lange et al., 2008; Brass, Schmitt, Spengler, & Gergely, 2007; Buccino et al., 2007; Pelphrey, Morris, & McCarthy, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004; Castelli, Happé, Frith, & Frith, 2000). This region responds to actions that are inconsistent with a prediction or expectation—for instance, to videos of someone turning off a light-switch with their knees when their hands are not otherwise occupied compared with when they are carrying something (Brass et al., 2007). In fact, the pSTS has the opposite response profile to the pIPL: It responds more to accidental actions than intentional ones (Buccino et al., 2005), likely because accidents are surprising to observe and create greater interpretational demands. The analysis of what is expected or unexpected, as computed in this region, is informed by a

large variety of factors—actions that are generally unusual, such as lifting a mug to one’s ear (De Lange et al., 2008), that are incongruent with a facial expression (Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009) or incorrect with respect to a task instruction (Pelphrey et al., 2004) that stimulate activity in pSTS. Semantic and syntactic anomalies in sentences also activate similar parts of cortex (Friederici, Rüschemeyer, Hahne, & Fiebach, 2003). Thus, the response of the pSTS to unintentional relative to intended actions suggests that it might draw upon knowledge about typical intentions of actions among a wide scope of other knowledge to generate an expectation for or analyze observed events or other incoming information—its more general role. The present results suggest that the stored knowledge of action-goal concepts, on the other hand, is represented in pIPL.

The present proposal is that the posterior parietal region observed here is part of the brain’s system for conceptual knowledge. However, although this region exhibited some content specificity, in that it responded to information about action intentions, but not body movements, not every kind of property was tested, so it is possible that this region represents multiple kinds of semantic attributes.

Past research regarding the role of posterior parietal cortex in semantics overall favors the notion that it is involved in a range of semantic tasks but is preferentially engaged for specific contents: those about events and actions. Meta-analysis has shown that posterior parietal cortex (angular gyrus) is one of the most consistent regions involved in semantic processing, that is, in comparisons of more versus less semantically demanding tasks (Watson et al., 2013; Binder, Desai, Graves, & Conant, 2009), including when requiring a similar activation profile across modalities of input (Price, Bonner, Peelle, & Grossman, 2013; Bonner, Peelle, Cook, & Grossman, 2013; Fairhall & Caramazza, 2013). However, these studies mostly do not explicitly test for content-generalities, and the averaged activations could be driven by some (sufficiently pervasive) subset of items. This possibility is made more likely by positive findings of content-specificity in the angular gyrus. One line of work has linked the angular gyrus to thematic knowledge—the kind of knowledge that relates objects in similar events or contexts (e.g., that spatulas and ovens are used for baking), when compared with taxonomic knowledge (e.g., that apples and pears are both fruit). Both fMRI and patient work have linked thematic (vs. taxonomic) conceptual processing to angular gyrus (Schwartz et al., 2011; Kalénine et al., 2009). Angular gyrus activation has also been observed in studies of tool use knowledge, where responses to novel tools are compared before and after training on how they are used (Creem-Regehr, Dilda, Vicchirilli, Federer, & Lee, 2007; Weisberg, van Turennout, & Martin, 2007) because of increased knowledge of either function or manipulation. Lastly, Fairhall, Anzellotti, Ubaldi, and Caramazza (2013) found that the angular gyrus responded more to retrieving knowledge about unique landmarks (e.g., the Eiffel tower) relative to famous people

across both verbal and visual presentation. This also strongly suggests some content-selectivity, in this case, for contexts or events. On the whole, many distinct findings point to a role of the angular gyrus in conceptual knowledge of some particular kind. A reasonable working hypothesis is that the kind of knowledge it represents is primarily that of events and actions, including their overall goals and the functions of objects that appear in them. The present results extend the domain of actions to those that take place in the mind and in interpersonal space, rather than only with the body or in physical space. Further work should attempt to characterize more precisely the extent and boundaries of the content the pIPL represents.

Further work should also test whether the role of pIPL extends beyond retrieval of self-generated action intentions. Desmurget et al. (2009) stimulated various parts of the IPL of awake surgical patients, which led them to report a conscious experience of the desire to move particular parts of their body. This was in contrast with pFC stimulation, which caused actual or illusory movements. Although the scope of parietal cortex that was stimulated was large, it is possible that the effects were driven by the same region as described in the present experiments. If true, this would support the interpretation of pIPL as participating in encoding intentions and would also suggest that it is involved in the generation of action plans. Although conceptual knowledge of actions is relevant to action planning, the present experiments do not rule out the possibility that pIPL is involved in the process of generating an action intention, even covertly. Future work should explore the role of this region in kinds of conceptual attributes or tasks—ones that do not engage first-person action retrieval.

Broader Implications

The present findings have broader implications for how semantic knowledge is represented and organized. Prior work has established that semantic knowledge is distributed across multiple subsystems, some of which are selective to particular domains, such as living or nonliving things (Caramazza & Shelton, 1998; Hart & Gordon, 1992; Hillis & Caramazza, 1991; Warrington & McCarthy, 1987; Warrington & Shallice, 1984), and others to particular attributes, such as motion or color (Kellenbach, Brett, & Patterson, 2001; Miceli et al., 2001; Chao, Haxby, & Martin, 1999; Martin et al., 1995). A commonly expressed view is that the principle underlying this distributed organization is sensory modality—that the distinctions between semantic subsystems falls exactly along the same lines as our sensory systems: Properties we detect with our eyes are stored in the “visual semantic” system, properties we hear are stored in the “auditory semantic system,” and these make up the sum of our conceptual knowledge (Beauchamp & Martin, 2007; Goldberg, Perfetti, & Schneider, 2006; Thompson-Schill, 1999). This view either explicitly denies or leaves out the possibility of attribute-selective systems that are not related to a sensory modality. However, this

theoretical idea cannot be evaluated without a search for systems that represent non-modality-related attributes. Such attempts are rare (though see Contreras, Banaji, & Mitchell, 2012; Zahn et al., 2007), and most work on abstract knowledge groups together all kinds of abstract knowledge into a single category (Rodríguez-Ferreiro, Gennari, Davies, & Cuetos, 2011; Skipper, Ross, & Olson, 2011; Duñabeitia, Avilés, Afonso, Scheepers, & Carreiras, 2009; Goldberg, Perfetti, Fiez, & Schneider, 2007; Binder, Westbury, McKiernan, Possing, & Medler, 2005; Noppeney & Price, 2002), which may not be a well-defined, coherent kind, and perhaps as a result, findings are inconsistent across studies. Instead, it is likely that nonobservable semantic knowledge, just like concrete semantic knowledge, is divided into attribute-selective systems. The present experiments are some of the first to attempt to consider this possibility, and their effectiveness suggests this may be a fruitful way forward. More importantly, they imply that the semantic system does contain subsystems that respond to attributes unrelated to any sensory or motor modality, challenging the view described above.

Lastly, the present results provide evidence against proposals that conceptual (i.e., modality-general) knowledge of goal attributes is represented within motor regions; for instance, the mirror neuron theory (Rizzolatti & Sinigaglia, 2010). Representations of goal attributes that spanned both motoric and nonmotoric content were instead represented in the pIPL, a region that we found does not represent body movement. Of course, we do not deny that motoric aspects of actions are represented as well, elsewhere. We also reported regions that showed effects of goal-directedness for motor verbs only; such regions might represent motor-specific aspects of goal-directed actions. Thus, we do not exclude a role for the motor system in action knowledge but suggest that any such role is specific to concrete actions and that conceptual understanding of goals in general is represented in a nonmotor area.

Overall Conclusions

By considering a broad range of actions—from those that involve the body to those involving only the mind—the present experiments separately varied the presentation of intention attributes and that of motoric attributes, as elicited by action verbs. A portion of posterior parietal cortex, near the angular gyrus, responded to intention information (but not body movement information) and did so equally across both motoric and nonmotoric actions. We propose that this region represents conceptual knowledge about why actions are typically performed, perhaps as part of a more general role in event and action semantics. Importantly for theoretical considerations about the organization of semantic knowledge, it serves as a specific example of an attribute-selective conceptual system that is unrelated to any sensory or motor modality. The existence of such a system and its robustness of response (visible in

individual participants) are expected from the simple observation that the meaning of many of our action concepts is given largely by what they intend to accomplish, rather than on the movements of one's body—and from the sheer number of action concepts that refer to types of mental processes and interpersonal interactions—learning, dreaming, empathizing, teaching. This may arise from the general principle that nonobservable attributes—not just sensory features—matter greatly to human concepts.

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Notes

1. In one framework, multiple sensory-specific attributes are bound together by a central “hub” (Simmons & Martin, 2009; Patterson, Nestor, & Rogers, 2007; Rogers et al., 2006); the question of the existence of a hub is a separate one from the representation of attributes not included in any sensory-specific systems.
2. Whether these hypothesized object-purpose and action-purpose systems would be related is an enticing possibility (Pillon & D'Honinckun, 2010, 2011; Vannuscorps & Pillon, 2011).
3. A similar profile was found in right TPJ and precuneus, the two other ROIs tested from the theory of mind network.

REFERENCES

- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2003). fMRI responses to video and point-light displays of moving humans and manipulable objects. *Journal of Cognitive Neuroscience*, *15*, 991–1001.
- Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex*, *43*, 461–468.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*, 527–536.
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*, 2767–2796.
- 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. *Journal of Cognitive Neuroscience*, *17*, 905–917.
- Bloom, P. (1996). Intention, history, and artifact concepts. *Cognition*, *60*, 1–29.
- Bloom, P., & Markson, L. (1998). Intention and analogy in children's naming of pictorial representations. *Psychological Science*, *9*, 200–204.
- Bonner, M. F., Peelle, J. E., Cook, P. A., & Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. *Neuroimage*, *71*, 175–186.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Brass, M., Schmitt, R. M., Spengler, S., & Gergely, G. (2007). Investigating action understanding: Inferential processes versus action simulation. *Current Biology*, *17*, 2117–2121.
- Buccino, G., Baumgaertner, A., Colle, L., Buechel, C., Rizzolatti, G., & Binkofski, F. (2007). The neural basis for understanding non-intended actions. *Neuroimage*, *36*(Suppl. 2), T119–T127.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, *24*, 355–363.
- Buxbaum, L. J., Veramontil, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing “what for” but not “how.” *Neurocase*, *6*, 83–97.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain the animate-inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.
- Castelli, F., Happé, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, *12*, 314–325.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Citron, F. M. M., Gray, M. A., Critchley, H. D., Weekes, B. S., & Ferstl, E. C. (2014). Emotional valence and arousal affect reading in an interactive way: Neuroimaging evidence for an approach-withdrawal framework. *Neuropsychologia*, *56C*, 79–89.
- Contreras, J. M., Banaji, M. R., & Mitchell, J. P. (2012). Dissociable neural correlates of stereotypes and other forms of semantic knowledge. *Social Cognitive and Affective Neuroscience*, *7*, 764–770.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, an International Journal*, *29*, 162–173.
- Creem-Regehr, S. H., Dilda, V., Vicchirilli, A. E., Federer, F., & Lee, J. N. (2007). The influence of complex action knowledge on representations of novel graspable objects: Evidence from functional magnetic resonance imaging. *Journal of the International Neuropsychological Society*, *13*, 1009–1020.
- Csibra, G., & Gergely, G. (1998). The teleological origins of mentalistic action explanations: A developmental hypothesis. *Developmental Science*, *1*, 255–259.
- Davies, M. (2011). *N-grams and word frequency data from the Corpus of Historical American English (COHA)*. Retrieved from www.ngrams.info.
- De Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology*, *18*, 454–457.
- De Renzi, E., & Lucchelli, F. (1988). Ideational apraxia. *Brain: A Journal of Neurology*, *111*, 1173–1185.
- De Zubicaray, G., Arciuli, J., & McMahon, K. (2013). Putting an “end” to the motor cortex representations of action words. *Journal of Cognitive Neuroscience*, *25*, 1957–1974.
- Decety, J., & Porges, E. C. (2011). Imagining being the agent of actions that carry different moral consequences: An fMRI study. *Neuropsychologia*, *49*, 2994–3001.
- Den Ouden, D. B., Fix, S., Parrish, T. B., & Thompson, C. K. (2009). Argument structure effects in action verb naming in static and dynamic conditions. *Journal of Neurolinguistics*, *22*, 196–215.

- Denkova, E., Dolcos, S., & Dolcos, F. (2013). The effect of retrieval focus and emotional valence on the inferior frontal cortex activity during autobiographical recollection. *Frontiers in Behavioral Neuroscience*, *7*, 192.
- Desmurget, M., Reilly, K. T., Richard, N., Szathmari, A., Mottolese, C., & Sirigu, A. (2009). Movement intention after parietal cortex stimulation in humans. *Science*, *324*, 811–813.
- Dodell-Feder, D., Koster-Hale, J., Bedny, M., & Saxe, R. (2011). fMRI item analysis in a theory of mind task. *Neuroimage*. doi:10.1016/j.neuroimage.2010.12.040.
- Duñabeitia, J. A., Avilés, A., Afonso, O., Scheepers, C., & Carreiras, M. (2009). Qualitative differences in the representation of abstract versus concrete words: Evidence from the visual-worlds paradigm. *Cognition*, *110*, 284–292.
- Fairhall, S., Anzellotti, S., Ubaldi, S., & Caramazza, A. (2013). Person- and place-selective neural substrates for entity-specific semantic access. *Cerebral Cortex*, *24*, 1687–1696.
- Fairhall, S., & Caramazza, A. (2013). Brain regions that represent amodal conceptual knowledge. *Journal of Neuroscience*, *33*, 10552–10558.
- Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, *13*, 170–177.
- Garcea, F. E., & Mahon, B. Z. (2012). What is in a tool concept? Dissociating manipulation knowledge from function knowledge. *Memory & Cognition*, *40*, 1303–1313.
- Gelman, S. A., & Wellman, H. M. (1991). Insides and essences: Early understandings of the non-obvious. *Cognition*, *38*, 213–244.
- Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends in Cognitive Sciences*, *7*, 287–292.
- Goldberg, R. F., Perfetti, C. A., Fiez, J. A., & Schneider, W. (2007). Selective retrieval of abstract semantic knowledge in left prefrontal cortex. *Journal of Neuroscience*, *27*, 3790–3798.
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006). Perceptual knowledge retrieval activates sensory brain regions. *The Journal of Neuroscience*, *26*, 4917–4921.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*, 711–720.
- Gutheil, G., Bloom, P., Valderrama, N., & Freedman, R. (2004). The role of historical intuitions in children's and adults' naming of artifacts. *Cognition*, *91*, 23–42.
- Hart, J., & Gordon, B. (1992). Neural subsystems for object knowledge. *Nature*, *359*, 60–64.
- Hauk, O., Davis, M. H., Kherif, F., & Pulvermüller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *European Journal of Neuroscience*, *27*, 1856–1866.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301–307.
- Hesse, M. D., Sparing, R., & Fink, G. R. (2009). End or means—The “what” and “how” of observed intentional actions. *Journal of Cognitive Neuroscience*, *21*, 776–790.
- Hillis, A. E., & Caramazza, A. (1991). Category-specific naming and comprehension impairment: A double dissociation. *Brain: A Journal of Neurology*, *114*, 2081–2094.
- Kalénine, S., Peyrin, C., Pichat, C., Segebarth, C., Bonthoux, F., & Baciuc, M. (2009). The sensory-motor specificity of taxonomic and thematic conceptual relations: A behavioral and fMRI study. *Neuroimage*, *44*, 1152–1162.
- Keil, F. C., Smith, W. C., Simons, D. J., & Levin, D. T. (1998). Two dogmas of conceptual empiricism: Implications for hybrid models of the structure of knowledge. *Cognition*, *65*, 103–135.
- Kelemen, D., & Carey, S. (2007). The essence of artifacts: Developing the design stance. In S. Laurence & E. Margolis (Eds.), *Creations of the mind: Artifacts and their representation*. Oxford, UK: Oxford University Press. Also printed in Hungarian in Csaba Pleh (2007). *Essence*, 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. *Cognitive, Affective & Behavioral Neuroscience*, *1*, 207–221.
- Kemler Nelson, D. G. K., Franken, A., Morris, C., & Blair, E. (2000). Young children's use of functional information to categorize artifacts: Three factors that matter. *Cognition*, *77*, 133–168.
- Koster-Hale, J., & Saxe, R. (2013). Functional neuroimaging of theory of mind. In S. Baron-Cohen, M. Lombardo, & H. Tager-Flusberg (Eds.), *Understanding other minds: Perspectives from developmental social neuroscience* (3rd ed., pp. 132–163). Oxford: Oxford University Press.
- Lingnau, A., & Petris, S. (2012). Action understanding within and outside the motor system: The role of task difficulty. *Cerebral Cortex*, *23*, 1342–1350.
- Majdandžić, J., Grol, M. J., van Schie, H. T., Verhagen, L., Toni, I., & Bekkering, H. (2007). The role of immediate and final goals in action planning: An fMRI study. *Neuroimage*, *37*, 589–598.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, *58*, 25–45.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and process. *Current Opinion in Neurobiology*, *11*, 194–201.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 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. *Nature Neuroscience*, *4*, 662–667.
- Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, *18*, 1586–1594.
- Nicholson, T., Roser, M., & Bach, P. (2013). Action goal understanding is primarily driven by object, not motor, information. *Poster presented at the Concepts, Actions, and Objects Workshop*, 23–26 May, Rovereto, Italy.
- Noppeney, U., & Price, C. J. (2002). Retrieval of visual, auditory, and abstract semantics. *Neuroimage*, *15*, 917–926.
- Ochipa, C., Rothi, L. J. G., & Heilman, K. M. (1989). Ideational apraxia: A deficit in tool selection and use. *Annals of Neurology*, *25*, 190–193.
- 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. *Nature*, *8*, 976–989.
- Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience*, *16*, 1706–1716.
- Perner, J., Aichhorn, M., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Thinking of mental and other representations: The roles of left and right temporo-parietal junction. *Social Neuroscience*, *1*, 245–258.
- Pillon, A., & D'Honinchtun, P. (2010). The organization of the conceptual system: The case of the “object versus action” dimension. *Cognitive Neuropsychology*, *27*, 587–613.
- Pillon, A., & D'Honinchtun, 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. *Cognitive Neuropsychology*, *28*, 37–41.
- Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitecturally defined primary and premotor cortices. *Neuroimage*, *43*, 634–644.
- Price, A. R., Bonner, M. F., Peelle, J. E., & Grossman, M. (2013). The neuroanatomical basis for combinatorial semantic processing: Evidence from neurodegenerative disease patients. Poster presented at the Concepts, Actions, and Objects Workshop, 23–26 May, Rovereto, Italy.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264–274.
- Rodríguez-Ferreiro, J., Gennari, S. P., Davies, R., & Cuetos, F. (2011). Neural correlates of abstract verb processing. *Journal of Cognitive Neuroscience*, *23*, 106–118.
- Rogers, T. T., Hocking, J., Noppeney, U., Mechelli, A., Gorno-Tempini, M. L., Patterson, K., et al. (2006). Anterior temporal cortex and semantic memory: Reconciling findings from neuropsychology and functional imaging. *Cognitive, Affective, & Behavioral Neuroscience*, *6*, 201–213.
- Ruby, P., Sirigu, A., & Decety, J. (2002). Distinct areas in parietal cortex involved in long-term and short-term action planning: A PET investigation. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *38*, 321–339.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in “theory of mind.” *Neuroimage*, *19*, 1835–1842.
- Saxe, R., & Wexler, A. (2005). Making sense of another mind: The role of the right temporo-parietal junction. *Neuropsychologia*, *43*, 1391–1399.
- Saxe, R., Xiao, D.-K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, *42*, 1435–1446.
- Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., et al. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 8520–8524.
- Shultz, S., Lee, S. M., Pelphrey, K., & McCarthy, G. (2011). The posterior superior temporal sulcus is sensitive to the outcome of human and non-human goal-directed actions. *Social Cognitive and Affective Neuroscience*, *6*, 602–611.
- Simmons, W. K., & Martin, A. (2009). The anterior temporal lobes and the functional architecture of semantic memory. *Journal of the International Neuropsychological Society*, *15*, 645–649.
- Sirigu, A., Duhamel, J.-R., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. *Brain*, *114*, 2555–2573.
- Skipper, L. M., Ross, L. A., & Olson, I. R. (2011). Sensory and semantic category subdivisions within the anterior temporal lobes. *Neuropsychologia*, *49*, 3419–3429.
- Spunt, R. P., & Lieberman, M. D. (2012). Dissociating modality-specific and supramodal neural systems for action understanding. *The Journal of Neuroscience*, *32*, 3575–3583.
- Spunt, R. P., Satpute, A. B., & Lieberman, M. D. (2011). Dissociable neural systems support retrieval of how and why action knowledge. *Journal of Cognitive Neuroscience*, *23*, 63–74.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.
- Thompson, C. K., Bonakdarpour, B., Fix, S. C., Blumenfeld, H. K., Parrish, T. B., Gitelman, D. R., et al. (2007). Neural correlates of verb argument structure processing. *Journal of Cognitive Neuroscience*, *19*, 1753–1767.
- Thompson-Schill, S. L. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, *37*, 671–676.
- Träuble, B., & Pauen, S. (2007). The role of functional information for infant categorization. *Cognition*, *105*, 362–379.
- Träuble, B., & Pauen, S. (2011). Cause or effect: What matters? How 12-month-old infants learn to categorize artifacts. *The British Journal of Developmental Psychology*, *29*, 357–374.
- Vander Wyk, B. C., Hudac, C. M., Carter, E. J., Sobel, D. M., & Pelphrey, K. A. (2009). Action understanding in the superior temporal sulcus region. *Psychological Science*, *20*, 771.
- 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*, 2321–2341.
- Vigliocco, G., Kousta, S.-T., Della Rosa, P. A., Vinson, D. P., Tettamanti, M., Devlin, J. T., et al. (2014). The neural representation of abstract words: The role of emotion. *Cerebral Cortex*, *24*, 1–11.
- Vigliocco, G., & Vinson, D. (2007). Semantic representation. In G. Gaskell (Ed.), *Oxford handbook of psycholinguistics*. Oxford: Oxford University Press.
- Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Neurocase*, *110*, 1273–1296.
- Warrington, E. K., & Shallice, T. (1984). Category-specific semantic impairments. *Brain*, *107*, 829–854.
- Watson, C., Cardillo, E., Ianni, G., & Chatterjee, A. (2013). Action concepts in the brain: An activation-likelihood estimation meta-analysis. *Journal of Cognitive Neuroscience*, *25*, 1191–1205.
- Weisberg, J., van Turenout, M., & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex*, *17*, 513–521.
- Zahn, R., Moll, J., Krueger, F., Huey, E. D., Garrido, G., & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *104*, 6430–6435.