Action Concepts in the Brain: An Activation Likelihood Estimation Meta-analysis

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Abstract

■ Many recent neuroimaging studies have investigated the representation of semantic memory for actions in the brain. We used activation likelihood estimation (ALE) meta-analyses to answer two outstanding questions about the neural basis of action concepts. First, on an "embodied" view of semantic memory, evidence to date is unclear regarding whether visual motion or motor systems are more consistently engaged by action concepts. Second, few studies have directly investigated the possibility that action concepts accessed verbally or nonverbally recruit different areas of the brain. Because our meta-analyses did not include studies requiring the perception of dynamic depictions of actions or action execution, we were able to determine whether conceptual processing alone recruits visual motion and motor systems. Significant concordance in brain regions within or adjacent to visual motion areas emerged in all meta-analyses. By contrast, we did not observe significant concordance in motor or premotor cortices in any analysis. Neural differences between action images and action verbs followed a gradient of abstraction among representations derived from visual motion information in the left lateral temporal and occipital cortex. The consistent involvement of visual motion but not motor brain regions in representing action concepts may reflect differences in the variability of experience across individuals with perceiving versus performing actions. ■

INTRODUCTION

Until recently, studies of concrete objects and the words that refer to them motivated most theories of the organization of semantic memory. In part bolstered by the discovery of "mirror neurons" (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), the realm of semantics has lately expanded to include another kind of conceptual knowledge: the meanings of human actions and events (e.g., Gallese & Lakoff, 2005; Vigliocco, Vinson, Lewis, & Garrett, 2004; Pulvermüller, 1999). Current thinking about the mental representation of action concepts is typically framed by theories of "embodied" or "grounded cognition" (see Barsalou, 2008, for a review). On this view, sensory and motor states acquired during real-world experience are reactivated or "simulated" during later conceptual processing (Decety & Grèzes, 2006; Barsalou, 1999). In neural terms, this means that object concepts may be represented in areas of the brain specialized for processing the salient visual features of objects, like their color or shape (e.g., Martin & Chao, 2001). Analogously, concepts that correspond to human actions may be represented in the same areas of the brain responsible for planning and executing movements (Gallese & Lakoff, 2005; Pulvermüller, 1999).[1]

Indeed, a growing body of research has focused on the involvement of the motor system in recognizing the actions of others (see Rizzolatti & Craighero, 2004, for a review). For instance, a recent meta-analysis of neuroimaging studies of action recognition found that viewing dynamic depictions of human actions is consistently associated with activity in frontoparietal motor circuits (Caspers, Zilles, Laird, & Eickhoff, 2010; see also Grosbras, Beaton, & Eickhoff, 2012). On one influential hypothesis, cells that fire during both action execution and observation ("mirror neurons") support action recognition. Areas exhibiting "mirror" behavior in humans include premotor cortex, inferior frontal gyrus (IFG), and the inferior parietal lobule (IPL; e.g., Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti, Fadiga, Matelli, et al., 1996). However, more symbolic representations of actions, like static depictions of actions or action words, also engage the motor system. Viewing and naming pictures of actions evokes activity in motor and premotor cortices relative to pictures of objects (Berlingeri et al., 2008; Liljeström et al., 2008; Damasio et al., 2001), and the comprehension of action language can also draw upon the motor system (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Noppeney, Josephs, Kiebel, Friston, & Price, 2005; Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004). For instance, Raposo, Moss, Stamatakis, and Tyler (2009) observed significant activation of motor and premotor cortices when participants listened to action verbs presented in isolation (e.g., "kick") or in sentences (e.g.,

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"kick the ball") but not when they were presented in idiomatic sentences (e.g., "kick the bucket").

But sources of information outside the motor system may also contribute to the neural representation of action concepts. In particular, an area of the brain specialized for processing visual motion (area MT+; Watson et al., 1993) is active when participants view static depictions of actions (Kourtzi & Kanwisher, 2000; Senior et al., 2000), although no visual motion is present in the stimuli. Area MT+ is also active when participants make semantic decisions about pictured actions (Kable, Lease-Spellmeyer, & Chatterjee, 2002). Furthermore, visual motion areas can be recruited by action language: Saygin, McCullough, Alac, and Emmorey (2010) found that listening to sentences describing actions with associated motion yielded greater activity in functionally localized area MT+ relative to sentences describing static events. On an embodied perspective, visual motion accompanies many actions, so areas of the brain that process visual motion may be re-activated during later conceptual processing (Watson & Chatterjee, 2011; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005). However, the recruitment of visual motion areas for semantic purposes, although consistent with an embodied perspective, is not compatible with the hypothesis that the motor system alone supports the comprehension of actions (e.g., Rizzolatti & Sinigaglia, 2010; Buccino, Binkofski, & Riggio, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996).

Individual neuroimaging experiments suggest that both the motor system and visual motion areas can be engaged when participants access action semantics. However, an outstanding question is the relative importance of each type of information for representing action concepts. Inconsistencies among findings in this domain contribute to the confusion. For instance, not all studies using action images (Kable et al., 2002) or action words (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Kable et al., 2002, 2005) observe significant activity in motor or premotor cortices. Similarly, area MT+ is active when participants listen to action verbs in sentences (Saygin et al., 2010) but not in isolation (Bedny et al., 2008; Kable et al., 2005). Thus, current evidence is inconclusive with respect to whether one source of modality-specific information is more consistently involved in representing action concepts. Yet, the answer to this question has more general implications for theories of embodied cognition: If the recruitment of sensory or motor systems during conceptual processing is variable, the embodiment of meaning is not necessary and instead fluctuates either within or between individuals.

The way in which action concepts are accessed may also affect the degree to which sensory and motor systems—or other cortical areas, instead—are engaged. In particular, static, visual depictions of actions may evoke different brain responses than action language. For example, Kable et al. (2005) found that making semantic judgments about action words relative to object words was associated with greater activity in the left posterior middle temporal gyrus (pMTG) and posterior STS (pSTS). The peak of this activation within lateral temporal cortex was located anterior and dorsal to the peak activation for action pictures relative to object pictures. And whereas action pictures activated bilateral area MT+, action words activated adjacent, but not overlapping, cortical areas (Kable et al., 2002, 2005). These results suggest that more abstract representations of action concepts, such as those accessed by language, may be represented near the sensory or motor cortices from which the representations are derived (Chatterjee, 2008; Kable et al., 2005; see also Vigliocco et al., 2004; Simmons & Barsalou, 2003; Plaut, 2002). Additionally, because of the left hemisphere's critical role in language processing, accessing action concepts with words rather than images may produce a more strongly left-lateralized pattern of neural activity. By contrast, on a "strong" embodied view, the sensory and motor states re-enacted during conceptual processing are constitutive of a concept (Barsalou, 1999; Pulvermüller, 1999). Action images and action words should therefore evoke similar neural responses in areas of the brain representing conceptual content. Despite the relevance for theories of embodied cognition, very few neuroimaging studies have directly investigated the neural similarities between concepts accessed by verbal or nonverbal means (i.e., Esopenko et al., 2012; Shinkareva, Malave, Mason, Mitchell, & Just, 2011), and both of these studies used object, rather than action, stimuli.

In the current study, we used a series of activation likelihood estimation (ALE) meta-analyses (Eickhoff et al., 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002) to determine (1) the consistency with which action concepts engage sensory and motor systems and (2) the similarities and differences between action concepts accessed either by images or words. Although individual experiments in this domain have yielded inconsistent results, the meta-analysis method offers the potential to identify patterns that emerge as consistent across many studies. Other meta-analyses have examined the observation of dynamic depictions of human actions and action execution (e.g., Grosbras et al., 2012; Caspers et al., 2010), but we focus on studies using static depictions of human actions and studies without overt action execution requirements (other than finger or mouth movements required to respond). By looking at this subset of studies, we can accurately assess the involvement of sensory and motor systems in conceptual processing rather than overt visual motion processing or motor execution. We have also included studies using action language, and we focus only on experiments in which action verbs were presented in isolation. In doing so, we can clearly identify the concepts evoked by the action words rather than other words in a sentence.

In Meta-analysis 1, we looked for consistency across all fMRI and PET studies in which participants likely accessed action concepts via images or words. In Meta-analysis 2, we took a finer-grained approach and looked for consistency among a subset of studies in which participants

were instructed to access action concepts as part of an experimental task. By contrast, participants not actively engaged in a task (e.g., passive viewing) may not engage the semantic system as deeply or at all. In Meta-analysis 3, we looked for similarities and differences in neural activity associated with processing either static depictions of action images or action words.

METHODS

Inclusion of Studies

We identified a preliminary list of articles for inclusion by searching PsycInfo and PubMed article databases. Our search criteria were (1) a word in the abstract denoting a neuroimaging method (e.g., "fMRI," "fMRI," "BOLD," "PET") and (2) the words "action," "actions," "verb," or "verbs". We also added studies to the list manually by examining the reference sections of relevant articles. In total, this broad preliminary search yielded a list of 749 studies.

Next, we examined the abstracts of these articles to determine which studies appeared to meet our criteria for inclusion. This process narrowed the list down to 102 studies. Finally, we examined each study in detail to determine if it met all criteria for inclusion. (The number of papers eliminated by each criterion is given in square brackets). Experiments were included if they (1) were published in a peer-reviewed journal ($n = 1$), (2) reported data from multiple, neurologically healthy adult participants ($n = 3$), and (3) reported peak coordinates from whole-brain, group-level, voxel-wise analyses (corrected or uncorrected for multiple comparisons at the whole-brain level) in either Montreal Neurologic Institute (MNI) or Talairach standardized brain spaces ($n = 32$). Criterion 3 eliminated studies reporting only ROI analyses and studies in which small-volume corrections had been applied to whole-brain analyses.

In addition to these general methodological criteria, we established six criteria related to our questions of interest. We applied these criteria on a by-contrast basis: If at least one contrast in a study met the criteria, it was included in the meta-analysis even if other contrasts from the study were excluded. We only included contrasts that (4) did not involve explicit motor imagery tasks (i.e., tasks in which participants were instructed to imagine themselves performing actions; $n = 1$), (5) did not involve tasks in which participants overtly executed body actions ($n = 0$), other than those required to speak a response or manually press response button, and (6) presented to participants action-related tasks or stimuli ($n = 17$). Criterion 6 mostly eliminated studies in which stimuli were verbs, in general, rather than action verbs, in particular. Additionally, we only included contrasts in which (7) stimuli were static depictions of human actions (drawings or photographs), single verbs referring to human actions, or object words or images only if the task focused attention on the human actions performed with those objects ($n = 10$). In the last

case, although the stimuli are objects, participants have to access action knowledge to perform the task, for instance, to generate the name of an action associated with an object (i.e., verb generation) or to decide if pairs of objects are used with the same action. Given Criterion 4, however, we nevertheless excluded any contrasts in which participants were instructed to imagine using an object. Finally, we excluded contrasts in which (8) action-related neural activity was removed via the subtraction method ($n = 5$) or (9) response-related activation in the condition of interest was not controlled for by the baseline task ($n = 4$). For instance, we eliminated a contrast in which the generation of common actions was compared with the generation of uncommon actions (Seger, Desmond, Glover, & Gabrieli, 2000) because this contrast highlighted neural activity related to "common-ness" rather than "action-ness." An example of a contrast eliminated by Criterion 9 is covert action picture naming versus fixation.

These task- and stimulus-related criteria were necessary to ensure that we could adequately assess the involvement of sensory or motor systems in conceptual processing. Both of these areas, by definition, are activated by lower-level processes (visual perception and motor execution). To correctly infer that these areas are also involved in semantic processing, we therefore had to eliminate contrasts in which activation in sensory or motor areas could be attributed to a lower level of processing. For instance, if visual motion is present in the stimuli (i.e., videos of actions) or if a body action is overtly executed, activity in modality-specific areas cannot be attributed to semantic processing. Explicit motor imagery, too, has been shown to activate premotor and primary motor cortices (Porro et al., 1996; Roth et al., 1996), so we also excluded contrasts involving this task.

Similarly, we excluded contrasts in which the task of interest required a manual response or overt/covert vocalization but the task to which it was compared did not; in these cases, activation can arise in the motor system from participants' responses rather than from semantic processing (see Aziz-Zadeh et al., 2006; Palmer et al., 2001, for evidence that covert speech recruits motor areas of the brain). Other researchers have used similar criteria (e.g., Binder, Desai, Graves, & Conant, 2009; Vigneau et al., 2006), and baselines that control for speech and low-level visual processing may actually more sensitively reveal semantic processing in the brain (Price, Devlin, Moore, Morton, & Laird, 2005).

Additionally, we only included contrasts in which action verbs were presented in isolation and not as part of a phrase or sentence. Our meta-analyses are focused on the conceptual representations of actions, and including sentences or phrases containing other kinds of words (e.g., nouns, adjectives) prevents us from drawing focused conclusions about the neural basis of action concepts, in particular.

After this elimination process, 29 individual experiments remained (Table 1). Note that some studies contain

Table 1. Studies Included in Final Meta-analyses

Study	Study No.	Contrast No.	Participants	Foci	Task Type	Stimuli Type	Meta-analysis No.
Bedny et al. (2008)	1	1	12	1	Lexical-semantic	Action verbs	1, 2, 3
Bedny, Caramazza, Pascual-Leone, & Saxe (2012)	2	2	20	2	Lexical-semantic	Action verbs	1, 2, 3
		3	20	5	Lexical-semantic	Action verbs	1, 2, 3
Berlingeri et al. (2008)	3	4	12	30	Lexical-semantic	Action verbs	1, 2, 3
		5	12	18	Lexical-semantic	Action verbs	1, 2, 3
		6	12	26	Lexical-semantic	Action images	1, 2, 3
		7	12	28	Lexical-semantic	Action images	1, 2, 3
Boronat et al. (2005)	4	8	15	5	Lexical-semantic	Object nouns	1, 2
		9	15	7	Lexical-semantic	Object images	1, 2
Buxbaum, Kyle, Tang, & Detre (2006)	5	10	15	3	Lexical-semantic	Object images	1, 2
		11	15	2	Lexical-semantic	Object images	1, 2
		12	15	5	Lexical-semantic	Object images	1, 2
Canessa et al. (2008)	6	13	15	3	Lexical-semantic	Object images	1, 2
Crescentini, Shallice, & Macaluso (2010)	7	14	14	2	Verb generation	Object nouns	1
Damasio et al. (2001)	8	15	20	12	Lexical-semantic	Action images	1, 2, 3
		16	20	12	Lexical-semantic	Action images	1, 2, 3
		17	20	1	Lexical-semantic	Action images	1, 2, 3
Grèzes and Decety (2002)	9	18	10	6	Verb generation	Object images	1
Hamzei et al. (2003)	10	19	12	3	Passive	Action images	1, 3
Hauk et al. (2004)	11	20	14	7	Passive	Action verbs	1, 3
Kana and Travers (2012)	12	21	26	11	Lexical-semantic	Action images	1, 2, 3
Kellenbach et al. (2003)	13	22	9	9	Lexical-semantic	Object images	1, 2
Kemmerer, Castillo, Talavage, Patterson, & Wiley (2008)	14	23	16	23	Lexical-semantic	Action verbs	1, 2, 3
		24	16	8	Lexical-semantic	Action verbs	1, 2, 3
		25	16	14	Lexical-semantic	Action verbs	1, 2, 3
		26	16	23	Lexical-semantic	Action verbs	1, 2, 3
		27	16	9	Lexical-semantic	Action verbs	1, 2, 3
Liljeström et al. (2008)	15	28	15	10	Lexical-semantic	Action images	1, 2, 3
Martin, Haxby, Lalonde, Wiggs, & Ungerleider (1995)	16	29	12	10	Verb generation	Object images	1
Osaka, Matsuyoshi, Ikeda, & Osaka (2010)	17	30	14	4	Lexical-semantic	Action images	1, 2, 3
		31	14	3	Lexical-semantic	Action images	1, 2, 3
Péran et al. (2010)	18	32	12	4	Verb generation	Object images	1
		33	12	1	Verb generation	Object images	1
Pierno et al. (2009)	19	34	15	4	Passive	Action images	1, 3
		35	15	8	Passive	Action images	1, 3

Table 1. (*continued*)

Study	Study No.	Contrast No.	Participants	Foci	Task Type	Stimuli Type	Meta-analysis No.
Raposo et al. (2009)	20	36	14	2	Passive	Action verbs	1, 3
Rodríguez-Ferreiro, Gennari, Davies, & Cuetos (2011)	21	37	14	7	Lexical-semantic	Action verbs	1, 2, 3
		38	14	3	Lexical-semantic	Action verbs	1, 2, 3
Rüschemeyer, Brass, & Friederici (2007)	22	39	20	9	Lexical-semantic	Action verbs	1, 2, 3
		40	20	2	Lexical-semantic	Action verbs	1, 2, 3
Saccuman et al. (2006)	23	41	13	3	Lexical-semantic	Action images	1, 2, 3
		42	13	4	Lexical-semantic	Action images	1, 2, 3
		43	13	2	Lexical-semantic	Action images	1, 2, 3
		44	13	5	Lexical-semantic	Action images	1, 2, 3
		45	13	8	Lexical-semantic	Action images	1, 2, 3
Sanjuán et al. (2010)	24	46	18	7	Verb generation	Object nouns	1
Tyler et al. (2003)	25	47	12	18	Lexical-semantic	Action verbs	1, 2, 3
		48	12	17	Lexical-semantic	Action verbs	1, 2, 3
		49	12	3	Lexical-semantic	Action verbs	1, 2, 3
		50	12	5	Lexical-semantic	Action verbs	1, 2, 3
van Dam, Rüshemeyer, & Bekkering (2010)	26	51	14	5	Lexical-semantic	Action verbs	1, 2, 3
Van Dam et al. (2012)	27	52	19	3	Lexical-semantic	Object nouns	1, 2
		53	19	6	Lexical-semantic	Object nouns	1, 2
Warburton et al. (1996)	28	54	9	6	Verb generation	Object nouns	1
	29	55	9	5	Verb generation	Object nouns	1

multiple experiments performed with different participants, so these were treated as independent experiments. In total, these experiments contained 55 relevant contrasts and 439 foci. Depending on the questions addressed by a particular meta-analysis, a single experiment could contribute foci from more than one relevant contrast. If foci from the same experiment but different contrasts were included in a single meta-analysis, these coordinates were aggregated together to avoid erroneously inflating the number of independent experiments (Turkeltaub et al., 2012).

Using the final set of experiments, we performed three separate meta-analyses. First, we examined convergence across all experiments, an analysis that included 29 experiments and 439 foci. For the second meta-analysis, we performed a more stringent investigation of the neural basis of action concepts: We examined convergence across studies in which participants were instructed to do lexical-semantic tasks while in the scanner (18 experiments and 374 foci). For instance, when making semantic relatedness judgments, performing semantic categorization, or naming, participants need to think about action concepts to

do the task. By contrast, passive viewing of images and reading of words may elicit but do not necessarily require semantic processing. In the second meta-analysis, we also excluded contrasts in which participants performed verb generation. The task demands of verb generation are very different from other included tasks in that participants must select a single concept from a pool of many possible, viable responses. Therefore, some areas implicated by verb generation may be those typically observed with increased demands for cognitive control rather than semantic processing per se (e.g., the anterior cingulate; Barch, Braver, Sabb, & Noll, 2000). Finally, we performed a third meta-analysis to contrast studies using two different kinds of stimuli, irrespective of task: static images of actions versus action verbs (18 experiments and 385 foci).

ALE Analyses

To determine convergence across studies, we used the ALE method (Eickhoff et al., 2009; Turkeltaub et al., 2002), implemented in the GingerALE 2.1.1 software

(brainmap.org). Before performing the analyses, any coordinates reported in Talairach space were converted to MNI space using GingerALE. With the ALE method, each coordinate in an experiment is modeled as a three-dimensional Gaussian probability distribution. The size of this probability distribution reflects the spatial uncertainty associated with each experiment and is determined by empirical estimates of between-subject and between-template (between-lab) variances derived by Eickhoff et al. (2009). Thus, the FWHM differs by experiment: Experiments with few participants have wide FWHMs, whereas experiments with many participants have narrower FWHMs. (The FWHM function used by GingerALE is plotted graphically at brainmap.org/ale/). Next, these peaks are combined within an experiment, using a recent modification to the ALE algorithm (Turkeltaub et al., 2012) that minimizes the contribution of within-experiment effects (i.e., multiple, similar coordinates reported in the same experiment) and makes the ALE method more amenable to inclusion of multiple contrasts calculated from the same set of participants. Within-experiment peaks are then combined across experiments to produce a whole-brain map of ALE scores. Finally, the ALE map is compared with the null distribution (computed nonparametrically by permuting the data) to determine if the null hypothesis—that the results of the studies are spatially unrelated to each other—can be rejected (Eickhoff et al., 2009). In Meta-analysis 3, we also performed a subtraction between two ALE maps to determine areas in which the two maps differed significantly. GingerALE also computes the conjunction between the two individual ALE maps using the logic of the minimum statistic for conjunctions (Nichols, Brett, Andersson, Wager, & Poline, 2005).

All analyses were corrected for multiple comparisons using a false discovery rate (FDR; Nichols & Holmes,

2002) of $q = .05$. We also used a minimum cluster size recommended by GingerALE for each analysis based on the total number of suprathreshold voxels: Clusters small enough to be comprised entirely of false positives (i.e., less than 5% of the total) were eliminated. For the conjunction analysis, created from two ALE maps already corrected for multiple comparisons, we excluded clusters with fewer than 50 voxels.

RESULTS

Meta-analysis 1: All Experiments

First, we looked for concordance among all experiments (i.e., contrasts) that met our criteria—in essence, experiments in which participants had the potential to access the conceptual representations of actions. Across all studies, a primarily left-lateralized pattern emerged (Table 2, Figure 1). The largest cluster of concordance occurred in the left pMTG and extended posteriorly to lateral temporal cortex and superiorly to posterior superior temporal gyrus and supramarginal gyrus. In the right hemisphere, a cluster of concordance in lateral occipital cortex emerged but did not extend outside the occipital cortex. Other clusters of concordance emerged in the left insular cortex/IFG and left fusiform gyrus.

Meta-analysis 2: Experiments Using Lexical-semantic Tasks Only

Next, we looked for concordance only among the studies that placed the strongest demands on semantic processing by instructing participants to perform lexical-semantic tasks while in the scanner. This analysis similarly revealed a strongly left-lateralized pattern of concordance (Table 2,

Table 2. Significant Activation Likelihood Clusters for Meta-analyses 1 and 2

Cluster No.	Location of Peak Voxel	x	y	z	ALE Value	Volume (mm^3)
Meta-analysis 1: All Experiments						
1	Left pMTG	−54	−50	−4	0.027	26688
2	Left insular cortex	−36	20	2	0.023	21920
3	Right lateral occipital cortex	54	−70	2	0.023	7096
4	Left fusiform gyrus	−40	−40	−22	0.020	5736
Meta-analysis 2: Experiments Using Lexical-semantic Tasks Only						
1	Left pMTG	−58	−50	6	0.022	10224
2	Left inferior/superior parietal cortex	−32	−56	54	0.016	7704
3	Right lateral occipital cortex	54	−70	2	0.023	7528
4	Left IFG (pars orbitalis)	−44	32	−16	0.014	6744

Coordinates are reported in MNI standardized space.

Figure 1. ALE values from Meta-analysis 1 (all studies). Maps have been corrected for multiple comparisons at FDR q = .05 with a minimum cluster size threshold equal to 5% of suprathreshold voxels. Coordinates are reported in MNI standardized space.
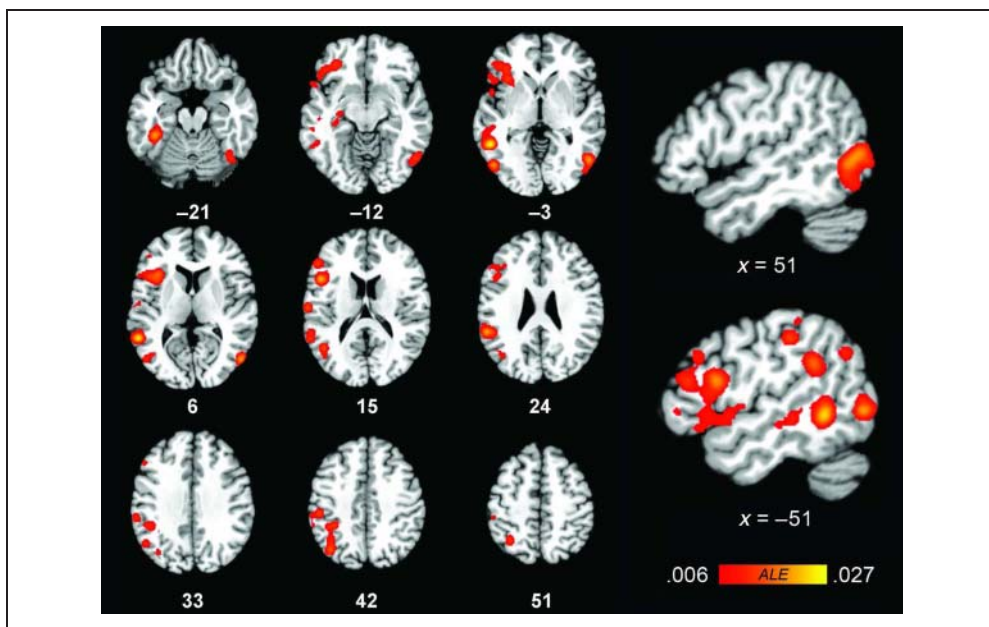

Figure 2). The largest cluster emerged in the left pMTG and also included posterior superior temporal gyrus, supramarginal gyrus, and the middle portion of the middle temporal gyrus (MTG). We also observed significant con-cordance within the left parietal cortex along the intraparietal sulcus and within the left IFG (pars orbitalis). Finally, a cluster in the right lateral occipital cortex reached significance.

Figure 2. ALE values from Meta-analysis 2 (studies using lexical-semantic tasks only). Maps have been corrected for multiple comparisons at FDR q = .05 with a minimum cluster size threshold equal to 5% of suprathreshold voxels. Coordinates are reported in MNI standardized space.
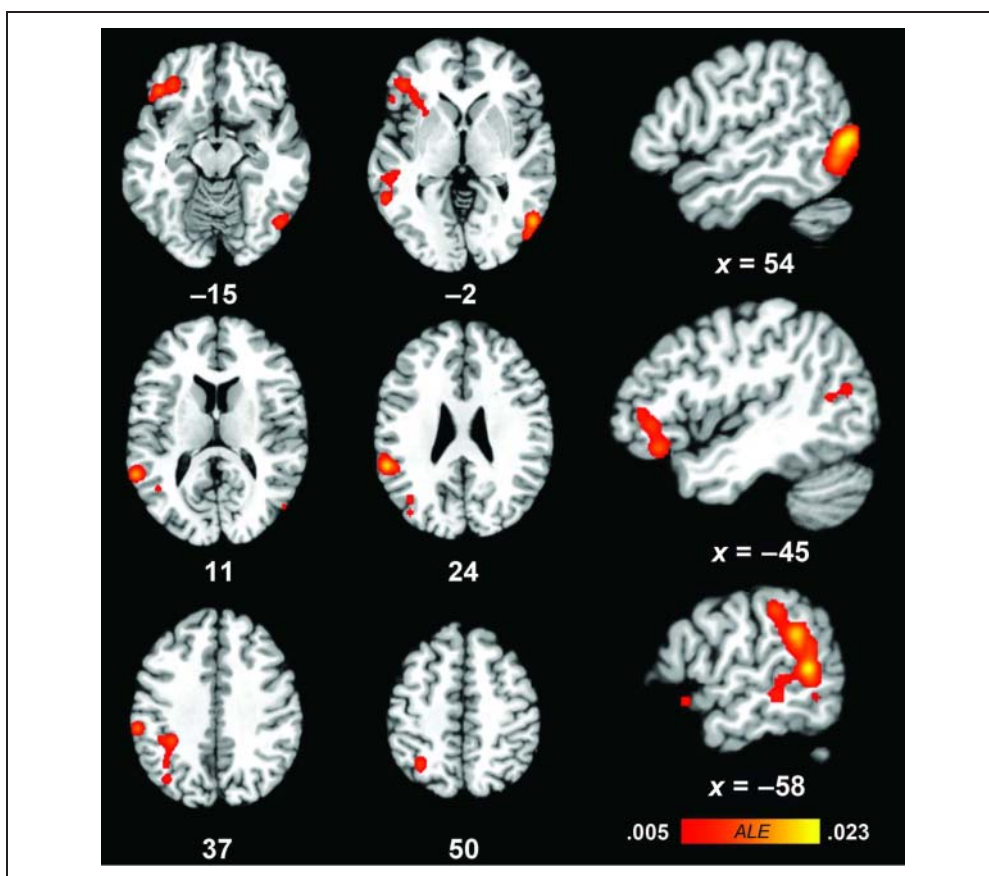
Meta-analysis 3: Subtraction/Conjunction Analysis across Visual and Verbal Input Formats

To investigate neural differences associated with accessing action concepts nonverbally or verbally, we contrasted ALE maps for experiments using action images or action verbs as stimuli (Table 3, Figure 3). We observed areas with greater concordance for action images relative to action verbs in bilateral lateral occipital cortex, extending posteriorly to the occipital poles. Areas with greater concordance for action verbs relative to action images were observed in the left middle MTG, fusiform gyrus/inferior temporal gyrus, and hippocampus. When the individual ALE maps for each input type were submitted to a conjunction analysis (Nichols et al., 2005), we observed significant overlap across stimuli types in the left pMTG and left insular cortex.

DISCUSSION

In the current study, we looked for the patterns of activity associated with action concepts that emerge as consistent across many neuroimaging studies. Specifically, we evaluated how consistently motor and visual motion areas of the brain are recruited by the conceptual processing of actions. We also tested the hypothesis that action images and action words activate distinct brain regions. Critically, none of the imaging studies included in our analyses involved the perception of dynamic depictions of actions or action execution. Instead, we limited ourselves to studies with tasks and stimuli that required participants to draw upon their long-term, semantic memory for actions. The most striking result from our analyses is the consistent involvement of brain areas overlapping with or adjacent to areas specialized for visual motion. By contrast, we observed no significant concordance in premotor or motor cortices in any analysis, despite recent research efforts indicating a role for the motor system in representing action semantics (e.g., Fischer & Zwaan, 2008; Pulvermüller, 2005).

## Meta-analyses 1 and 2: Involvement of Motor System and Visual Motion Areas

In Meta-analysis 1, we included all contrasts that met our criteria. As a result, this analysis had the most power to detect the recruitment of sensory or motor systems by action concepts. We observed significant concordance in bilateral lateral occipital cortex, overlapping with the usual location of area MT+ (Dumoulin et al., 2000). Our results are in agreement with those of Kourtzi and Kanwisher (2000) and others (Kable et al., 2002; Senior et al., 2000) who have observed activity in this area when participants view images that imply but do not actually contain visual motion. Because no individual study has found MT+ to be active when participants process action words in isolation (Bedny et al., 2008; Kable et al., 2002, 2005), the significance of area MT+ in Meta-analysis 1 is likely driven by the subset of studies that used action images as stimuli.

Table 3. Meta-analysis 3: Significant Activation Likelihood Clusters from the Contrast between Action Images and Action Verbs and Their Conjunction

Cluster No.	Location of Peak Voxel	x	y	z	Z score	Volume (mm^3)
Action Images > Action Verbs						
1	Right lateral occipital cortex	51	−70	1	3.04	5304
2	Left lateral occipital cortex	−47	−76	−2	3.04	3608
3	Right lateral occipital cortex	39	−77	7	3.04	1880
4	Left lateral occipital cortex	−39	−88	0	3.04	1840
Action Verbs > Action Images						
1	Left MTG (middle)	−48	−32	−12	2.10	264
2	Left fusiform gyrus/inferior temporal gyrus	−40	−34	−16	2.09	176
3	Left hippocampus	−35	−32	−9	2.13	96
4	Left inferior temporal gyrus	−50	−26	−20	1.81	64
Conjunction of Action Images and Action Verbs						
1	Left pMTG	−58	−50	6	–	1264
3	Left insular cortex	−36	22	2	–	456

Coordinates are reported in MNI standardized space.

Figure 3. *Z* scores and ALE values from Meta-analysis 3 (subtraction and conjunction analyses of studies using action images and action verbs as stimuli). Red-to-yellow spectrum denotes greater concordance for action images versus action verbs. Blue-to-light blue spectrum denotes greater concordance for action verbs versus action images. Purple denotes areas of significant concordance for both input types as revealed by a conjunction analysis. Maps have been corrected for multiple comparisons at FDR $q = .05$ with a minimum cluster size threshold of 50 voxels. Coordinates are reported in MNI standardized space.
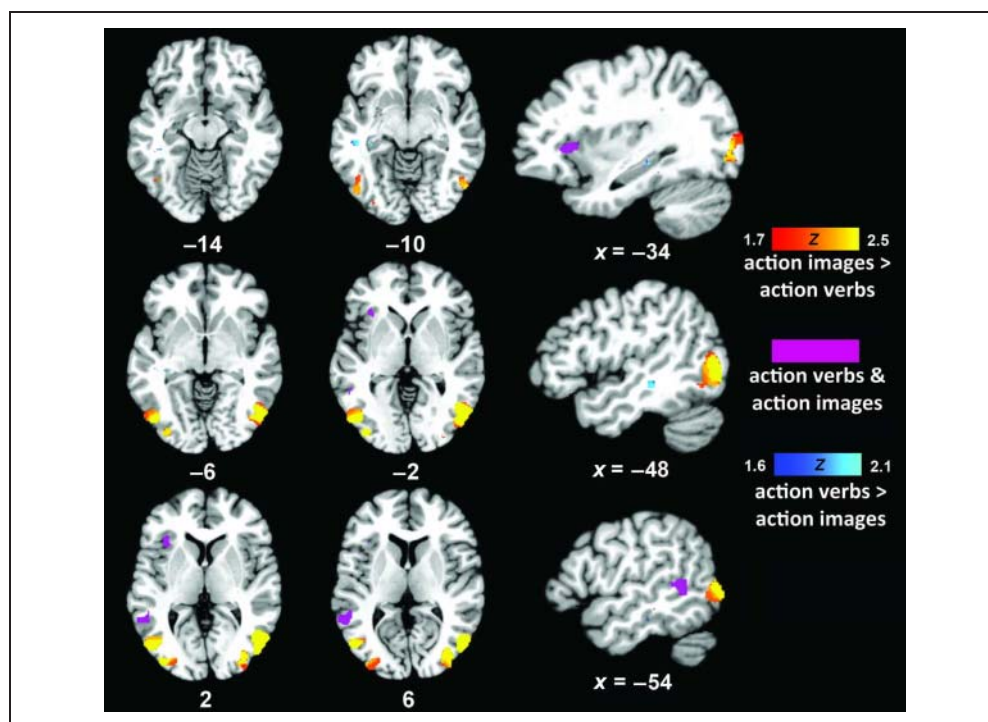
We also observed significant concordance in the left pMTG, adjacent to area MT+. Neuropsychological research suggests that pMTG plays a critical role in the representation of action concepts. For example, Kalénine, Buxbaum, and Coslett (2010) administered action recognition tasks to 43 left hemisphere stroke patients. Using voxel-based lesion symptom mapping (VLSM), they found that impairments for matching action verbs to their associated gestures correlated significantly with damage to left pMTG, leading them to conclude that this area of the brain "… supports the understanding of action meaning" (Kalénine et al., 2010, p. 3278; see also Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). Although pMTG is not itself a visual area specialized for processing motion, its proximity to area MT+ puts it in a position to develop more abstract representations derived from visual motion input (Watson & Chatterjee, 2011; see Plaut, 2002, for computational evidence of such an organization). However, Bedny et al. (2008) found that activity in posterior lateral temporal cortex did not differ between verbs associated with high and low amounts of visual motion. One explanation for this result is that even actions without associated visual motion come to be represented within pMTG by bootstrapping from action representations acquired earlier in development (Bedny et al., 2008). Consistent with such an explanation, patients with damage to lateral temporal cortex are impaired at understanding the thematic roles that underlie action events (i.e., who is doing what to whom?; Wu, Waller, & Chatterjee, 2007).

In contrast to visual motion areas of the brain, Meta-analysis 1 did not reveal consistent involvement of pre-motor or motor cortex in the conceptual processing of actions. Generally, null results should be interpreted with caution. However, because meta-analyses aggregate across multiple studies and do not reflect idiosyncratic patterns of results, we believe this method permits stronger conclusions to be made in the absence of an effect. Thus, although activation in premotor and motor cortices has been observed in individual neuroimaging studies of action knowledge (e.g., Raposo et al., 2009; Berlingeri et al., 2008; Hauk et al., 2004), these areas appear to be only weakly or inconsistently involved when the results of many studies are considered.

The inconsistent involvement of the motor system in action concepts may, in part, be a result of the somatotopic organization of motor and premotor cortices. If stimuli within or across studies refer to actions executed with different effectors (e.g., leg, arm, face), then the power to detect a spatially coherent effect within somatotopically organized areas will be diminished. By contrast, no such somatotopy exists within area MT+. So, in principle, it may be easier to detect an embodied response within visual motion relative to motor areas.

More generally, a limitation of meta-analyses is that only whole-brain, voxel-wise results can be considered, leading to the exclusion of ROI analyses, analyses performed within functionally defined masks, or analyses applying small volume corrections. In essence, the method excludes strongly hypothesis-driven analyses. With regard to the questions at hand, this limitation is particularly salient: We excluded studies examining activity within functionally defined visual motion or motor ROIs. Yet this kind of

analysis offers the strongest test for whether or not action concepts recruit sensory or motor systems.

Nevertheless, the emergence of concordance within visual motion but not motor areas indicates that some embodied responses can be detected at the whole-brain level. Indeed, the lack of consistency within motor areas may reveal limits on embodiment. On an embodied perspective, activity in sensory and motor systems during conceptual processing reflects prior real-world experiences with dynamic actions. We suggest that the pattern of results observed in Meta-analysis 1 reflects inherent variability in the motor but not visual experiences people have with actions. In support of this interpretation is evidence that the motor system is more strongly recruited during action recognition by actions that observers themselves can perform. Calvo-Merino et al. (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005) found that premotor cortex (and also parietal cortex, STS, and the cerebellum) was more active when expert dancers viewed movements within their motor repertoires versus ones that were not. If first-person experiences with actions vary across individual stimuli and across participants, then premotor and motor cortex will not emerge as consistently involved in the processing of action concepts. On the other hand, participants' experiences perceiving actions visually are likely to be more consistent.

Nevertheless, we note that meta-analyses focusing on the observation of dynamic depictions of human actions have revealed significant concordance in premotor and primary motor cortices (Grosbras et al., 2012; Caspers et al., 2010). Also, word stimuli that have strong associations with both actions and colors (e.g., tennis ball) can flexibly engage the motor system as a function of task: Only when participants are asked to think about the words' action properties is the motor system more strongly engaged relative to abstract words (Van Dam, Van Dijk, Bekkering, & Rüschemeyer, 2012; see Lingnau & Petris, 2012, for related findings). Thus, although our results indicate that premotor and motor cortex are not consistently engaged by action concepts, factors such as one's familiarity with an action, the dynamicity of the visual input, and task demands/context make it more likely that action concepts will engage the motor system.

Although neither premotor nor motor cortex emerged as significant in Meta-analysis 1, we did observe a cluster of concordance encompassing parts of the left insula and IFG, an area of the brain hypothesized to contain "mirror neurons" (Rizzolatti, Fadiga, Matelli, et al., 1996; but see Dinstein, Thomas, Behrmann, & Heeger, 2008, for a critique). But unlike premotor and motor cortex, many nonmotor (and nonmirror) functions are ascribed to IFG. For instance, this area of the brain is involved in selecting among competing representations in memory (Moss et al., 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). One explanation for this region's consistent involvement in accessing action concepts is that doing so

places higher demands on selection processes than other categories of concepts (e.g., objects). In support of this view, Siri et al. (2008; see also Longe, Randall, Stamatakis, & Tyler, 2007) found that when participants produced the names of pictured actions using different parts of speech (e.g., infinitive verb: "to run," action noun: "the running"), activity within IFG was modulated by the morphosyntactic difficulty of the response. They concluded that "differences in the left IFG activation emerge as a consequence of increasing linguistic and/or general processing demands" (Siri et al., 2008, p. 171). Thus, activation of IFG by action concepts may not necessarily reflect the simulation of motor attributes. Instead, the emergence of concordance in IFG in Meta-analysis 1 may reflect the tendency for actions or action verbs to place greater demands on morphosyntactic or selection processes.

Meta-analysis 1 included all studies and so had the most statistical power to reveal neural patterns associated with action concepts. Meta-analysis 2, however, included only studies in which participants were instructed to perform lexical-semantic tasks. As a result, this analysis offered a more focused test of the claim that sensory and motor systems are involved in representing the meanings of actions. In fact, if some action-related brain regions are recruited only by deep or difficult semantic processing (Lingnau & Petris, 2012), then these areas may be more likely to emerge in Meta-analysis 2. Consistent with the results of Meta-analysis 1, we observed a primarily left-lateralized pattern of activity associated with semantic processing of actions. Concordance in the left pMTG, parietal cortex, IFG, and right lateral occipital cortex remained significant although only contrasts involving overt tasks were considered. As in Meta-analysis 1, we failed to detect significant concordance in premotor or motor cortices. As detailed above, the significant involvement of brain regions overlapping with or adjacent to areas specialized for processing visual motion—but not premotor or motor cortices—may reflect consistency across participants in viewing human actions and their associated visual motion. And, significant concordance in the left IFG in Meta-analysis 2 may reflect activity within the human "mirror system," but, as above, it may also reflect this region's known role in morphosyntactic processing and the selection of information from semantic memory.

In both Meta-analyses 1 and 2, we observed significant concordance in inferior and parts of superior parietal cortices. Inferior parietal cortex (IPL) is hypothesized to subserve the production of skilled object-directed actions (e.g., "hammering"; Buxbaum, Kyle, Grossman, & Coslett, 2007). However, this area of the brain also participates in comprehending these kinds of actions. For instance, lesions to IPL are associated with deficits in recognizing object-directed actions (Kalénine et al., 2010; Buxbaum, Kyle, & Menon, 2005). Neuroimaging studies have shown that IPL is active when participants view object-directed actions (Buccino et al., 2001) or think about the meanings of objects that have familiar action associations (e.g., tools;

Boronat et al., 2005; Kellenbach, Brett, & Patterson, 2003; Martin & Chao, 2001). The many studies included in our analyses that used object-directed actions as stimuli likely contributed to the significant involvement of IPL in Meta-analyses 1 and 2.

Meta-analyses 1 and 2: Other Findings

In Meta-analysis 1, we also observed significant concordance in the left fusiform gyrus. However, the cognitive process attributed to this area is not unique to action concepts: The left fusiform cortex is engaged by orthographic processing irrespective of semantic category (see Dehaene & Cohen, 2011, for a review). Therefore, consistency within this region likely reflects the use of word stimuli in some experiments rather than processing specific to action concepts.

Meta-analysis 3: Differences between Visual and Verbal Action Stimuli

In Meta-analysis 3, we looked for similarities and differences between areas of the brain consistently recruited by either static depictions of actions or action words. Our results suggest that action words and images activate distinct but partially overlapping neural networks. Action images relative to action words were associated with greater concordance in bilateral lateral occipital cortex, including area MT+ in both hemispheres. This result accords with earlier studies in which area MT+ was activated by static depictions of actions (e.g., Kourtzi & Kanwisher, 2000) and also confirms that the involvement of lateral occipital cortex in Meta-analyses 1 and 2 is driven by studies with action images as stimuli. Action words relative to action images, on the other hand, were associated with greater concordance in several left hemisphere areas. Consistent with a graded view of embodied representation (e.g., Chatterjee, 2008, 2010), we observed concordance for action words in the middle part of the left MTG. This cluster was located anterior to areas associated with action images and to visual area MT+.

The implications of this pattern of results are twofold. First, action words and action images evoke (partly) distinct neural responses within the left lateral temporo-occipital cortex. Thus, although an image and a word may refer to the same action, the conceptual representations evoked by each depend on the format of the input—a finding inconsistent with a strong view of embodied semantics. Second, concordance in the left MTG for action words is anterior to areas associated with action images and area MT+.[2] One explanation for this result is that the proximity of action word areas to areas representing visual motion information indicates that more abstract representations of action meaning are derived from information in unimodal sensory cortices (Watson & Chatterjee, 2011; Chatterjee, 2008, 2010; but see Bedny et al., 2008).

Using a computational model, Plaut (2002) demonstrated how such an organization might develop: Parts of the semantic system proximal to particular input or output modalities develop relative degrees of functional specialization for modality-specific knowledge. Parts of the semantic system located farther away from these modalities develop representations that are increasingly amodal.

However, the neural networks associated with processing action images and action words also partly overlap: A conjunction analysis revealed a cluster of overlap within the left pMTG. Given the hypothesized role of pMTG in action semantics (Kalénine et al., 2010; Kable et al., 2002, 2005), the shared activation of pMTG by images and words indicates an area that houses conceptual representations recruited by both formats. In support of this claim, an fMRI study in which participants made semantic decisions about visually or auditorily presented action words found that left pMTG and anterior intraparietal cortex responded similarly to action words irrespective of their format (Noppeney et al., 2005). Noppeney et al. (2005) suggest that these brain areas "play the role of amodal semantic regions" for actions (see also Buxbaum & Kalénine, 2010). Other researchers have proposed that pMTG is an area responsible for the multimodal integration of all semantic information (Visser, Jefferies, Embleton, & Lambon Ralph, 2012; Binder et al., 2009; Willems, Özyürek, & Hagoort, 2009). Why, then, is pMTG consistently activated when participants think about actions relative to other semantic categories? We suggest that the need to link multiple sources of information (i.e., vision, proprioception, audition) together to form meaning may be greater for spatially and temporally changing actions than for objects.

Meta-analysis 3: Other Findings

In Meta-analysis 3, we also observed greater concordance for action words relative to action images in the left fusiform and inferior temporal gyri, brain areas activated by word reading (Dehaene & Cohen, 2011; Jobard, Crivello, & Tzourio-Mazoyer, 2003). Action words also yielded greater concordance in the left hippocampus. Although the hippocampus is typically linked to episodic memory, there is evidence to suggest that it plays a role in supporting semantic memory, as well (Manns, Hopkins, & Squire, 2003; Squire & Zola, 1998). Thus, all of these brain regions appear to reflect processing that is not action specific.

We also observed concordance outside our areas of interest in the conjunction analysis in Meta-analysis 3. Left insula is not typically associated with the conceptual processing of actions, in particular. Instead, the involvement of this area may reflect the things to which action stimuli are often compared. When the task of interest involved a manual or speech response, we eliminated contrasts in which the baseline task did not (e.g., fixation). However, given the role of the insula in internal verbalization and articulatory speech planning (Jezzini, Caruana, Stoianov, Gallese, & Rizzolatti, 2012; Dronkers, 1996), it remains

possible that action-related conditions taxed internal speech or speech planning processes to a greater degree than baseline tasks.

Conclusion

In the present series of meta-analyses, we identified brain regions associated with the conceptual processing of actions across many studies. Action concepts consistently activated brain areas within or adjacent to visual motion area MT+. Furthermore, action images and words were associated with patterns of activity in the left lateral temporal cortex that reflect a gradient of abstraction among representations derived from visual motion information. On the other hand, we did not find evidence for consistent involvement of premotor or motor cortices in the representation of action concepts. At the very least, this finding argues against the hypothesis that premotor or motor cortex activations are inherent to the process of understanding action concepts. From our results, one might further argue that conceptual understanding of actions, if framed as being embodied, relies on visual motion more so than motor systems. However, such a conclusion might be premature. We suspect that the recruitment of both motor and visual motion systems depends on individuals' experience with observing and executing these actions. In the experiments from which we drew our data, greater similarities between individuals with perceiving actions than performing them may have led to the consistent recruitment of visual motion and adjacent areas.

Notes

1. In addition to sensory areas important for all concrete objects, objects that are familiar and associated with skilled manipulations (e.g., a hammer) may also be partly represented within motor and visual motion systems (e.g., Beauchamp, Lee, Haxby, & Martin, 2003; Chao & Martin, 2000).
2. Although we focused on studies using action word stimuli in isolation, action verbs presented within sentences (Wallentin, Lund, Østergaard, Østergaard, & Roepstorff, 2005) or narratives (Wallentin et al., 2011) also elicit activation in MTG anterior to MT+.

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