63 Concepts of Actions and Their Objects

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ABSTRACT We take concepts to be mental representations involving stored knowledge with some level of generality and modality invariance. Here we explore the neural organization of action concepts. In the neuropsychological literature on action production and comprehension, a *mechanical reasoning* system diverges from a system based more on object identity, and within the latter system, only rarely is the understanding of tool action selectively impaired relative to concepts of the object involved in an action. The more frequent co-occurrence of action and tool knowledge deficits reflects the close proximity or even extensive overlap of their corresponding neural representations. Neuroimaging work has identified at least two loci important for (primarily concrete) action concepts: in the posterior middle temporal gyrus (pMTG) and the inferior parietal lobe (IPL). Yet both loci seem equally central to aspects of knowledge about tools. Shared neural territory between concrete action concepts and tools seems to reflect more than the fact that tools cue actions. Rather, we argue that it reflects the fact that possibilities for action are inherent attributes of tools and that action concepts inherently specify their typical instruments as part of their predicate structure.

This chapter is about action concepts, but we begin with the inherent problems of the terms *concepts* and *action*. *Concepts* has different uses in the literature: here, we take concepts to be representations with certain properties, rather than any information retrieved during "conceptual tasks" (Leshinskaya & Caramazza, 2016). Specifically, concepts involve stored knowledge that captures some generality about the world and can be accessed from different modalities of stimuli. Just how general is a theoretical issue. Is a view-invariant representation of a specific chair a concept, or must it span many different chairs? We suspend this issue and take a broader, inclusive view.

What is an *action*? In sensorimotor content, the distinction between static shapes (*objects*) and body movements (*actions*) is clear, but at the conceptual level, different distinctions emerge. Movement is neither necessary nor sufficient in action concepts: we do not have concepts for meaningless movements; meanwhile, mental actions have no physical motion at all. Furthermore, action concepts often specify relations among participating objects as instruments or targets, and likewise, many artifacts have physical features that are imbued with relevance for action. Thus, at the conceptual level, the distinction of object versus action may not be primary.

The evidence we review regarding the neural organization of action concepts reflects this: neural representations of action concepts are entangled with those of objects—specifically, tools. Although content-selective conceptual deficits have long been reported in object domains such as animate and inanimate (Capitani, Laiacona, Mahon, & Caramazza, 2003; Caramazza & Shelton, 1998), they rarely seem to selectively affect action concepts. This raises the question of what organizing principles govern conceptual representations of actions; we describe some possibilities in our review of concepts *for* action and concepts *of* action. Neuroimaging has identified at least two loci important for action concepts; below, we attempt to better understand their representational roles. We find that neither is characterized by pure selectivity to action concepts per se but that both also contain information about tools. Furthermore, both are embedded within complex functional landscapes spanning multiple specialized areas; we suggest that these adjacency relations may be important clues to their broader function.

Dissociations among Action Knowledge Systems

Concepts for action Deficits in knowledge that support action planning are typically probed using *pantomime tasks*. An object is named or shown to a patient, then taken away; patients must demonstrate how they would typically use it with their hands. A deficit in this ability, along with intact basic motor and visual function, is termed *apraxia* (Heilman, Maher, Greenwald, & Rothi, 1997). In these tasks, the object serves as a cue to the relevant stored knowledge about action. The neuropsychological evidence suggests the existence of dissociations among such knowledge into two distinct systems: one based on object identity and the other on *mechanical reasoning*.

One way to solve the pantomime task is to recognize the object, retrieve one's knowledge about how to use this kind of object, and act accordingly (the object identity route). However, it can alternatively be solved by *mechanical reasoning*: computing actions on the basis of information about an object's physical properties—its shape, weight, rigidity, and so on (Goldenberg & Hagmann, 1998; Riddoch, Humphreys, & Price, 1989). Rather than relying on knowledge of the identity of an object, this system enables inferences from the object's physical characteristics available from its visible properties. When patients successfully perform pantomime tasks in response to objects they don't recognize, it is possible they use this mechanical-reasoning system.

A direct way to test the mechanical system is with a *novel tools* task: patients are asked to reason about novel tools whose conventional function is not known, such as a set of unconventional hooks, to determine which tool can lift another object out of a container (Heilman et al., 1997) or open a box (Hartmann, Goldenberg, Daumüller, & Hermsdörfer, 2005). By requiring only the *selection* of the novel tool, deficits cannot be due to motor execution problems. Such tasks can be solved at ceiling by patients who have deficits in object recognition—that is, who cannot name familiar tools or retrieve other semantic information about them (Bozeat, Lambon Ralph, Patterson, & Hodges, 2002; Hodges, Spatt, & Patterson, 1999; Sirigu, Duhamel, & Poncet, 1991). This even includes those who cannot pantomime successfully to them. Conversely, novel tools performance can be impaired in patients with otherwise intact semantic knowledge (Goldenberg & Hagmann, 1998; Goldenberg & Spatt, 2009). Thus, either the object's identity or a mechanical reasoning system can be used to reason about action, and these appear dissociable.

This mechanical-reasoning system is sometimes characterized as *nonconceptual*, but it is not clear that it contains no conceptual content. This content must be independent of the knowledge of the identity of specific objects, but it might well be conceptually rich in other ways. It might contain general, intuitive physics principles relating object properties to inferences about support, containment, propulsion, and other forms of physical interaction. It could also represent how objects can interact with the hand to work as levers or enable reaching. A key direction for future research is to probe what patients with impairments in identifying objects do or do not know about various aspects of intuitive physics (see chapter 65). If their knowledge turns out to be conceptually rich, it would support the idea of a dissociable aspect of the conceptual system that is specifically important for intuitive physics concepts.

There are also cases of deficits to the object identity system that may be selective to action knowledge specifically. Such patients exhibit conceptual errors when using objects with conventional functions, such as brushing the teeth with a spoon (De Renzi & Lucchelli, 1988; Heilman et al., 1997; Ochipa, Rothi, & Heilman, 1989; Sirigu, Duhamel, & Poncet, 1991). These errors appear to result from conceptual confusion about what to do, rather than errors in a mechanical-reasoning system. Ochipa, Rothi, and Heilman's (1989) patient, who made such errors in action, was also poor at describing those objects' typical functions but able to name objects and actions. These cases are suggestive of a specialized conceptual system involved in the knowledge of the conventional functions of objects but distinct from both mechanical reasoning and the ability to name those objects, though the latter part of this dissociation remains tentative (see Bozeat et al., 2002; Daprati & Sirigu, 2006 for discussion).

In summary, a least two varieties of conceptual representations support acting with objects. Mechanical reasoning—the knowledge of intuitive principles linking physical properties of objects and inferences about action—doubly dissociates from other aspects of conceptual knowledge, which in turn allow the use of object-specific action knowledge by identifying the objects and retrieving their conventional functions.

A major limitation is that this work focuses specifically on transitive (object-based) actions. It remains possible that concepts of intransitive (non–object based) actions have different principles of organization. However, from the evidence on hand, it seems difficult to disentangle knowledge about action from that about objects; the mechanical-reasoning system has to make reference to the physical qualities of objects in order to support judgments about acting with them. And while a "concepts for *object-based* action" system is an alluring idea, evidence for it separate from conceptual knowledge regarding nonaction attributes remains tentative.

Concepts of actions Concepts *of* actions enable recognizing and understanding actions that one observes. Action recognition is typically tested by having patients match an action name to a video or picture, and it doubly dissociates from production abilities, as the in pantomime tests described above (Negri et al., 2007; Tarhan, Watson, & Buxbaum, 2016). Action recognition can fail for multiple reasons, however, and not all are due to deficits at the conceptual level. For example, visual agnosia is an impairment specific to the visual modality, leaving intact the ability to make judgments about actions presented as names. Agnosia can selectively affect action or object stimuli (Rothi, Mack, & Heilman, 1986; Tarhan, Watson, & Buxbaum, 2016), suggesting there may be an action-selective component within the visual recognition system but not necessarily in the conceptual system.

Attempts to avert these issues and look for conceptual-level deficits to action concepts per se have failed to provide conclusive evidence. One study (Pillon & D'Honincthun, 2011) reports on a patient with broad, crossmodal conceptual deficits and intact lower-level visual, motor, and lexical abilities. For example, he could discriminate meaningful from meaningless gestures. However, when asked to name pictures, select related pictures, or verify properties of named objects, he showed a consistent pattern of impairment, performing the worst on living things and significantly better on man-made objects and actions, which in turn did not differ from each other. This was the case even for actions that did not involve objects (e.g., between two people). Another study (Vannuscorps & Pillon, 2011) reports a complementary performance profile of a patient with a conceptual-level impairment regarding tools, nontool artifacts, and actions to equal degree, with spared abilities for animals, plants, and famous people and buildings. Thus, rather than a selective semantic system for actions, these findings demonstrate selectivity within the semantic system for actions and artifacts together. The authors argue that a common domain-selective system exists supporting conceptual knowledge for actions and artifacts; collectively, perhaps, it represents concepts that pertain to goals or purposes. This argument relies on the observation that actions and artifacts were damaged to a similar degree across these patients and the premise that this coincidence is not due to damage to adjacent but functionally independent neural structures. Reports do exist of inanimate object impairment without impairment to actions, but these domains were not compared directly (Bi, Han, Shu, & Caramazza, 2007). In a direct comparison of performance in naming the action (sewing) versus the instrument (needle) in an action, there is a report of a patient with a clear dissociation between the two (Shapiro & Caramazza, 2003). The patient performed quite well in naming the objects but very poorly in naming the actions with those objects. Importantly, the difference in performance could not be attributed to differences in the grammatical class of the words (nouns vs. verbs) since the patient showed normal grammatical class (morphosyntactic) processing. Altogether, more evidence is needed to fully resolve whether there is a content-selective system for concepts of actions, and its exact relation to concepts of objects.

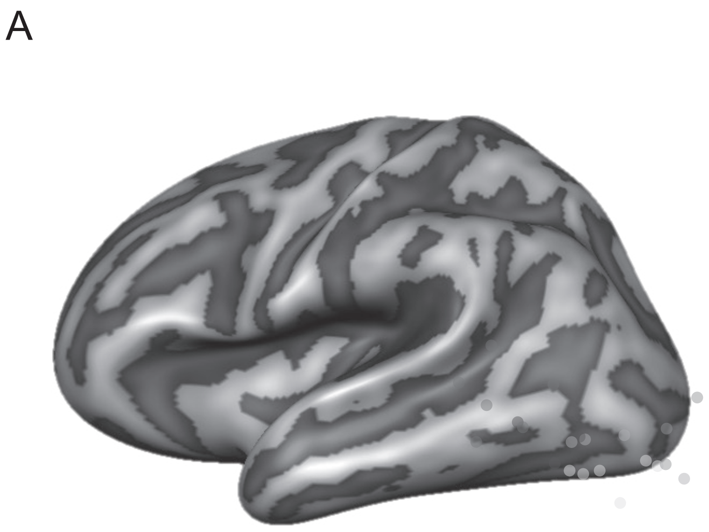
Neural Organization of Action Concepts

Dissociations among impairments in action-related tasks, as reviewed above, have shed light on which cognitive components are neurally separable, though leaving many issues unresolved. Neuroimaging and lesion-mapping evidence provide additional insight into cortical organization by demonstrating how action knowledge is spatially arranged in cortex.

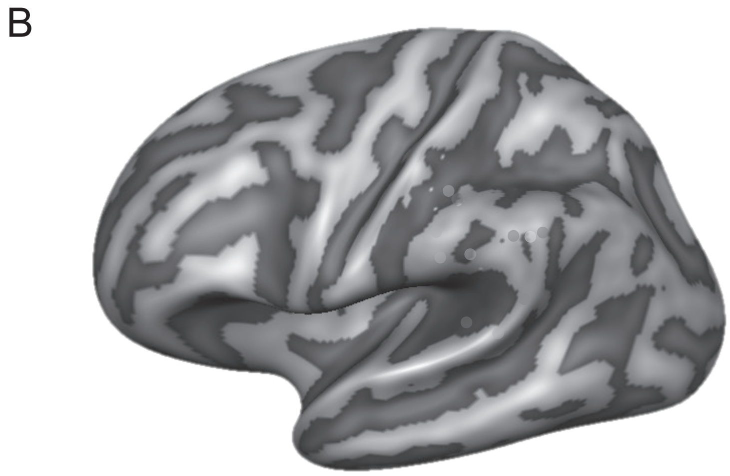
The principal findings from this work are centered on areas in lateral temporal and lateral parietal cortex (figure 63.1). It has become clear that parts of these areas represent conceptual content about actions but that these, too, reflect object knowledge, specifically about tools, as would be expected under an account of action concepts as predicates and their arguments. The most compelling facts of these data are that representations about actions and tools are closely entangled in neural space rather than strictly separated, even as the broader roles of those areas—comprising multiple specializations—are best described as serving action planning and understanding.

Concepts of actions A large set of experiments suggests that a relatively anatomically consistent area in the left lateral posterior temporal cortex preferentially responds when participants retrieve action knowledge (Watson, Cardillo, Ianni, & Chatterjee, 2013). We term this area *action-MTG*, to designate a functional area in and around the pMTG with this profile. Activation in this area is increased when participants name actions that correspond to pictures or names of tools, relative to naming their typical colors (Martin et al., 1995); effects at nearby coordinates are seen for retrieving action attributes relative to size attributes, for both tools and fruit (Phillips, Noppeney, Humphreys, & Price, 2002) and for semantic judgments about names of actions versus names of objects (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002).

Is action-MTG an area specifically involved in action concepts, and what about them does it represent? It could reflect action concepts, or the grammatical category of verbs, or motion imagery. To approach this question, one must describe it in the context of a complex landscape of responses in the broad cortical area surrounding it—we refer to this anatomical region spanning multiple functional areas as the lateral occipitotemporal cortex (LOTC). Essential to this effort is evidence that directly compares functional activations within the same group of subjects, and we rely on evidence from such comparisons to assess whether different functions are attributable to the same area.



Study	Tal X	Tal Y	Tal Z
Action attribute retrieval			
Martin et al., 1995 (Study 1)	-50	-50	4
Martin et al., 1995 (Study 2)	-54	-62	8
Phillips et al., 2002	-50	-62	5
Kable et al., 2005	-53	-60	-5
Verbs			
Bedny et al., 2008	-53	-41	3
Peelen et al., 2012	-49	-53	12
Shapiro et al., 2006	-57	-40	9
Bedny et al., 2013	-60	-51	11
Hernandez et al., 2014	-45	-43	7
Bedny et al., 2011	-53	-49	6
Tools			
Beauchamp et al., 2002 (Study 1)	-38	-63	-6
Beauchamp et al., 2002 (Study 2)	-46	-70	-4
Valyear et al., 2007	-48	-60	-4
Peelen et al., 2013	-50	-60	-5
Bracci et al., 2011 (Study 1)	-48	-65	-6
Bracci et al., 2011 (Study 2)	-46	-68	-2
Feature-general action representation			
Wurm & Lingnau, 2015	-41	-76	-4
Wurm et al., 2017	-44	-64	3
Oosterhof et al., 2010	-49	-61	2
Wurm & Caramazza, 2018	-54	-61	4
Basic motion			
Bedny et al., 2008	-46	-71	7
Zeki et al. 1991	-38	-74	8
Bracci et al., 2011	-44	-72	-1



Study	Tal X	Tal Y	Tal Z
Tool experience			
Creem-Regehr et al., 2007	-56	-29	29
Valyear et al., 2012	-43	-39	43
Vingerhoets et al., 2011	-42	-32	42
Weisberg et al., 2007	-42	-43	38
Feature-general action representation			
Oosterhof et al., 2010	-44	-31	44
Oosterhof et al., 2012	-49	-31	42
Hafri et al., 2017	-56	-36	28
Wurm & Lingnau, 2015	-51	-29	36
Wurm et al., 2017	-47	-27	37
Feature-general object function			
Leshinskaya & Caramazza, 2015	-62	-38	38
Tools			
Garcea & Mahon, 2014	-43	-43	41

FIGURE 63.1 Peak coordinates of action-related effects in MTG (*A*) and IPL (*B*) reported in studies discussed in the section on the neural organization of action concepts. The different kinds of effects are based on the following contrasts/classifications: action attribute retrieval (*blue*) = tasks requiring the retrieval of actions or action attributes versus action-unrelated attributes (e.g., color) from pictures or names of actions or manipulable objects; tool experience (*magenta*) = familiar/typical versus unfamiliar/atypical tool use knowledge; verbs (*red*) = verbs versus nouns (various contrast; see the text); basic motion (*orange*) = moving versus static dots; feature-general action representation (*light blue*) = multivoxel pattern classification of action videos across perceptual features; feature-general object function (*green*) = multivoxel pattern classification of abstract categories of functions; tools (*yellow*) = images or videos of tools versus nonmanipulable artifacts or animals. Note that peaks do not reflect the spatial extent or the overlap of effects. (See color plate 85.)

Posteriorly in LOTC is the functional area MT+, which is selective to moving versus static stimuli across content domains (Zeki, Kennard, Watson, Lueck, & Frackowiak, 1991). Anterior to MT+ in left LOTC is another area, which preferentially responds to images of tools relative to human bodies (Beauchamp, Lee, Haxby, & Martin, 2002) and other categories (Valyear, Cavina-Pratesi, Stiglick, & Culham, 2007), and which we term *tool-MTG*. Within-study functional comparisons show that tool-MTG diverges from motion-sensitive MT+ (Beauchamp et al., 2002); the effects of action attribute retrieval—that is, action-MTG—also diverge from MT+ (Kable et al., 2005). Thus, tool and action responses in the MTG do not reflect the retrieval of simple visual motion. One possibility is that they reflect retrieval of more complex kinds of motion. Indeed, tool-MTG responds more strongly to functionally moving tools than to static tools or moving human bodies (Beauchamp et al., 2002). However, tool responsiveness in the MTG is preserved in congenitally blind participants, who have no visual experience (Peelen et al., 2013), suggesting that responses in this area are unlikely due only to the visual imagery of tool motion.

Tool- and action-MTG areas are anatomically nearby; both are reliably anterior to MT+. Critically, a within-subject functional region of interest (ROI) analysis showed that tool-MTG also responds to action attribute retrieval (Perini, Caramazza, & Peelen, 2014). Thus, we suggest that overlapping tool and action responses likely reflect the same functional area (tool/action-MTG hereafter)—one that exhibits preferential responses to tools, particularly moving ones, and the retrieval of action attributes. However, this area is not driven specifically by visual experience, and its content is not reducible to low-level visual or kinematic features. It is thus consistent with being a conceptual-level representation, though not definitively so.

The observation of seemingly shared neural space between responses to actions and tools converges with some of the above-reviewed findings from neuropsychology: that conceptual representations of artifacts and actions sometimes pattern together in semantic impairment (but see Shapiro & Caramazza, 2003). However, there are important differences: tool-MTG is more responsive to tools than to other artifacts (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2011; Valyear et al., 2007) and is not the locus of all tool-related knowledge (see chapter 64 on tool concepts). Thus, tool/action-MTG may be just one locus of shared neural territory between action and artifact knowledge.

This shared territory could reflect a common representation accessed by both action attributes and tools; tool images might simply be cues to actions, for example. An alternative is that it reflects something about both tools and actions per se. Recent work finds that tool-MTG represents information about not only the physical uses of tools but also their taxonomic category, such as musical instruments versus garage tools (Bracci, Daniels, & Op de Beeck, 2017), which might support the latter view. Nonetheless, such categories might also reflect action knowledge because playing music versus repairing a house are also distinct categories of actions. Our work also finds that information in and around the MTG represents whether an object or a person is a participant in an action (Wurm & Caramazza, 2018; Wurm, Caramazza, & Lingnau, 2017). In short, what aspects of actions and objects are represented in the MTG remains an open question, but the evidence does not allow the conclusion that the information represented in this area is only about actions and not also about tools.

There is further evidence that responses in and around the anatomical location of tool/action-MTG reflect conceptual similarity among actions, although it is not known whether they occur in exactly the same functional area. For example, in posterior parts of the LOTC, videos of opening actions elicit reliably distinct response patterns from videos of closing actions, while kinematically and perceptually different opening actions (opening a bottle vs. a jar) elicit relatively similar patterns (Wurm & Lingnau, 2015). This suggests that regions around tool/action-MTG encode the distinction between meaningfully different actions, generalizing across perceptually different instantiations of an action. Other whole-brain studies report similar effects nearby: actions like “lift” versus “tilt” elicit reliably distinguishable responses while generalizing across visual viewpoints and different hand configurations (Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010) and the effector used to carry out the action (Vannuscorps, Wurm, Striem-Amit, & Caramazza, 2018). In more anterior LOTC, spanning tool/action-MTG, representations generalize across specific actions and encode more general attributes, such as whether an action involves interaction with manipulable objects or another person (Wurm, Caramazza, & Lingnau, 2017). Moreover, these representations have been shown to generalize across videos and sentences (Wurm & Caramazza, 2019), controlling for the possible effects of verbalization or imagery. In summary, a large set of recent findings shows effects in posterior LOTC that reveal abstract representation of action information.

Action concepts are often, but not necessarily, expressed with a certain grammatical category in language: verbs. Responses to verbs over nouns are also found in anterior and superior areas surrounding the MTG, which we term *verb-MTG* (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Peelen, Romagno, & Caramazza, 2012; Shapiro, Moo, & Caramazza, 2006). Verb-selective responses are preserved in the congenitally blind (Bedny, Dravida, & Saxe, 2013) and cannot be explained by differences in the amount of visual motion they denote (Bedny et al., 2008). Notably, these effects range over a wide range of verb types beyond just action verbs, including those referring to mental states (Bedny et al., 2008; Bedny, Caramazza, Pascual-Leone, & Saxe, 2011), abstract states (*include, exist*; Peelen, Romagno, & Caramazza, 2012), perception (*gaze*), and emission (*clang*; Bedny, Dravida, & Saxe, 2013). They thus reflect more than action concepts per se. In addition, these responses scale with transitivity, the number of objects a verb requires: *take* requires more arguments than *die* (Hernandez, Fairhall, Lenci, Baroni, & Caramazza, 2014). This suggests that verb-MTG has a role in representing predicate-argument structures, a function that is both grammatical and semantic.

A critical question is whether verb-MTG overlaps with tool/action-MTG. In support of their overlap, action-responsive MTG also responds strongly to names of tools (Kable et al., 2005). On the other hand, preferential responses to verbs over nouns, holding semantics constant (state verbs vs. nouns), are found in a more anterior portion of lateral posterior temporal cortex than preferential responses to action semantics (action vs. state verbs; Peelen, Romagno, & Caramazza, 2012). An analysis of coordinates reported in the work cited here shows a reliable anterior to posterior difference in verb and tool effect coordinates ($M = 18.1$ mm, $t(8) = 6.45$, $p < .001$), with verb effects anterior to tool effects. Thus, representations of verbs as a semantic/grammatical category seem to diverge from those of tools/actions.

Nonetheless, the coincidence of responses to tools, action concepts, and verbs in such close quarters raises the possibility that they reflect the operation of a broader functional area in LOTC. We suggest that this broader function would be about neither “actions” nor “tools” alone but rather relate objects to action concepts and action concepts to predicate-argument structures. Verbs typically denote objects as agents or patients (Pinker, 1989), and objects possess properties that are informative about their action possibilities. Sensitivity to verbs, action attributes, action-relevant objects, and the predicate structures of verbs may be adjacent because of their common participation in the process of understanding actions and speaking about them.

Concepts for actions The visuomotor planning of actions critically relies on parietal cortex (Goodale & Milner, 1992), and lesion mapping shows that selective impairments in mechanical reasoning arise from IPL damage (Goldenberg & Spatt, 2009). Like LOTC, IPL clearly contains multiple adjacent specializations within it: while some components represent visuomotor information, others have signatures of a conceptual role. But although the IPL is functionally heterogeneous, the relationship between different functions is rarely assessed directly, and it is unclear whether all conceptual effects arise from the same area. Below, we consider the possibility that parts of the IPL may “contain” conceptual representations, with their exact location unclear, rather than attributing any singular representational type to the IPL as a whole.

Parts of the IPL are sensitive to factors like action familiarity and conventionality during action planning, all consistent with a conceptual role (Creem-Regehr, Dilda, Vicchrilli, Federer, & Lee, 2007; Valyear, Gallivan, McLean, & Culham, 2012; Vingerhoets, Vandekerckhove, Honoré, Vandemaele, & Achten, 2011; Weisberg, van Turennout, & Martin, 2007). Furthermore, the kinds of representations these areas exhibit during action planning are not only motoric or kinematic, and can also be driven by different kinds of stimulus inputs. For example, Gallivan, McLean, Valyear, and Culham (2013) cued participants to perform reaching and grasping actions with either hands or reverse tongs and found that posterior parts of the IPL contained information discriminating reaching and grasping but common to both hands and tongs, even though these have opposite kinematics. These representations are thus not of motor kinematics. Moreover, IPL representations during action planning can be shared with those during action observation, suggesting they are not tied to specifically visual or motor features of the stimuli: Oosterhof et al. (2010) and Oosterhof, Tipper, and Downing (2012) found that anterior parts of the IPL show similar patterns of responses when the same action type (e.g., lift) is executed and observed while showing distinct patterns of response to different actions (e.g., tilt). These results are consistent with the possibility that conceptual factors are reflected in the IPL.

We reported more direct evidence toward this conclusion (Leshinskaya & Caramazza, 2015). Participants evaluated a set of objects toward one of four functions: keeping her or his body warm; protecting objects from water; decorating a house; and dressing up for a night out. Patterns of response in the anterior IPL were similar between pairs of functions that belonged to similar broader categories, Decorate and Protect, without sharing a similar physical manner of execution (e.g., *decorate house* and *dress up* elicited more similar neural patterns relative to dress up and protect body). This finding suggests that the IPL contains conceptual-level representations about actions, which are not driven by motoric or visual properties.

Despite its importance in action planning, anterior parts of the IPL respond in a similar way to the MTG in studies of action observation, showing discriminable response patterns for actions like "kick," "push," "open," and "close" while generalizing across specific visual differences among instances of those actions (Hafri, Trueswell, & Epstein, 2017; Oosterhof, Tipper, & Downing, 2012; Oosterhof et al., 2010; Wurm, Caramazza, & Lingnau, 2017; Wurm & Lingnau, 2015). However, there are also notable differences between the MTG and the IPL, in that only the former seems to encode action representations that generalize across observed actions and sentences describing actions (Wurm & Caramazza, 2019).

The conceptual effects we outlined hardly account for the entirety of the IPL, which has a highly diverse set of functions in different parts (e.g., Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Notably, any conceptual representation would seem to reside near specifically visuomotor ones (Gallivan et al., 2013; Tunik, Frey, & Grafton, 2005; Valyear et al., 2007). This is critical evidence against a singular kind of representation in the IPL and for the idea that the IPL may represent multiple representations with different levels of abstraction. Thus, like LOTC, this area contains multiple specializations that cannot be reduced to each other. However, the reason they are adjacent may be due to participation in a common broader function.

In combination with its role in mechanical reasoning (Fischer, Mikhael, Tenenbaum, & Kanwisher, 2016; Goldenberg & Spatt, 2009), one possible common function for this set of areas is that they all support "how" reasoning—understanding how objects can be used to accomplish certain outcomes—both when this reasoning is about kinematic or mechanical information or abstract properties like aesthetic quality (Leshinskaya & Caramazza, 2015; Spunt, Satpute, & Lieberman, 2011). This account would predict little specialization in the IPL for knowledge about action to the exclusion of knowledge about objects (and how they support action), reflecting the inherent entanglement between action and object properties supporting action.

In support of this idea, the IPL and the MTG are both core parts of a set of regions responding preferentially to tools (Garcea & Mahon, 2014). Like the MTG, parts of the IPL exhibit representations characterizing the associated motor action and taxonomic categories of objects, albeit in a task-dependent manner (Bracci, Daniels, & de Beeck, 2017). Moreover, transcranial magnetic stimulation to the IPL impairs the ability to name tools more than living items (Pobric, Jefferies, & Lambon Ralph, 2010). This indicates that the IPL contains knowledge about tools beyond their roles in cueing action knowledge. Future research should better characterize the specific roles of the IPL and the MTG in action and tool cognition.

General Conclusion

We have described several specialized neural systems involved in action concepts but have not excluded their also being involved in concepts about objects—specifically, tools. This shared neural territory has been most commonly investigated by concrete, transitive action concepts, so this result might therefore not be too surprising. Nonetheless, we marshaled some evidence that these areas represent information about tools per se, and not only as simple cues to their associated actions, and that relatively abstract knowledge about actions can be represented there. Thus, this neural overlap or adjacency might reflect the fact that possibilities for action are inherent attributes of tools/artifacts and that action concepts inherently specify their typical instruments. Neuropsychological evidence that action and tool concepts dissociate is rare, and such impairments can often pattern together.

We conclude that the neural organization of concepts is not drawn primarily along a clear object versus action boundary, given the entanglement between tools and concrete action concepts in neural territory. Moreover, these entangled conceptual representations are further embedded in functionally diverse landscapes in both temporal and parietal cortex. These diverse areas' ways of interacting, their organizing principles, and their broader roles in cognition are major directions for future work.

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