**The lateral occipitotemporal cortex in action**

Lingnau, A.1,2 & Downing, P.E.3\*

1. Center for Mind/Brain Sciences (CIMeC), University of Trento, Rovereto, 38068, Italy

2. Department of Psychology and Cognitive Science, University of Trento, Rovereto, 38068, Italy

3. Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK

*\*Corresponding author:*

p.downing@bangor.ac.uk

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*Abstract*

Understanding and responding to other people’s actions is fundamental for social interactions. Whereas many studies emphasize the importance of parietal and frontal regions for these abilities, several lines of recent research show that the human lateral occipitotemporal cortex (LOTC) represents varied aspects of action, ranging from perception of tools and bodies and the way they typically move, to understanding the meaning of actions, to performing overt actions. We highlight common themes across these lines of work, which have informed theories related to high level vision, concepts, social cognition, and apraxia. We propose that patterns of activity in LOTC form representational spaces, the dimensions of which capture perceptual, semantic, and motor knowledge of how actions change the state of the world.

*Action representations in the lateral occipitotemporal cortex*

Consider a scenario in which two people are working together to prepare a meal. This mundane situation places a variety of demands on the cooks: they will read a recipe in a cookbook and plan a series of steps accordingly; they must grasp and carefully use a range of implements correctly to prepare the ingredients; one of them (a novice) might watch the other (an expert) to better learn how to quickly dice an onion. Many of these demands depend on perceptual, conceptual, and motoric knowledge of action. Several diverse lines of evidence show that the lateral occipitotemporal cortex (LOTC; Figure 1; Box 1) encodes many related dimensions of action. These include representations of: simple and complex patterns of motion; the appearance, uses, and characteristic motions of manipulable artifacts such as tools; the shape of human bodies and body parts as well as their movements; and verbal material referring to actions symbolically. Further, activity in this region is also implicated in preparing and executing overt, goal-directed movements.

Here we draw together this evidence, which arises from several sub-disciplines that often proceed in parallel, to consider its implications as a whole. Our approach is deliberately “bottom-up” in the sense that we are led initially by a collection of empirical observations that converge anatomically in the LOTC, rather than by a single theoretical view. Building on previous efforts [1-5], this overview leads us to a comprehensive perspective on this broad region’s role as a hub in which perceptual, semantic, and movement-related sources of action information converge.

*The LOTC: key findings*

*Visual motion*. A core area of LOTC is the motion selective human middle temporal (MT) complex [6,7] often referred to as “hMT+”. Due to its sensitivity to a variety of visual motion properties such as different types of optic flow [8] and stimulus speed [9], hMT+ is well suited for representing aspects of complex movements. Some subregions of hMT+ respond to auditory [10] or tactile [11] motion, to motion implied in static images (such as a snapshot of a sprinter launching herself from the starting blocks) [12], and to somatosensory stimulation [13], further demonstrating a broad contribution to representing dynamic information. Anatomically, hMT+ is an important anchor point in LOTC, in that it provides a stable and readily localized landmark (close to the intersection of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus) by which to triangulate other regions [14].

*Tools*. LOTC has long been associated with the perception and use of tools [15]. Viewing patterns of motion that are characteristic of tools, performing simple visual or memory tasks on pictures of tools, reading the names of tools, or preparing to perform tool-related gestures or actions, all preferentially activate regions of LOTC [16-20]. In congenitally blind individuals, highly similar activity is evoked by auditory presentation of tool-related words [21], suggesting that tool-related activity in LOTC does not rely on visual experience. Accordingly, damage to regions of the LOTC can impair aspects of performance on tool-related tasks, such as naming [22], adopting correct limb postures [1] or pantomiming correct movements [23]. Likewise, action judgments about tools are impaired when transcranial magnetic stimulation (TMS) is used to interrupt activity in an fMRI-defined tool-selective region [24]. Thus LOTC activity is implicated in perceptual, semantic, and motor aspects of tool knowledge.

*Bodies and Hands*. fMRI studies reveal an LOTC region -- the “extrastriate body area” (EBA) in the posterior inferior temporal sulcus and the middle temporal gyrus -- that responds selectively to images of human bodies and body parts, relative to faces, animals, objects, scenes, and other visual stimuli [25,26]. Brain stimulation applied over EBA selectively interferes with successful body detection and perception [27-29]. Likewise, brain injury involving this region or its connections with the fusiform body area (FBA [30,31]) selectively impairs body processing [32] (but see [33]). EBA is also recruited in congenitally blind participants who have been trained to discriminate shapes of bodies in comparison to other objects by means of a sensory substitution device [34]. Other recent studies have identified multiple LOTC body representations, such as a cluster of distinct “limb-selective” regions in a regular array around hMT+ [5] including a left-hemisphere hand-specific region [35]. Further related work reports a much broader pattern of subtle biases for different parts of the human body that encompasses but extends beyond EBA to cover much of the LOTC [36]. These broad visual representations of the human body may also extend to include other animals [37]. Taken together, this evidence demonstrates that there is strong representation, or multiple representations, of the shape of the body and its parts within the LOTC.

*Action observation.* Many neuroimaging studies implicate regions of the LOTC in perception of the body in action. We can broadly distinguish the perception of body movement (often referred to as “biological motion”), which generally encompasses simple behaviors that are sometimes meaningless and often intransitive [38], from action observation, which generally refers to goal-directed behaviors [39]. The literature on biological motion was led by early findings of single cells in the macaque temporal cortex that respond to specific movements of the body, head, and eyes [40], and by studies of minimal “point-light” displays [41]. Action observation, in contrast, is often examined in the context of the “action observation network”, a proposed homologue of the “mirror neuron system” found in macaques [42,43]. Findings from both lines of work converge in the temporal lobes, with an emphasis on the posterior superior temporal sulcus but often implicating LOTC regions as defined here, where neural activity is evoked by observing actions from simple finger movements through to complex dance pieces [44-46].

*Action performance*. Although it lies distant from classical motor-control regions, a few findings show that LOTC regions are recruited during the planning and execution of actions. LOTC activity increases during the preparation and execution of unseen limb movements [47,48], particularly the hands [49]. When subjects perform simple (unseen) movements of different parts of the body, activity increases in the corresponding parts of a broad LOTC-wide visual body map [36]. Finally, increased average activity levels [50] and local activity patterns in subregions of LOTC are related to the type, laterality, and sequence of upcoming actions with the hands [51,52] or with tools [18] that are prepared by the subject. In summary, these studies suggest that LOTC encodes information about upcoming movements such as the effector, the type of movement, and/or the anticipated perceptual effects of the movement.

*Action concepts*. LOTC regions are further implicated in accessing conceptual knowledge related to movement and action. In neuropsychological patients, deficits on tasks that require making a variety of judgments about actions (e.g. comparisons on properties such as how fatiguing they are, matching verbs to action photographs or to movement patterns) with a variety of simple stimuli (words, pictures, animations) are associated with damage in several sites, including left LOTC [43,53,54]. In neuroimaging, early PET studies showed LOTC activity in tasks requiring participants to generate an appropriate verb that matches an object represented by its name or a picture [55]. More recent studies show a more subtle relationship between the meaning of action stimuli and LOTC activity. For example, activity within LOTC distinguishes between viewed grasps of objects that are appropriate or inappropriate for the object [56]. Similarly, LOTC responds more strongly when participants judge the goal of an action (e.g. throw / kick a ball vs. punch / kick a person) in comparison to the effector (arm, leg) [46]. And LOTC is sensitive to the type of movement (e.g. lift vs. push), irrespective of viewpoint [57]. Together these studies demonstrate the role of this region in representing conceptual knowledge about action.

*Grammatical class*. The understanding of verbs and of nouns can be dissociated in neuropsychological patients, who sometimes exhibit severe deficits in retrieving or comprehending verbs, but not nouns [58,59]. Neuroimaging studies have identified a stronger response to verbs than to nouns in the LOTC [2,60,61]. Furthermore, LOTC is recruited during semantic processing tasks involving various types of verbs related, for example, to human movement, communication, or state-changes in objects [62]. Because verbs typically refer to actions, whereas nouns often refer to objects, it is debated whether this selectivity for verbs reflects a distinction on the basis of grammatical class (something structural about verbs *per se*), or whether it reflects a distinction on the basis of semantics (the kinds of concepts that verbs typically describe) [63-66]. A recent study found stronger responses within LOTC for state verbs (to believe) and event verbs (to walk) in comparison to state and event nouns (the value, the concert), but no preference for event nouns or verbs in comparison to state nouns or verbs [67]. In contrast, in a more posterior sector that showed no overall verb preference, stronger responses were seen for event in comparison to state verbs. Taken together, these results suggest that both grammatical class (verbs) and semantics (events/actions) are encoded in LOTC, in distinct but adjacent representations (see also[68]).

*Entangled representations of action in LOTC*

 The above findings show the diversity of action-related processes that implicate regions within the LOTC. In practice, these processes must frequently act in concert as we seek to understand and act in our surroundings. Several recent studies provide key evidence demonstrating the functional and anatomical entanglements of action-related representations in LOTC.

 With respect to tools, the left LOTC hand-selective representation has been shown to overlap closely with a region activated by tools [69], particularly those that are used in the hand to interact with the world as an extension of the body [70]. This suggests one way in which hand and object representations are tightly integrated: LOTC activity partly reflects a single integrated representation (hand-using-tool-as-effector), rather than distinct neural coding of hands and tools. Further, this joint representation of hands and tools interacts with parietal regions implicated in tool knowledge and use [69,71] in line with accounts of cortical organization that emphasize the influence of inter-regional connectivity [72-74].

Detailed examination of activity in the extrastriate body area suggests that this region (in concert with the fusiform body area) encodes a static representation of body shape and posture [26,75] that is not directly engaged in motor behavior [48,76]. However, another study found that EBA activity increases during preparation of unseen hand (vs. face) movements [49]. And broad LOTC visual representations of the limbs, including and extending beyond EBA, are also engaged by the execution of movements with those limbs [36] and are sensitive to the kinetic properties of observed movements [77]. These findings illustrate further ways in which LOTC encoding of the shape and posture of the body may be closely interrelated with representations of the properties of planned and executed movements.

These results are also congruent with recent evidence that LOTC is not only engaged by observing actions and by performing actions [78,79], but further is sensitive to the correspondence between what is seen and what is performed. For example, many imaging studies have shown LOTC activity in imitation tasks, which require participants to monitor viewed actions and to match their ongoing motor activity to what they see [23,39,80]. Similarly, activity in a region of LOTC increases when the effector used to make a response (hand or foot) matches the effector of an action that is concurrently viewed in a video, compared to a mismatch [81]. And a series of studies using whole-brain multi-voxel pattern analysis (MVPA) identified regions in which local patterns of brain activity are similar for a given action, whether seen or performed, but different for different actions [4,57]. Both anterior parietal and LOTC regions consistently showed these properties. Together, all of these findings imply that the LOTC’s roles in supporting action perception and overt action performance are closely related. In this regard, LOTC may have a larger role to play in the human action observation network [39] than typically conceived in accounts that focus on fronto-parietal regions [82].

Finally, turning to motion sensitive hMT+, this region overlaps with areas recruited when participants perform matching judgments about action pictures (compared to object pictures) [2]. Likewise, several studies reported an overlap between hMT+ and activations obtained when participants read sentences describing motion in comparison to sentences describing static events [65,83] (but see [63,84,85]). And a recent study found a stronger response to third- (“*prende”*, he grasps) in comparison to first-person (“*prendo”*, I grasp) verbs in hMT+ [86]. Collectively, these studies suggest that motion sensitive regions in LOTC are recruited during tasks that make demands beyond low-level visual motion perception.

Together, the findings reviewed in this section indicate how multiple sources of perceptual, conceptual, and motor information about actions can interact in the LOTC, sometimes in complex ways. Although this evidence adds weight to the view that LOTC can be seen as a hub of action encoding in the brain, it also highlights the complexity of the current picture and the need for synthesis.

*Theoretical views that implicate LOTC*

Because of the diverse ways in which LOTC activity represents many aspects of action, it is implicated in a variety of theoretical perspectives (Figure 2). These relate principles of neuroanatomical organization to propositions about the functional aspects of how actions are encoded. These different perspectives have in common the view that LOTC is well suited to integrate different types of information that are relevant for understanding and interacting with our environment.They vary in their relative emphasis on anatomy or function; in their focus on inter-regional connections (Figure 2A) or on local organizing principles (Figure 2B); and with respect to the overall computational goals that they propose the brain must solve. These theoretical perspectives are not mutually exclusive. Rather than selecting among them, our aim is to develop a more general framework that accommodates the diversity of properties and organizing principles that have been proposed to exist in LOTC.

 Theorists oriented towards high-level vision have focused on how occipitotemporal representations extract visual representations of objects that are useful for recognition (e.g. [87-89]). One proposed broad organizational scheme of particular relevance for LOTC focuses on the differential engagement of ventral and lateral occipitotemporal regions by the presence and type of visual motion [16]. Broadly, activity on the ventral temporal surface was found to be driven by static images and organized by visual category, while laterally, extending across the LOTC region considered here, activity was found to depend on the interaction of form with motion, with a further distinction between the motion of objects and of people.

For researchers concerned with the brain’s representation of meaning, the theoretical interest in LOTC has been around how our understanding of actions may be grounded in perception. Sensory-based embodiment accounts highlight the role of sensory regions for understanding related concepts [90]. For example, when seeing a pair of scissors, the sensory aspects of scissors (e.g. typical shape, size, material, typical movement when used) are assumed to be activated and to play an important part in understanding what scissors are, and are for. In the context of LOTC, researchers have focused on whether and how visual motion selective cortex is engaged by tasks requiring the understanding of dynamic aspects of actions and their perceptual consequences. Some supportive evidence comes from different tasks requiring various judgments about tools [17,61] and about verbal material describing motion [65,83] although there are contradictory findings [63,84].

Theoretical perspectives arising from social neuroscience focus on how LOTC representations help us to understand the actions of other individuals, with the ultimate aim of inferring their mental states (such as goals). In one view, for example, body and action representations of LOTC form the perceptual anchor of a pathway that extends beyond the LOTC into the superior temporal cortex and the temporal parietal junction [91]. Along this gradient, increasingly rich representations of the posture, movements, actions, and mental states of other people are constructed. In another perspective [92], a ventral pathway connecting the middle temporal gyrus (MTG) and posterior inferior frontal gyrus (IFG) supports action understanding in concert with the dorsal “action observation network” [42,43]. According to this view, representations in the middle temporal gyrus and the anterior inferior frontal gyrus jointly retrieve the most likely goal of an observed action on the basis of contextual information (including objects that are present; scissors indicate that a cutting action is likely [93,94]). This information is then used by the dorsal action observation network to generate predictions about the specific actions most strongly associated to that goal. Thus, in this view, LOTC representations contribute to our ability to relate the current percept to stored knowledge, in order to understand and anticipate the perceived actions of other people.

Finally, theorizing that concerns the use of action knowledge in the service of overt behavior has focused on how LOTC represents the characteristic ways in which objects (including tools) are used. For example, to account for the patterns of deficits seen in neuropsychological patients on a range of action tasks including pantomiming and mimicry, a tri-partite extension of the classic two-stream model of vision [95,96] has been proposed [97], in line with anatomical data [98]. This is highly consistent with a similar perspective motivated mainly by the organization of selective regions identified in neuroimaging experiments [5]. In this extended model, a “ventro-dorsal” stream stores information about the correct functional use of objects such as tools [1,23] and bridges visual and multimodal action representations [5].

*Representation of action and the organization of LOTC*

Here we consider how the evidence and theoretical frameworks that we have reviewed may be synthesized to produce an integrated understanding of how the LOTC represents action. The lateral occipitotemporal cortex hosts, in parallel, action representations of varying levels of complexity. A mosaic of focal, but partially overlapping, selective regions in LOTC represents specific information – about the shape of bodies, patterns of motion, affordances of tools, etc. -- that forms the components of action representations. Where task demands require it, these local representations can be called upon in order, for example, to detect motion [99], to detect people in complex scenes [29], or to reason about tools [24]. More broadly, diffuse patterns of activity across LOTC integrate these multiple local representations. Perceptual, semantic, and motoric information related to a given specific action will evoke relatively similar patterns, which in turn will be distinct from those patterns produced by other actions. Together, the distribution of these activity patterns defines a “space” (or indeed multiple spaces [89,100]).

The dimensions of these hypothesized spaces will reflect some key psychological aspects of the semantics of action [101] (Figure 3A). The action representations of LOTC are suited, but not limited, to encode the means (e.g. kinematics, hand posture, position of the hand with respect to the object) by which actions are carried out. In addition to such concrete properties, LOTC representations draw together actions that may have different local kinematic or perceptual features, but that share the aim to change the state of the world in a particular way, irrespective of how exactly this change of state is achieved. By contrast, inference of higher-level goals or the intentional states that motivate them are more closely attributed to parietal regions [102] or the “mentalizing” system [103]. As an example, viewing a lifting movement and performing a lifting movement produce similar patterns in LOTC, which in turn are distinct from the pattern produced by viewing or performing a slapping movement. These similarity relationships hold whether actions are viewed in a first- or third-person perspective, demonstrating an aspect of the generality of action representations in this region across specific sensory properties [57]. By contrast, the possible different intentions behind such movements (e.g. to open a water bottle to drink or to water the plants) are not likely to be distinguished in LOTC (cf. [104]).

A potential source of further hypotheses about the key dimensions of distributed action encoding in LOTC comes from a recent study examining the psychological organization of action semantics. Participants sorted photographs of tools according to the actions typically associated with their uses, and rated the tools on a number of action-related scales [105] (Figure 3B). Using multidimensional scaling analysis, the authors observed two important dimensions: the magnitude of the hand movement (i.e. distance and force) and hand configuration (e.g. “clench” vs. “palm”). A similar approach has been applied to examine the category structure of actions involving social interactions [106]. Thus it may be possible to identify important dimensions of action knowledge from behavioral tasks and judgments, and test how these are mapped systematically onto distributed patterns of brain activity [107]. This approach has been used in work in which models of “face space” (e.g. with dimensions of trustworthiness and dominance [108]) are defined on the basis of behavioral data and then related to measures of neural activity [109]. A similar approach has been successfully applied to the perception of objects [110], space [111], and biological classes [112].

Fronto-parietal regions involved in planning and executing action display systematic gradients in the mapping of representations to the cortical surface. For example, in human posterior parietal cortex there is evidence for a posterior-to-anterior gradient, with more posterior regions being engaged by the sensory aspects of a movement (e.g. target location), whereas anterior regions are more sensitive to movement-related information (e.g. which effector to use) [113]. In other species, microstimulation reveals further organization in parietal and precentral cortex, such as clustering by ethologically relevant action categories that include defensive movements, hand-to-mouth movements, and reaching movements [114,115].

With respect to LOTC, subregions of LOTC also differ in the characteristics of action they represent. In line with the proposals reviewed above, we expect that representations of action in this region follow multiple gradients, reflecting gradual changes e.g. in types of preferred motion [16], or preference for specific body parts [36]. Some of these gradients may be matched by, and possibly driven by, the profile of connectivity from LOTC to wider brain networks [73]. In line with this idea, a study of resting-state functional connectivity [116] found that MTG connectivity varies, with anterior regions showing more widespread connectivity than posterior regions, suggesting an anatomical basis for increasingly abstract, multimodal representations in the anterior direction.

*Concluding remarks*

 By taking an anatomically led approach, rather than focusing on a particular sub-discipline or a particular theoretical perspective, we have been able to draw together a wide range of findings to highlight the rich roles that the lateral occipitotemporal cortex plays in the perception, understanding, and production of action. We believe this approach is valuable in that it reveals links that were not otherwise obvious, speaks to ongoing theoretical debates about the functional and neuroanatomical organization of action representations, and suggests clear directions for future studies (see Outstanding Questions). It leads us to a view of LOTC as combining multiple sources of specific information into a distributed representation that is organized to capture psychologically relevant dimensions of knowledge about how actions change the states of the world. A similar approach may also prove useful in characterizing the functional organization of other brain regions.

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**Box 1: Defining and mapping the lateral occipitotemporal cortex**

Many diverse tasks that involve perceptual, conceptual, and motor aspects of action involve the lateral occipitotemporal cortex (LOTC). To what extent is this a genuine region, and how would we define its borders?

Many neuroimaging studies adopt functional localizers - independent data sets analyzed with simple contrasts to identify a focal region of interest according to its functional properties. For example, the typical paradigm to identify human hMT+, a visual-motion selective area, is to compare responses to moving vs. static dots; similarly, the “extrastriate body area” is identified by comparing bodies versus objects. One could identify LOTC as the collection of such focal regions. However, the engagement of LOTC by action (broadly construed) often extends beyond these “hot spots” (see Figure 1); indeed, their borders are not always clear (e.g. [117-119]). Further, other more complex tasks and stimuli elicit LOTC activity that is not easily localized to focal regions, for example where multi-voxel pattern analyses of distributed activity, which have low spatial precision, are employed.

More physiologically-motivated approaches use criteria such as cytoarchitecture and connectivity to define brain areas [120,121], but we are not aware of any studies examining the cytoarchitectonics in human LOTC specifically. With respect to anatomical connectivity, diffusion tensor imaging demonstrates that the middle temporal gyrus is connected with Brodmann area (BA) 47, with the posterior superior temporal sulcus and the angular gyrus (BA 39), and with the anterior superior temporal gyrus/BA 22. Functional connectivity reveals links between LOTC and a number of regions, including: superior temporal cortex; angular gyrus and superior parietal lobe; and the middle frontal gyrus and the dorsal portion of the precentral gyrus, as well as different portions of the inferior frontal gyrus, including BA44 and 45. These findings show that LOTC is richly connected with areas implicated in biological motion, language, and the selection, planning, and control of movements [116].

Thus, while the localization evidence from imaging and neuropsychology, and findings from connectivity studies, puts the LOTC in an ideal position for integrating information related to action, these findings do not clearly delineate LOTC as a distinct region. Therefore we adopt a pragmatic definition of lateral occipitotemporal cortex; in line with previous studies (e.g. [5]) we place the anterior boundary in the middle portion of the MTG; the posterior boundary in the lateral occipital sulcus; the superior boundary in the superior temporal sulcus; and the inferior boundary on the inferior temporal gyrus.

**Outstanding questions**

1. To what extent is LOTC distinct from neighboring regions in terms of cytoarchitecture or in terms of unique footprints of connectivity with other brain regions?
2. To what extent do the LOTC regions that are engaged by action-related processing overlap with each other? Are they spatially related in reliable ways, within and across subjects? (see Figure 1)
3. To what extent do the patterns of action-related activity in LOTC follow anatomical/functional gradients? (see Figure 2B)
4. Do local patterns of action-related activity in LOTC form a multidimensional “space”, and if so what are the main dimensions of that space? (see Figure 3B)
5. To what extent does LOTC connect with other brain regions (e.g. inferior parietal cortex, posterior parietal cortex, premotor cortex) implicated in other dimensions of action? To what extent do the local profiles of activity patterns in LOTC predict wider patterns of connectivity? In addition to the neuroimaging measures of functional and anatomical connectivity, brain stimulation methods may also shed light on these questions. For example, repetitive transcranial magnetic stimulation applied to the left posterior LOTC has been shown to abolish the difference between action and non-action verbs in the precentral gyrus [122]. In contrast to motor-based accounts of conceptual knowledge [123], this finding suggests that the sensitivity to the difference between action and non-action verbs measured in precentral gyrus is driven by the processing of semantics in the posterior LOTC.
6. To what extent do the properties of LOTC representations relate to individual differences in behavioral performance on various action-related tasks?
7. To what extent are the action-related representations of LOTC shaped by major neurodevelopmental factors such as congenital blindness or handedness [124]?
8. What are the key differences between left and right hemisphere LOTC? For example, EBA is known to be strongly right-lateralized (particularly in right handers [125]), whereas tool- and language-related modulations are typically stronger in left LOTC. Do these biases relate to wider organizational properties such as the lateralization of language?

**Figure Captions**

**Figure 1.** Approximate borders of the human lateral occipitotemporal cortex (LOTC), the focus of the present review. **A:** Outlines of LOTC superimposed on the segmented and inflated left hemisphere of an individual participant. Locations of key sulci and gyri are given for reference. **IFG**, inferior frontal gyrus; **CS**, central sulcus; **IPS**, intraparietal sulcus; **STS**, superior temporal sulcus; **MTG**, middle temporal gyrus; **ITS**, inferior temporal sulcus; **ITG**, inferior temporal gyrus; **MOG**, middle occipital gyrus; **LOS**, lateral occipital sulcus. **B**: Outlines of LOTC (red line), together with activation peaks reported in a variety of studies covered in this review (peaks reported in meta-analyses are indicated by black outline). Peaks derived as follows: basic motion [6,7,14,69]; biological motion [38]; tool viewing [17,69]; body parts [25,48,69,117]; hands [69,70]; action observation [39]; action imitation [1,39]; action planning [47,48,50,51]; actions crossmodal [57]; action concepts [46,126]; verbs [64,67,68,86]. Note that peaks do not reflect the typical spatial extent of activations nor overlap among them.

**Figure 2.** Some conceptions of the organization of action-related neural representations captured by activity in LOTC and their relationship to other brain regions. **A.** Solid lines: tripartite organization into dorso-dorsal, ventro-dorsal, and ventral stream [97,98]. Dashed line: two-pathway model of action understanding [92]. **B. Top left:** Posterior (concrete) to anterior (abstract) gradient [126]. **Top right:** posterior (visual) to anterior (multimodal) gradient [5]. **Middle left**: gradient from ventral temporal cortex (perception of socially relevant stimuli from static images of bodies) to the temporal parietal junction (intentions) [91]. **Middle right**: gradient from ventro-lateral (object motion) to dorso-lateral regions (human motion) [16]. **Bottom left.** Gradient of fMRI responses evoked by viewing legs (dorsal) to arms and faces (ventral) [36]. **Bottom right:** LOTC is likely to contain additional functional gradients (see Outstanding Questions).

**Figure 3.** **A.** Representational similarity analysis [101] can be used to examine different levels of action representations in LOTC. **Left panel:** Representational dissimilarity matrix (RDM). Each cell contains the dissimilarity between pairs of experimental conditions (measured as 1 minus the correlation). In this example, the RDM depicts a cortical region (or model for that region) that shows low dissimilarity (or high similarity) between similar effectors depicted visually, but not for effectors described verbally, indicating effector-specific representations that are limited to the visual domain. **Right panel:** Example RDM showing low dissimilarity between similar effectors, both when presented visually and when described verbally. This example indicates effector-specific representations that do not depend on the type of material (visual, verbal). **B:** Graphical representation of a multidimensional scaling analysis (adopted from [105]). To reveal the organization of actions, participants are instructed to sort stimuli along a critical dimension (e.g. the typical movement associated with the use of the depicted tools), or to directly rate movement similarity for each pairwise comparison on a Likert scale. The resulting similarity values are then entered into a multidimensional scaling analysis to reveal the underlying N-dimensional similarity structure.

 These similarity measures can be used to test how they are mapped systematically onto distributed patterns of brain activity.

 **Glossary**

**Brodmann area:** a cortical area defined on the basis of cytoarchitectonic maps originally suggested by Brodmann in 1909

**Conceptual knowledge:** e.g. knowing that a cow typically has four legs, eats grass and produces milk

**Diffusion tensor imaging:** a method to examine white-matter fiber bundles; in brief, this method exploits the fact that diffusion (i.e. the probability of displacement with time) of water molecules varies across different types of tissue

**Embodiment:** the idea that higher cognitive functions reside on sensory and motor representations

**Encoding**: converting information in such a way that it can be stored and used again

**Functional connectivity**: a measure of connections between different brain areas based on how their activity covaries over time

**Hub**: a brain region with rich anatomical connections serving as an interface between other regions

**Local patterns of brain activity:** defined as the profile of activation across a brain region; as an example, activation might be high in voxel 1, 2 and 4 and low in voxel 3 and 5 in condition A, whereas it might be high in voxel 1 and 3 and low in voxel 2, 4 and 5 in condition B

**Mentalizing system:** a set of regions, consisting of the medial prefrontal cortex and the temporo-parietal junction, recruited during tasks that require inferring the intentions or beliefs of other people

**Mirror-neuron system:** a set of regions, consisting of macaque premotor area F5 and macaque areas PF and PFG in the inferior parietal lobule, that contain neurons that are active both when the monkey observes an action (e.g. grasping), and when the monkey performs a similar movement; the human homologue of the mirror-neuron system has been suggested to consist of the posterior portion of the inferior frontal gyrus, the inferior portion of the precentral gyrus and the rostral portion of the inferior parietal lobule

**Motor regions:** regions involved in movement planning and execution, consisting of the primary motor cortex, dorsal and ventral premotor cortex, supplementary motor area, frontal cortex, and superior parietal lobule

**MVPA (multi-voxel pattern analysis)**: a method that uses local patterns of brain activity (instead of analyzing data at each voxel independently) to distinguish between different neural processes

**Neural space**: refers to the idea that the patterns of activity across a brain region are related in a systematic way to some properties of a stimulus or of a mental process

**“Point-light” displays:** animations of movements such as walking, created by placing luminous points on key joints of the body and removing other cues about the surface features of the body

**Predication**: describes a feature of verbs, namely constituting the relationship between two nouns (e.g. Paul, paper -> Paul writes a paper)

**Resting state activity**: a measure of brain activation in the absence of a specific task that can be used to compute functional connectivity between different brain areas

**Semantic processing:** processing the meaning of a stimulus

**Structural connectivity:** a measure of connections between different brain areas based on white matter / axon fibers

**Voxels:** the basic unit of measurement of brain activity in functional brain imaging; typically on the order of 3x3x3 mm in size