The lateral occipitotemporal cortex in action

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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. Here, 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 LOTC

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; and 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 (see Glossary), and motoric knowledge of action. Several diverse lines of evidence show that LOTC (Box 1; Figure 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. Furthermore, 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 subdisciplines 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 the role of this broad region as a hub in which

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Glossary

Brodmann area: a cortical area defined on the basis of cytoarchitectonic maps originally suggested by Brodmann in 1909.
Conceptual knowledge: for example, 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 voxels 1, 2, and 4 and low in voxels 3 and 5 in condition A, whereas it might be high in voxels 1 and 3 and low in voxels 2, 4, and 5 in condition B.
Mentalizing system: a set of regions, comprising the medial prefrontal cortex and the temporoparietal junction, recruited during tasks that require inferring the intentions or beliefs of other people.
Mirror-neuron system: a set of regions, comprising 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 homolog of the mirror-neuron system has been suggested to comprise the posterior portion of the IFG, 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, comprising the primary motor cortex, dorsal and ventral premotor cortex, supplementary motor area, frontal cortex, and superior parietal lobule.
Multi-voxel pattern analysis (MVPA): 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 relation 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 and/or axon fibers.
Voxels: the basic unit of measurement of brain activity in functional brain imaging; typically on the order of 3×3×3 mm in size.

Box 1. Defining and mapping LOTC

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

Many neuroimaging studies adopt functional localizers, which are 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 versus 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' (Figure 1, main text); indeed, their borders are not always clear (e.g., [117–119]). Furthermore, other more complex tasks and stimuli elicit LOTC activity that is not easily localized to focal regions, for example where MVPA of distributed activity, which has low spatial precision, is used.

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 MTG 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 several 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 IFG, including BA44 and BA45. 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 LOTC; 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.

perceptual, semantic, and movement-related sources of action information converge.

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+'. Given 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 the 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 (MTG)] 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 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 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]. By contrast, action observation is often examined in the context of the 'action observation network', a proposed homolog of the 'mirror