

The neural bases of different levels of action understanding

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Marneweck M, Vallence AM. The neural bases of different levels of action understanding. *J Neurophysiol* 115: 1085–1087, 2016. First published September 2, 2015; doi:10.1152/jn.00819.2015.—Many have recently questioned whether all levels of actions understanding, from lower kinematic levels to the higher goal or intention levels of action understanding, are processed in the action observation network (a network of neurons that are active during action execution and observation). A recent study by Wurm and Lingnau (*J Neurosci* 35: 7727–7735, 2015) gave evidence to the contrary, by showing that higher levels of action understanding are processed in the lateral occipitotemporal cortex. An important next step is to differentiate between the role of the lateral occipitotemporal cortex in processing the visual form of an observed action and the goal of an observed action.

action understanding; action goals; fMRI; motor system; occipitotemporal cortex

IT IS WELL ACCEPTED THAT actions can be described, and therefore understood, at different levels. Lower levels of action understanding are based on kinematics and muscle activity, whereas higher levels of action understanding are based on action goals and intention. Action understanding can be specific to a concrete action element (e.g., open a specific box) or by any instantiation of that action independent of the concrete object (e.g., open), as was recently put forth by Wurm and Lingnau (2015). A concrete (open a specific bottle), intermediate (open bottle, irrespective of specifics of one type of bottle), and abstract understanding (open, irrespective of object category) of an action represents different levels of a conceptual action hierarchy. The action observation network (AON), comprising the ventral premotor cortex (PMv), inferior parietal lobule (IPL), and superior temporal sulcus (STS), has been proposed as a neural substrate for action understanding (see for review Rizzolatti et al. 2014). Mirror neurons in the AON are active during both the execution and the observation of actions. Proponents of the mirror neuron account of action understanding argue that if the same neurons that are active when an action is executed (i.e., when the intention of the action is known) are also active when an action is observed, then the intention of the observed action can be inferred, and thus the action understood. In recent years, many have questioned whether all levels of action understanding are solely reliant on this network (see for reviews Hickok 2013; Kilner 2011). In a recent edition of the *Journal of Neuroscience*, Wurm and Lingnau (2015) investigated brain regions important for action understanding at different levels of abstraction using cross-

conditional multivoxel pattern analysis (MVPA) of functional magnetic resonance imaging (fMRI) data.

Wurm and Lingnau (2015) aimed to identify the brain regions important for action representations at three levels of an action conceptual hierarchy: concrete, intermediate, and abstract. This group obtained fMRI data while participants observed video recordings of reach-and-grasp actions: opening and closing 1) a screw-cap water bottle, 2) a wine bottle with a cork, and 3) a box with a lid. The training classifier for the MVPA was the water bottle (open vs. close), and the test classifier differed across the levels of action representation: for concrete, the test classifier was the water bottle (open vs. close); for intermediate, the test classifier was the wine bottle (open vs. close); for abstract, the test classifier was the box (open vs. close). Thus the MVPA aimed to decode open-and-close trials of different objects (water bottle, wine bottle, box) with training on the same classifier (water bottle); for intermediate and abstract (but not concrete), the kinematics and object in the test classifier differed from the training classifier. Using this design, Wurm and Lingnau (2015) aimed to identify brain regions that represent action (in this case open or close), irrespective of object example (bottle type) and object category (bottles vs. box), thereby identifying which neural populations are important for understanding actions at different levels of abstraction. The results of the region-of-interest (ROI) MVPA showed that action understanding at the concrete level could be decoded by neural activity in PMv, IPL, and lateral occipitotemporal cortex (LOTc) but that action understanding at the intermediate and abstract levels could only be decoded by neural activity in IPL and LOTc.

A novel and interesting finding of Wurm and Lingnau (2015) is the ability to decode an action (in this case, open or close) at the abstract level from neural activity of LOTc. This finding is in direct contrast with the suggestion that the action understanding occurs exclusively within the three reciprocally connected areas in AON (PMv, IPL, and STS). A major criticism of the AON account for action understanding is that for this model to be able to infer the goal or intention of an action, that is, abstract action understanding, there would have to be a one-to-one mapping between the kinematics and the goal. This is not the case, because the same kinematics of an action can be used for many different goals and intentions, and the same goal can be achieved with many different actions (Hamilton and Grafton 2007; Kilner 2011). It has been suggested that, more likely than relying on the AON alone, abstract action understanding is dependent on the interaction between the AON and the ventral pathway that links middle temporal gyrus (MTG) with the anterior inferior frontal gyrus (IFG) (Badre and D'Esposito 2009; Binder et al. 2009; Turken and Dronkers 2011; Wagner et al. 2001). Wurm and Lingnau

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(2015) provide evidence to show that action understanding occurs beyond the AON; on the basis of their finding that neural activity in LOTC can decode actions at the abstract level, they argue for a cognitive account of action understanding whereby perceptual functions underlie action understanding, similar to object recognition. However, given the importance of LOTC in perception of visual form (see for review Loffler 2008), it is possible that this region is decoding differences in visual features between the to-be-decoded actions, rather than decoding differences in goal between to-be-decoded actions. Although the perceptual similarity analysis reported in Wurm and Lingnau (2015) showed that the perceptual differences between the to-be-decoded actions (i.e., open vs. close) were smaller than the perceptual differences between the same actions across conditions (i.e., open water bottle vs. open wine bottle vs. open box), there were still perceptual differences between the to-be-decoded actions. Similarly, although the movement trajectories of to-be-decoded actions were mirror-like, there were still differences in movement trajectories between the to-be-decoded actions. Therefore, LOTC activity could be explained, at least in part, by differences in visual features between to-be-decoded actions. In addition to LOTC, the results from the ROI MVPA show that intermediate and abstract actions could be decoded from neural activity in IPL (part of the AON), and results from the searchlight MVPA identified the posterior MTG as a region that could decode action at the abstract level. These results fit with the suggestions that interactions between the AON and the ventral pathway that links MTG with the IFG are important for abstract action understanding (see Kilner 2011). The findings of Wurm and Lingnau (2015) indicate that a network of regions, including areas of the AON, MTG, and LOTC, are important for action representation; however, the precise role of LOTC in abstract action understanding remains unknown.

A comprehensive operationalization of the different levels of action understanding was proposed by Kilner (2011): 1) the kinematic level: the trajectory and the velocity profile of a goal-directed action (e.g., the reach-to-grasp phase of opening a bottle); 2) the motor level: the processing and pattern of muscle activity required to produce the kinematics; 3) the goal level: the immediate purpose of the action (e.g., opening a bottle); and 4) the intention level: the overall reason for executing the action (e.g., to drink). The goal and intention levels reflect abstract action understanding. One method to further elucidate the role of LOTC in abstract action understanding would be to manipulate goal-directed attention and object-directed attention during fMRI. In an elegant study, Hamilton and Grafton (2007) used a repetition suppression design to infer neuronal population coding for different levels of action understanding. Three groups of subjects viewed a series of movie sequences during fMRI. Each movie sequence was defined as “novel” or “repeated,” depending on whether it matched the sequence that came before it, on each of three stimulus dimensions: 1) the goal object (dumbbell or wine bottle; notably, they defined the action goal by the identity of the object, and thus the object and action goal are intertwined in this condition); 2) the grasp type (whole hand or precision); and 3) the object weight (as revealed by lifting velocity). Key to differentiating the neural bases of different levels was that each group was asked during fMRI to attend to one of the three stimulus dimensions in each movie sequence. They found

evidence for a hierarchical system for understanding, suggesting that a visual representation of action kinematics resided in LOTC, with more activity in response to attending to novel grasp types and object weights compared with repeated grasp types and object weights. Conversely, they found more activity in IPL and IFG, and not in LOTC, in response to attending to novel than repeated object goals. Interestingly, a recent study by Finisguerra et al. (2015) provides some evidence to suggest a role of the primary motor cortex (M1) in action understanding at the level of the goal. This group showed an increase in corticospinal excitability measured from a forearm flexor, a muscle directly involved in closing the hand, during observed closing actions of the hand, mouth, and eye compared with observed opening actions of the hand, mouth, and eye. On the basis of this finding, the authors suggest that motor activity induced by action observation can map complex action features, such as “open” or “close” (i.e., action goals; Finisguerra et al. 2015). Together, this evidence suggests that LOTC is important for decoding visual features of action kinematics and that other regions, including IPL, IFG, MTG, and potentially M1, are important for decoding action goals.

The results of Hamilton and Grafton (2007), supporting the role of LOTC in decoding visual features of action kinematics, contrast the interpretation of Wurm and Lingnau (2015), that LOTC plays an important role in abstract action understanding. However, the strength of Wurm and Lingnau’s experimental paradigm is the capacity to decode action goals irrespective of the object example and object categories, to investigate actions at different levels of abstraction. Therefore, the role of LOTC in abstract action understanding could be further examined by manipulating the level of action understanding to which subjects are to attend (as per Hamilton and Grafton 2007) within the experimental paradigm of Wurm and Lingnau (2015). Specifically, individuals would watch movie sequences of the opening and closing of a water bottle, wine bottle, and box while attending to either the goal (i.e., open and close) or the object (i.e. bottle/box). If neural activity in LOTC during the goal-directed attention condition (but not object-directed attention condition) can decode action at the abstract level, it would suggest an important role of LOTC in abstract action understanding. However, if neural activity in LOTC during the object-directed attention condition (but not the goal-directed attention condition) can decode action at the abstract level, it would suggest a greater role of LOTC in perceptual processing of the visual form, rather than the goal of the action. Furthermore, given the findings of Wurm and Lingnau’s searchlight analysis, and Hamilton and Grafton’s ROI results, we might expect that neural activity in IPL can decode action at the abstract level for goal-directed but not object-directed attention, providing some insight into the complex neural network required for abstract action understanding. In summary, Wurm and Lingnau (2015) provided convincing results that LOTC is involved in the ability to perceive actions of others. A pertinent next step is to clarify the specific role of LOTC in action understanding, by differentiating its involvement in goal and visual analysis of actions.

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AUTHOR CONTRIBUTIONS

M.M. and A.-M.V. conception and design of research; M.M. and A.-M.V. interpreted results of experiments; M.M. and A.-M.V. drafted manuscript; M.M. and A.-M.V. edited and revised manuscript; M.M. and A.-M.V. approved final version of manuscript.

REFERENCES

- Badre B, D'Esposito M.** Is the rostro-caudal axis of the frontal lobe hierarchical? *Nat Rev Neurosci* 10: 659–669, 2009.
- Binder JR, Desai RH, Graves WW, Conant LL.** Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex* 19: 2767–2796, 2009.
- Finisguerra A, Maffongelli L, Bassolino M, Jacono M, Pozzo T, D'Ausilio A.** Generalization of motor resonance during the observation of hand, mouth and eye movements. *J Neurophysiol* (August 19, 2015); doi:10.1152/jn.00433.2015.
- Hamilton AF, Grafton ST.** The motor hierarchy: from kinematics to goals and intentions. In: *Attention and Performance XXII: Sensorimotor Foundations of Higher Cognition*, edited by Haggard P, Rosetti Y, Kawato M. Oxford, UK: Oxford University Press, 2007.
- Hickok G.** Do mirror neurons subserve action understanding? *Neurosci Lett* 540: 56–58, 2013.
- Kilner JM.** More than one pathway to action understanding. *Trends Cogn Sci* 15: 352–357, 2011.
- Loffler G.** Perception of contours and shapes: Low and intermediate stages mechanisms. *Vision Res* 48: 2106–2127, 2008.
- Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S.** Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiol Rev* 94: 655–706, 2014.
- Turken AU, Dronkers NF.** The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front Syst Neurosci* 5: 1, 2011.
- Wagner AD, Pare-Blagoev EJ, Clark J, Poldrack RA.** Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31: 329–338, 2001.
- Wurm MF, Lingnau A.** Decoding actions at different levels of abstraction. *J Neurosci* 35: 7727–7735, 2015.

