



HHS Public Access

Author manuscript

Wiley Interdiscip Rev Cogn Sci. Author manuscript; available in PMC 2016 November 01.

Published in final edited form as:

Wiley Interdiscip Rev Cogn Sci. 2015 November ; 6(6): 483–490. doi:10.1002/wcs.1367.

Rethinking Actions: Implementation and Association

Lorna C. Quandt and Anjan Chatterjee

Lorna C. Quandt: lquandt@mail.med.upenn.edu

Abstract

Action processing allows us to move through and interact with the world, as well as understand the movements performed by other people. In recent years, there has been increasing interest in the semantics of actions as differentiated from the semantics of objects. However, as the understanding of action semantics has evolved, it is evident that the existing literature conflates two senses of the word “action”—one that stems from studies of tool use and the other from event representation. In this paper, we suggest that this issue can be clarified by closely examining differences in how the human parietal and temporal cortices of the brain process action-related stimuli. By contrasting the posterior parietal cortex to the posterolateral temporal cortex, we characterize two complementary action systems in the human brain, each with its own specialization of function. We suggest that these two systems be referred to as the parietal Action Implementation System, and the posterolateral temporal Action Association System. While the fronto-parietal system is concerned primarily with how we perform actions, and simulate others’ actions, the temporal action system is more involved with processing actions from a third-person, conceptual standpoint. Recent work in cognitive neuroscience of perception and language, as well as the neuroanatomical organization of these brain regions support this distinction. We will discuss the implications of this work for cognition-, language-, and neuroscience-based action research.

ACTION IN THE BRAIN

Knowledge about actions allows us to guide and coordinate our own actions, as well as to understand other people’s movements, behaviors, and intentions. Action understanding is critical to our ability to communicate, learn, and act in the world. We argue that the existing scientific literature concerning action in the human brain conflates two types of action knowledge, one derived from investigations of tool use, and the other from investigations of event representation. We propose that action knowledge takes two distinct forms: an Action Implementation System (AIS) harbored within parietal cortices, specializing in controlling skilled bodily movements and relating others’ actions to the self, and an Action Association System (AAS) located in posterolateral temporal lobes, specializing in identifying actions and retrieving associated conceptual representations. These two systems can be characterized across different levels of organization, and each system consists of multiple functional regions that contribute to common processing goals. This functional specialization permits parallel processing of two different modes of action information.

Correspondence to: Lorna C. Quandt, lquandt@mail.med.upenn.edu.
no conflicts of interest

Earlier attempts have tried to delineate the contributions of different brain regions to action processing. The classic two-visual streams hypothesis postulates that visual processing diverges into interacting “where” and “what” pathways. In this view, the dorsal “where” stream, which projects from the occipital lobe into the parietal lobe, encodes spatial relations between visual objects¹. In contrast, the ventral “what” stream, which projects from the occipital lobe and continues into the temporal lobe, classifies visual stimuli into understandable categories with enduring properties. Goodale and Milner modified this hypothesis by emphasizing the importance of the “where” system to motor behavior, suggesting that this stream was better framed as a “how” system^{2,3}. The dorsal aspect of the two-visual-streams hypothesis has been refined further^{4,5}. Based on neurophysiological and behavioral work, Buxbaum and colleagues proposed that the dorsal stream is better conceptualized as containing two systems, a dorso-dorsal “reach to grasp” stream and a ventro-dorsal “use” stream involved in knowledge of how to use tools^{6,7}. Our model follows a similar framework, extending it with the proposal that a dorsal AIS pathway specializes in sensory-to-motor transformations of actions, and a ventral AAS system specializes in conceptual action associations. The presence of multimodal convergence zones in these two pathways is consistent with this model. We propose that the “grasp” and “use” systems are both components of the AIS, which is distinct from the AAS. Figure 1 characterizes the AIS and AAS at multiple structural and functional levels. An important feature of this functional distinction is distinguishing between a first-person and a third-person perspective in action knowledge. The AIS underlies action processing from a first-person perspective, relating observed actions to one’s existing motor repertoire. In contrast, the AAS processes actions from a third-person perspective, relating observed actions to stored semantic concepts, without regard to motor plans or one’s own experience with carrying out the action. In everyday life, these systems work in concert, allowing us to understand, imitate, and derive meaning from the actions we see.

ACTION IMPLEMENTATION AND FRONTO-PARIETAL CIRCUITRY

Parietal circuitry, in conjunction with connections to the frontal lobe, is critical for guiding one’s own actions, storing knowledge about how to perform actions, and simulating others’ actions, possibly by engaging the putative human mirror neuron system (MNS). Action Implementation refers to this mode of action knowledge, and encompasses both the dorso-dorsal “reach-to-grasp” system and the ventro-dorsal “use” system⁷. Virtual lesions created with transcranial magnetic stimulation have shown that the inferior parietal lobule (IPL) is involved in distinguishing “self” from “other”⁸, which is in line with the tendency for this region to specialize in relating actions to the self. Additionally, specific deficits in imitating others’ actions are linked to damage in somatosensory cortices, the angular gyrus, and the supramarginal gyrus,⁹ highlighting the role of the parietal lobe in carrying out actions without necessary reference to any stored semantic information.

On a basic level, the parietal lobe codes our intentions to act and then implements the relevant action. Many human functional neuroimaging studies have shown that parietal brain areas, particularly around the anterior intraparietal sulcus (aIPS), control one’s own actions¹⁰ by guiding reaching movements and storing knowledge of how tools are used⁷. The involvement of aIPS in goal-oriented reaching and grasping is shown by single-unit

recording in primates¹¹ and functional neuroimaging in humans¹². Reaching to grasp is inherently goal-oriented and its specific motor implementation is constrained by the spatial location and shape of visible objects. Damage to the aIPS can result in optic ataxia, a clinical syndrome in which people have difficulty reaching to the location of objects as guided by their vision⁵. In contrast, damage to the ventro-dorsal object-use stream produces ideomotor apraxia, which leads to difficulties with using and pantomiming the use of tools to perform skilled tasks¹³.

Actions performed by other people are also processed in the parietal lobe of the observer, leading to characterization of the parietal lobe as specialized for “perception-for-action”¹⁴. Multivariate pattern analysis of functional neuroimaging data has revealed a gradient of information content in the parietal lobe, in which posterior regions represent action goals while anterior areas favor the effector used to carry out an action¹⁵. Function-related information is stored in the anterior IPL, adjacent to manipulation-related regions¹⁶. These function-specific regions encode the ways in which a person might carry out a particular action. In support of this notion, recent neuroimaging work shows that the primary somatosensory and motor cortices respond to action stimuli in terms of how the actions might be executed, rather than the visual features of the stimuli¹⁷. Affordances of objects that guide how one might act upon them (e.g., whether an object is graspable) are also encoded in fronto-parietal regions. For instance, EEG recordings show that while the occipito-temporal cortex responds early (210–270 ms) to both graspable and non-graspable objects, premotor (210–270 ms) and primary somatosensory cortex (550–600 ms) responds more strongly to tools than to plants¹⁸. Finally, the occipitoparietal junction encodes object orientation, which is crucial for knowing how one would act upon the object, even though this region does not encode the identity of objects¹⁹.

The action observation network (AON) encompasses brain regions that are especially active during the observation of others' actions²⁰, and includes the IFG, dorsal premotor cortex, supplementary motor area, intraparietal cortex, posterior MTG, and fusiform face and body areas. The AON encompasses both the AIS and the AAS. The putative human mirror neuron system (MNS) is a part of the AON, and the MNS is distinctive because it is active both during the production of action, and during the observation of others' actions, indicating that people process others' actions by means of vicarious simulation. This simulation probably facilitates the observer's understanding of the action he or she is seeing²¹. The MNS comprises a largely fronto-parietal circuit²², with the IPL, the inferior frontal gyrus, and the STS traditionally considered central hubs of this network. The superior parietal lobe is particularly involved in the common coding of perception and action²³, while inferior parietal cortex is sensitive to the biological plausibility of actions²⁴, supporting the overall idea that in this region others' actions are processed in relation to the observer's own capacity to produce the action.

An observer's prior experience with the action being observed modifies the simulation of others' actions^{25, 26}. For example, the IPL is more activated by the observation of dance movements with which the observer has greater personal experience²⁷ or general familiarity²⁸. More specific types of experience with action also modulate subsequent parietal activity during action observation. For example, learning about sensorimotor

characteristics of object-directed actions (i.e., learning that an object is heavy or light) leads to differences in the parietal cortex while observing object-related gestures²⁹. Similarly, prior tactile experiences associated with actions modulate mirroring activity over central and parietal areas during action observation³⁰. This work demonstrates that specific details of one's prior action experiences can change subsequent action processing in the parietal lobe. Importantly, these studies have not found evidence for such effects in temporal lobe regions^{25, 27, 31}. Along with recent human functional neuroimaging evidence highlighting the role of one's own motor system in action understanding¹⁷, the accumulating evidence is consistent with the hypothesis that parietal action representations are self-referential.

ACTION ASSOCIATION AND THE POSTEROLATERAL TEMPORAL CORTICES

The temporal lobe is implicated in recognizing actions and retrieving associated conceptual representations. In this way, it serves as a perceptual and conceptual recognition system. The areas of the lateral temporal lobe that are most involved in this process in the macaque include the middle temporal gyrus (MTG), the superior temporal sulcus/gyrus (STS/STG), and lateral regions bordering the occipital lobe. A recent voxel-based lesion-symptom mapping study shows a pattern consistent with our proposed model. While patients with parietal damage had pronounced imitation deficits, patients with damage to the left posterior temporal gyrus had difficulties with tool-related tasks, which are unique in that they require associations of certain actions to certain tools⁹.

The posterolateral part of the inferior temporal gyrus (area MT/MST) is responsive to visual motion³². While area MT provides input to parietal action-related areas⁵, it is also a critical part of the AAS, feeding action information forward to the pMTG to be linked to abstract conceptual knowledge. Posterior regions of the STS are particularly sensitive to biological motion, like movement of the human body^{27, 33} and fMRI research has shown that different types of action observation (e.g., social communication or gaze perception) are differentially encoded in the right STS³⁴. Together, the coordinated function of these regions recognizes an action for what it is.

Regions in the temporal lobe link moving visual stimuli to conceptual information about the content or purpose of dynamic actions. For example, while seeing a human form moving in a certain pattern, an observer might identify the movement as "dance", or as "classical ballet". This conceptual knowledge of actions relies on the bilateral posterolateral temporal lobes³⁵. A wide array of functional neuroimaging work suggests that the posterior MTG contains a semantic system in which associative mechanisms pair visual input conveying actions (e.g., action words or images) with semantic action concepts^{35, 36}. Accordingly, a primary function of the posterior MTG is to link observed actions with stored event-related action knowledge³⁷. The storage of action concepts in this manner may follow a similarity-based framework, such as has been previously described for object concepts³⁸. That is, rather than storing an absolute representation of *jumping*, the brain encodes the concept of *jumping* based on the similarities and differences shared by *jumping* and other cases that share certain features (e.g., *vaulting*, *twirling*). Recent behavioral work shows that this sort of similarity-based structure underlies tool use knowledge³⁹. Under such a framework,

action concepts are stored as semantic, generalized concepts, largely separate from any direct relation to the self.

Action abstraction, wherein actions are generalized away from an actor or a specific exemplar of an action, is an important function of the AAS. The pMTG, which encodes conceptual action knowledge, abstracts away from the adjacent visual motion area MT⁴⁰. In addition to moving stimuli, static images depicting actions and images of action-associated objects (i.e., tools) also activate posterolateral temporal areas^{17, 41}, suggesting that these regions retrieve the action concepts associated with the image. Action representations may be stored along a gradient of abstraction, in which the lateral occipitotemporal cortex encodes concrete action representations (e.g. images depicting objects in motion) while more abstract action-related concepts (e.g., words that describe dynamic events) are located centripetally towards the perisylvian cortex^{42, 43}. In keeping with the spirit of dividing the dorsal stream into a dorso-dorsal “reach and grasp” and a ventro-dorsal “use” sub-stream⁶, we suggest that the ventral stream is divided into ventro-ventral “object association” and a dorso-ventral “action association” sub-streams.

ANATOMICAL FOUNDATIONS OF THE TWO SYSTEMS

Multimodal convergence zones in the parietal and temporal lobes help to conceptualize the differences between these two action-processing systems. In the AIS, signals from the external world are integrated with internal sensations and motor plans. In contrast, in the AAS, signals from the outside world converge, with little input from our internal senses. We suggest that types of sensory convergences that occur in parietal and temporal regions lay the foundation for higher-order AIS and AAS streams. Single-unit recordings and anatomical tracing studies show that in the primate ventral intraparietal area, exteroceptive inputs (e.g., vision) converge with interoceptive tactile, proprioceptive and vestibular inputs⁴⁴. In humans, the aIPS performs similar superadditive integration of visual and tactile inputs⁴⁵. In the macaque, somatosensory and visual signals converge in the IPS, integrating external and internal signals in a bidirectional manner⁴⁶. Taken together, the convergence of internal and external signals in the posterior parietal lobe forms a link between dynamic representations of our own body and the changing external environment. This low-level link may be the foundation on which action-relevant sensations from the external world are related to the self and mapped onto motor programs.

By contrast, in the posterolateral temporal lobe, exteroceptive visual and auditory signals converge⁴⁷. The visual and auditory sensations processed in this area confer information about the external world, and thus form the foundation of the AAS. In primates, single-cell recordings reveal neurons that are sensitive to both auditory and visual stimuli in the STS^{48, 49}. Overall, the lateral temporal lobe, which is the home of auditory processing and visual motion detection areas (MT/V5), integrates auditory and visual inputs from the external world, via connections with the superior colliculus⁴⁷. In humans, the STG is involved in speech comprehension, which relies on the integration of auditory and visual cues⁵⁰. The neural organization of audiovisual integration areas supports our proposal that this design of sensory convergences might be the low level link upon which actions are represented as independent from the self.

Despite being conceptually and anatomically distinct, AIS and the AAS are usually seamlessly coordinated. The way this integration occurs is not entirely understood, but likely involves both the posterior and anterior aspects of the respective streams. Connectivity analyses demonstrate that the AIS and AAS each make contributions to action observation, and that the strength of these connections changes as a result of experience with actions⁵¹. Additionally, recent findings suggest that parts of the occipito-temporal cortex, such as the extra-striate body area and adjacent object recognition areas are not just passively responsive to the perception of bodies and objects. Areas within occipito-temporal cortex that generally respond to visual representations of the limb and trunk are also partially responsive to first person movement of those same body parts⁵². Whether this activation is driven by actual input from motor programs, or by vivid imagery or proprioceptive signals that accompany motor movements, is not yet known.

The AIS and AAS may also exert modulations upon one another. For example, short-term movement intentions can override long-term semantic associations of how an object is typically used⁵³ (for review, see⁵⁴). In these cases, semantic information (reliant on the AAS) is selectively activated depending on whether it is in accord with the immediate goal of the actor (reliant on the AIS). In contrast, the AAS can modulate the functioning of the AIS. For instance, short-term movement goals may be executed more quickly if they are congruent with higher-level conceptual goals^{55,56}. Future research should more closely consider the contextual variables that influence these interactions and the neuroanatomical substrates upon which they rely.

Anatomical connections may provide additional hints about how the AIS and AAS function together. Anteriorly, the aSTG and parts of the dorsolateral prefrontal cortex are connected by the temporo-frontal extreme capsular fasciculus. The importance of this pathway, has not been adequately appreciated in recent research⁵⁷. First described by Petrides and Pandya in the macaque⁵⁸, the human analog of this connection has been confirmed in recent years⁵⁷. The temporo-frontal extreme capsular fasciculus may serve to organize the aSTG with prefrontal cortices into a coordinated functional unit and might integrate associative knowledge of actions with their implementation.

ACTION KNOWLEDGE AND LANGUAGE

The neural organization of action language parallels our proposed distinction between the AIS and AAS. Actions typically involve objects in dynamic relation to the observer or to other entities. In English, these dynamic relations are referred to by distinct linguistic constituents that identify how objects move, and where they are located⁵⁹. For example, in the sentence *The girl skips down the hill*, the verb “skips” describes the girl’s manner of motion, and the prepositional phrase “down the hill” refers to her locative path of motion. Attending to the manner of motion in visual events activates posterior inferior/middle temporal cortex while attention to path is associated with activity in the intraparietal sulcus and posterior middle frontal gyrus⁶⁰. This segregation of dynamic visual attributes extends to the functional-anatomic organization of their linguistic counterparts.

Action language processing in the temporal lobe is concerned with conceptual understanding of actions without relying on a first person reference. Posterolateral temporal brain regions including the MTG are tuned to the abstract action concepts conveyed by action verbs^{43, 61}. For example, Bedny and colleagues⁶² suggest that while reading action verbs, posterolateral temporal cortex abstracts away from sensorimotor information and groups words according to semantic categorizations or grammatical classifications. Furthermore, thematic role knowledge, which is the understanding of *who* is doing *what* to *whom*, is determined by how verbs organize meaning conveyed by a sentence. Patients who have damage to the MTG and STG have difficulty with this higher-order understanding of actions⁶³.

Given the AIS' specialization for linking our bodies' actions to the external world, it is not surprising that linguistic information conveying locative knowledge is aligned anatomically with this system. Locative knowledge encodes spatial relationships between entities (e.g., *between* or *under*). When planning movements, knowing whether to direct an action to an object *on* the table or *behind* a curtain is critical. Understanding locative prepositions such as these relies on the supramarginal gyrus^{64, 65}. Similarly, the end points of goal-directed actions rely on location information, which is processed in parietal and frontal regions⁶⁶. Thus, while the lateral temporal lobe specializes in action verbs that describe manners of motion that are independent of the self, parietal cortices are critical for situating actions in relation to one's own location in space.

Conclusion

Our knowledge of actions occurs at different levels of functional and anatomic organization in the brain that are integrated almost seamlessly. We understand familiar actions such as seeing somebody throw a ball—an action we may have performed many times. We might be at bat and prepare to hit a ball that the pitcher throws. Or we might watch a sport like curling, which we have never played, although we may understand the nature of the actions. We might see a snake slithering through the grass and react to the threat it poses, although we lack the motor capacity to slither. We might even appreciate the beauty of a swelling ocean wave, an action that lacks agency. Each of these instances of action processing draws upon the two action systems of the human brain, either by involving both processing streams simultaneously, or by relying on one more than the other. By conceptualizing actions in reference to the neural underpinnings of their implementation and association we are able to categorize their first- or third-person relevance, their relation to tool use or conceptual roles, and their links to different elements of language. This new way of looking at action processing has significant implications for the fields of visual perception, psycholinguistics, and cognitive neuroscience. Most critically, the descriptions of the AIS and the AAS should prevent the conflation of these two action systems as researchers pursue new avenues of inquiry. Future research should continue to explicitly contrast the functions of these two systems across a variety of domains.

Acknowledgments

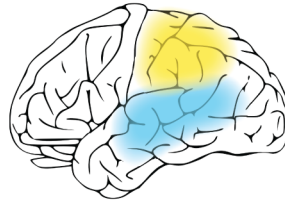
This work was supported by the following grants: NIH RO1 DC012511 and NSF Science of Learning Centers award 1041707 (subcontract 330161-18110-7341). The authors are grateful to Christine Watson, Anja Jamrozik, Steven Weisberg and Marguerite McQuire for their helpful comments.

References

1. Ungerleider, L.; Mishkin, M. Two cortical visual systems. In: Ingle, D.; Goodale, M.; Mansfield, R., editors. *Analysis of Visual Behavior*. Cambridge, MA: MIT Press; 1982. p. 549-586.
2. Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends Neurosci*. 1992; 15:20–25. [PubMed: 1374953]
3. Milner AD, Goodale MA. Two visual systems re-viewed. *Neuropsychologia*. 2008; 46:774–785. [PubMed: 18037456]
4. Hoeren M, Kaller CP, Glauche V, Vry M-S, Rijntjes M, Hamzei F, Weiller C. Action semantics and movement characteristics engage distinct processing streams during the observation of tool use. *Exp Brain Res*. 2013
5. Rizzolatti G, Matelli M. Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res*. 2003; 153:146–157. [PubMed: 14610633]
6. Buxbaum L, Kalénine S. Action knowledge, visuomotor activation, and embodiment in the two action systems. *Ann N Y Acad Sci*. 2010; 1191:201–218. [PubMed: 20392282]
7. Binkofski F, Buxbaum L. Two action systems in the human brain. *Brain Lang*. 2012
8. Uddin L, Molnar-Szakacs I, Zaidel E, Iacoboni M. rTMS to the right inferior parietal lobule disrupts self-other discrimination. *Soc Cogn Affect Neurosci*. 2006; 1:65–71. [PubMed: 17387382]
9. Buxbaum L, Shapiro A. Critical brain regions for tool-related and imitative actions: a componential analysis. *Brain*. 2014; 137:1971–1985. [PubMed: 24776969]
10. Tsakiris M, Longo M, Haggard P. Having a body versus moving your body: neural signatures of agency and body-ownership. *Neuropsychologia*. 2010; 48:2740–2749. [PubMed: 20510255]
11. Murata A, Gallese V, Luppino G, Kaseda M, Sakata H. Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J Neurophysiol*. 2000; 83:2580–2601. [PubMed: 10805659]
12. Binkofski F, Dohle C, Posse S, Stephan K, Hefter H, Seitz R, Freund H. Human anterior intraparietal area subserves prehension - A combined lesion and functional MRI activation study. *Neurology*. 1998; 50:1253–1259. [PubMed: 9595971]
13. Buxbaum L, Kyle K, Grossman M, Coslett H. Left inferior parietal representations for skilled hand-object interactions: Evidence from stroke and corticobasal degeneration. *Cortex*. 2007; 43:411–423. [PubMed: 17533764]
14. Decety J, Grezes J. Neural mechanisms subserving the perception of human actions. *Trends Cogn Sci*. 1999; 3:172–178. [PubMed: 10322473]
15. Oosterhof N, Wiggett A, Diedrichsen J, Tipper S, Downing P. Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *J Neurophysiol*. 2010; 104:1077–1089. [PubMed: 20538772]
16. Leshinskaya A, Caramazza A. Abstract categories of functions in anterior parietal lobe. *Neuropsychologia*. 2015:1–13.
17. Watson C, Cardillo E, Bromberger B, Chatterjee A. The specificity of action knowledge in sensory and motor systems. *Front Hum Neurosci*. 2014
18. Proverbio AM, Adorni R, D’Aniello GE. 250ms to code for action affordance during observation of manipulable objects. *Neuropsychologia*. 2011; 49:2711–2717. [PubMed: 21664367]
19. Culham JC, Valyear KF. Human parietal cortex in action. *Curr Opin Neurobiol*. 2006; 16:205–212. [PubMed: 16563735]
20. Caspers S, Zilles K, Laird AR, Eickhoff SB. ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*. 2010; 50:1148–1167. [PubMed: 20056149]
21. Rizzolatti G, Sinigaglia C. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*. 2010; 11:264–274. [PubMed: 20216547]
22. Fogassi L. Parietal lobe: From action organization to intention understanding. *Science*. 2005; 308:662–667. [PubMed: 15860620]
23. Wolpert DM, Kawato M. Multiple paired forward and inverse models for motor control. *Neural Netw*. 1998; 11:1317–1329. [PubMed: 12662752]

24. Blakemore S, Decety J. From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*. 2001; 2:561–567. [PubMed: 11483999]
25. Quandt L, Marshall P. The effect of action experience on sensorimotor EEG rhythms during action observation. *Neuropsychologia*. 2014; 56:401–408. [PubMed: 24568874]
26. Calvo-Merino B, Glaser D, Grezes J, Passingham R, Haggard P. Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb Cortex*. 2005; 15:1243–1249. [PubMed: 15616133]
27. Cross E, Hamilton A, Kraemer D, Kelley W, Grafton S. Dissociable substrates for body motion and physical experience in the human action observation network. *Eur J Neurosci*. 2009; 30:1383–1392. [PubMed: 19788567]
28. Plata Bello J, Modroño C, Marcano F, González Mora JL. Observation of simple intransitive actions: The effect of familiarity. *PLoS ONE*. 2013; 8:e74485. [PubMed: 24073213]
29. Quandt L, Marshall P, Shipley T, Beilock S, Goldin-Meadow S. Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation. *Neuropsychologia*. 2012; 50:2745–2751. [PubMed: 22910276]
30. Quandt L, Marshall P, Bouquet C, Shipley T. Somatosensory experiences with action modulate alpha and beta power during subsequent action observation. *Brain Res*. 2013; 1534:55–65. [PubMed: 23994217]
31. Calvo-Merino B, Grèzes J, Glaser DE, Passingham RE, Haggard P. Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation. *Curr Biol*. 2006; 16:1905–1910. [PubMed: 17027486]
32. Newsome WT, Pare EB. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J Neurosci*. 1988; 8:2201–2211. [PubMed: 3385495]
33. Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R. Brain areas involved in perception of biological motion. *J Cognitive Neurosci*. 2000; 12:711–720.
34. Pelphrey K, Morris J, Michelich C, Allison T, McCarthy G. Functional anatomy of biological motion perception in posterior temporal cortex: an fMRI study of eye, mouth and hand movements. *Cereb Cortex*. 2005; 15:1866–1876. [PubMed: 15746001]
35. Kalenine S, Buxbaum L, Coslett H. Critical brain regions for action recognition: lesion symptom mapping in left hemisphere stroke. *Brain*. 2010; 133:3269–3280. [PubMed: 20805101]
36. Noppeney U. The neural systems of tool and action semantics: A perspective from functional imaging. *J Physiol-Paris*. 2008; 102:40–49. [PubMed: 18479891]
37. Kable J, Lease-Spellmeyer J, Chatterjee A. Neural substrates of action event knowledge. *J Cogn Neurosci*. 2002; 14:795–805. [PubMed: 12167263]
38. Edelman S. Representation is representation of similarities. *Behav Brain Sci*. 1998; 21:449–467. [PubMed: 10097019]
39. Watson C, Buxbaum L. Uncovering the architecture of action semantics. *J Exp Psychol Hum Percept Perform*. 2014; 40:1832–1848. [PubMed: 25045905]
40. Watson C, Chatterjee A. The functional neuroanatomy of actions. *Neurology*. 2011; 76:1428–1434. [PubMed: 21502604]
41. Watson C, Cardillo E, Ianni G, Chatterjee A. Action concepts in the brain: An activation likelihood estimation meta-analysis. *J Cogn Neurosci*. 2013; 25:1191–1205. [PubMed: 23574587]
42. Chatterjee A. The neural organization of spatial thought and language. *Semin Speech Lang*. 2008; 29:226–238. [PubMed: 18720319]
43. Kable J, Kan I, Wilson A, Thompson-Schill SL, Chatterjee A. Conceptual representations of action in the lateral temporal cortex. *J Cogn Neurosci*. 2005; 17:1855–1870. [PubMed: 16356324]
44. Lewis JW, Van Essen DC. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J Comp Neurol*. 2000; 428:112–137. [PubMed: 11058227]
45. Gentile G, Petkova V, Ehrsson H. Integration of visual and tactile signals from the hand in the human brain: an FMRI study. *J Neurophysiol*. 2011; 105:910–922. [PubMed: 21148091]
46. Avillac M, Ben Hamed S, Duhamel J. Multisensory integration in the ventral intraparietal area of the macaque monkey. *J Neurosci*. 2007; 27:1922–1932. [PubMed: 17314288]

47. Barraclough NE, Xiao D, Baker CI, Oram MW, Perrett DI. Integration of visual and auditory information by superior temporal sulcus neurons responsive to the sight of actions. *J Cogn Neurosci*. 2005; 17:377–391. [PubMed: 15813999]
48. Benevento LA, Fallon J, Davis BJ, Rezak M. Auditory-visual interaction in single cells in the cortex of the superior temporal sulcus and the orbital frontal cortex of the macaque monkey. *Exp Neurol*. 1977; 57:849–872. [PubMed: 411682]
49. Hikosaka K, Iwai E, Saito H, Tanaka K. Polysensory properties of neurons in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *J Neurophysiol*. 1988; 60:1615–1637. [PubMed: 2462027]
50. Wright T, Pelphrey K, Truett A, McKeown M, McCarthy G. Polysensory interactions along lateral temporal regions evoked by audiovisual speech. *Cereb Cortex*. 2003; 13:1034–1043. [PubMed: 12967920]
51. Gardner T, Goulden N, Cross ES. Dynamic modulation of the action observation network by movement familiarity. *The Journal of neuroscience: the official journal of the Society for Neuroscience*. 2015; 35:1561–1572. [PubMed: 25632133]
52. Astafiev SV, Stanley CM, Shulman GL, Corbetta M. Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat Neurosci*. 2004; 7:542–548. [PubMed: 15107859]
53. Van Elk M, van Schie HT, Bekkering H. Short-term action intentions overrule long-term semantic knowledge. *Cognition*. 2009; 111:72–83. [PubMed: 19230870]
54. van Elk M, van Schie H, Bekkering H. Action semantics: A unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. *Physics Life Rev*. 2014; 11:220–250.
55. Ondobaka S, de Lange FP, Newman-Norlund RD, Wiemers M, Bekkering H. Interplay Between Action and Movement Intentions During Social Interaction. *Psychol Sci*. 2012; 23:30–35. [PubMed: 22157675]
56. Ondobaka S, Bekkering H. Hierarchy of idea-guided action and perception-guided movement. *Front Psychol*. 2012; 3
57. Petrides, M. *Neuroanatomy of Language Regions of the Human Brain*. Academic Press; 2013.
58. Petrides M, Pandya DN. Association fiber pathways to the frontal cortex from the superior temporal region in the rhesus monkey. *J Comp Neurol*. 1988; 273:52–66. [PubMed: 2463275]
59. Talmy, L. *Toward a cognitive semantics: Concept structuring systems*. Vol. 1. Cambridge, MA: The MIT Press; 2000.
60. Wu D, Morganti A, Chatterjee A. Neural substrates of processing path and manner information of a moving event. *Neuropsychologia*. 2008; 46:704–713. [PubMed: 18023824]
61. Bedny M, Caramazza A, Pascual-Leone A. Typical neural representations of action verbs develop without vision. *Cereb Cortex*. 2012; 22:286–293. [PubMed: 21653285]
62. Bedny M, Caramazza A, Grossman E, Pascual-Leone A, Saxe R. Concepts are more than percepts: The case of action verbs. *J Neurosci*. 2008; 28:11347–11353. [PubMed: 18971476]
63. Wu D, Waller S, Chatterjee A. The functional neuroanatomy of thematic role and locative relational knowledge. *J Cogn Neurosci*. 2007; 19:1542–1555. [PubMed: 17714015]
64. Kemmerer D, Tranel D. A double dissociation between the meanings of action verbs and locative prepositions. *Neurocase*. 2003; 9:421–435. [PubMed: 14972757]
65. Amorapanth P, Widick P, Chatterjee A. The neural basis for spatial relations. *J Cogn Neurosci*. 2010; 22:1739–1753. [PubMed: 19642889]
66. Kranjec A, Cardillo E, Schmidt G, Lehet M, Chatterjee A. Deconstructing events: The neural bases for space, time, and causality. *J Cogn Neurosci*. 2012; 24:1–16. [PubMed: 21861674]



Object Association	Action Association	Action Implementation	
Ventral		Dorsal	
Exteroceptive		Intero-exteroceptive	
3rd person		1st person	
Ventro-ventral	Dorso-ventral	Ventro-dorsal	Dorso-dorsal
Nouns	Verbs		Prepositions

Figure 1. Schematic image depicting the Action Implementation and Action Association Systems, along with the Object Association system. Separate and shared characteristics of these systems are shown. Dorso-dorsal “reach-to-grasp” and ventro-dorsal “use” streams correspond to those described by Buxbaum and colleagues ⁶.