

## ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Cognitive Neuroscience***Perception, action, and word meanings in the human brain: the case from action verbs**Marina Bedny<sup>1</sup> and Alfonso Caramazza<sup>2,3</sup><sup>1</sup>Brain and Cognitive Sciences Department, Massachusetts Institute of Technology, Cambridge, Massachusetts. <sup>2</sup>Department of Psychology, Harvard University, Cambridge, Massachusetts. <sup>3</sup>Center for Mind/brain Sciences CIMEC, University of Trento, Trento, Italy

Address for correspondence: Marina Bedny, Brain and Cognitive Sciences Department, Massachusetts Institute of Technology, 43 Vassar St., room 46-4021, Cambridge, Massachusetts 02139. mbedny@mit.edu

Among other things, humans talk about what they perceive and do, like “glowing,” “hopping,” and “squeaking.” What is the relationship between our sensory-motor experiences and word meanings? Does understanding action-verbs rely on the same neural circuits as seeing and acting? The available evidence indicates that sensory-motor experience and word meanings are represented in distinct, but interacting systems. Understanding action-verbs does not rely on early modality-specific visual or motor circuits. Instead, word comprehension relies on a network of amodal brain regions in the left frontal, temporal, and parietal cortices that represent conceptual and grammatical properties of words. Interactions between word meanings and sensory-motor experiences occur in higher-order polymodal brain regions.

**Keywords:** sensory-motor; experience; action-verbs; word meaning; concept; neural

**Introduction**

We learn the meaning of many words through our senses and use words to describe the world that we perceive.<sup>1</sup> What is the relationship of word-meaning representations and sensory-motor systems that support sensation and perception? According to strong embodied views of cognition, word meanings are built from sensory-motor experiences and are themselves the reactivations of sensory-motor “memories” of experience.<sup>2–4</sup> For example, the meaning of the word “to run” might consist in part of the motor program for running, the visual image of running, and the sound of running. Alternatively, word-meaning representations may be abstract, modality independent, and organized according to conceptual distinctions (e.g., entities versus events). These abstract representations may, nevertheless, dynamically interact with our sensory and motor systems during communication and thinking.<sup>5–7</sup> Finally, word meanings could interact with sensory representations only indirectly.<sup>8</sup> The origins of these viewpoints date back

to empiricist and nativist philosophers.<sup>9–11</sup> In modern science, these views have been the target of linguistic and psychological research,<sup>5,6,12–14</sup> and, most recently, measurements of human brain function have been used to weigh in on this longstanding debate.<sup>2,3,7,15–18</sup> In this article, we will review some of the insights gained from these neuroscientific inquiries.

Our discussion will focus specifically on what has been learned about the relationship between word-meanings and sensory experience from studies of the neuroanatomical basis of word knowledge. First, neuroanatomical data allow us to assess the degree to which word-meanings and sensory-motor experience rely on the same neural mechanisms. To the extent that these different processes rely on the same neural machinery, it is more likely that word meanings are recapitulations of sensory experiences, at some level of description. Second, neuroanatomical data provide insights into whether the sensory modality of learning has a direct influence on the format of word-meaning representations? Representations that have a different neuroanatomical

basis are more likely to have distinct representational formats. Therefore, we can ask whether the sensory modality of learning determines the neuroanatomical basis of word meanings. To address this question, we will review recent studies comparing the neural basis of word meanings in congenitally blind and sighted individuals.

Rather than surveying the entire literature on the neural basis of word meaning representation, we will use action verbs as a window onto word meanings more generally. This focused approach allows us to consider specific neuroanatomical and cognitive hypotheses.

Action-verbs are a useful test case in part because there are relatively specific neuroanatomical and cognitive hypotheses regarding the sensory representations that are relevant to their meaning.<sup>3,19–23</sup> Specifically, action-verbs are distinguished from many other word classes in that they have a preponderance of motor and visual-motion features. It has therefore been hypothesized that understanding action verbs relies on motor and visual motion systems.<sup>24,25</sup>

The strongest version of an embodied account of word meanings makes a number of clear predictions. First, action-verb comprehension should rely primarily on early, modality-specific, sensory-motor brain regions (in the visual motion system and motor control system). These sensory-motor brain regions should be engaged automatically during word comprehension, largely irrespective of task and context. This account also predicts that growing up blind should result in changed or missing visual representations of action-verb meanings.

A modality-independent (amodal) account of word meanings instead predicts that word comprehension depends on brain regions that are not associated with a specific sensory modality or the motor system. These brain regions distinguish between word types along abstract dimensions (e.g., events versus entities), rather than sensory dimensions (e.g., visual versus auditory). This account also suggests that the word meanings of blind and sighted individuals are represented in the same format.

To distinguish between these accounts of word-meaning representation, we first briefly review the cortical regions involved in visual-motion perception and motor control. We then ask whether sensory brain regions are involved in action-verb com-

prehension, and if so during which kinds of tasks. Next we review evidence for modality-independent representations of action verbs. Finally, we compare the neural basis of action-verbs in congenitally blind and sighted individuals.

## Action verbs and motion vision

We learn about actions and events, in part, by observing motion in our environment. For example, we can tell if someone is strutting or sauntering by looking at them. Action-verbs are also more likely to refer to motion in the environment than other kinds of words. As a result, many embodied accounts of word meaning propose that understanding action verbs depends on the visual motion system.<sup>17,18,20</sup>

Putative support for this hypothesis comes from behavioral studies of motion perception and action-verb comprehension. For example, a number of studies have shown interference or facilitation between visual motion tasks and linguistic tasks.<sup>43,44</sup> In one study, participants performed a visual lexical decision task with verbs that refer to motion in the upward direction, downward direction, and control words with no dominant vertical direction (e.g., climb, fall, and run, respectively). Upward and downward moving dots were displayed on the screen superimposed onto the written words. When the motion of the dots was inconsistent with the direction of the verb, participants were slower to say the verb was a real word. Furthermore, they were more accurate than baseline when the direction of the dots and the verb were the same.<sup>45</sup> The reverse effect of language on perception has also been observed. Meteyard and colleagues found a reduction in participants' ability to detect coherent motion of dots embedded in noise (decreased  $d'$ ) when participants heard action-verbs whose dominant direction of motion was inconsistent with the visual stimulus.<sup>46</sup> Based on these findings, the authors suggest that action-verb comprehension may depend on visual motion areas, including medial temporal area/medial superior temporal area (MT/MST).<sup>45</sup> Similarly, many other behavioral studies have also shown either effects of language on perception or effects of sensory-motor tasks on language performance.<sup>47–49</sup>

These behavioral studies provide clear evidence that action-verb comprehension and motion perception interact in online tasks. However, they provide only indirect insights into the neural structures

that are responsible for the behavioral interactions. That is, these results provide evidence of interaction, but not of isomorphism between word meanings and perception. First, it is possible that interaction between perception and comprehension happens in secondary perceptual regions such as the parietal cortex. Although verb meanings affect motion sensitivity ( $d'$ ), motion sensitivity is a product of processing at many levels within the motion perception stream, including higher-level multimodal brain regions.<sup>50</sup> Furthermore, language–perception interactions may occur not because action-verb meanings are represented in visual motion areas, but because verb meaning representations prime visual motion representations during contemporaneous linguistic and perceptual tasks. This might occur through top–down modulation of perceptual brain regions. For example, activity in motion perception regions is modulated by top–down processes such as imagery and attention.<sup>51</sup> Feedback projections from higher-order cortical areas involved in attention and executive control may relay information from language regions to perceptual regions when such information is potentially relevant to the perceptual task. Similarly, processing in language areas themselves could be influenced by information from perceptual systems.<sup>52</sup>

Interactions between different kinds of representations have been described for the visual motion and auditory systems. For example, high-pitch tones facilitate perception of upward motion, whereas low-pitch tones facilitate the perception of downward visual motion.<sup>53</sup> These results do not imply that auditory pitch perception is mediated by the visual system or that visual motion perception is mediated by the auditory system. Rather, such findings suggest that the visual and auditory systems interact. Analogously, brain circuits that represent action verbs meanings may interact with the visual motion system. Finally, interaction of perception and verb comprehension could occur at the decision stage, rather than in perception or language circuits.

The available behavioral data are therefore consistent with the possibility that action-verb meanings and sensory representations are distinct, and interact only indirectly. The behavioral demonstration of interaction between language and sensory-motor processes does not allow us to determine the locus of the interaction within the cognitive-perceptual-

motor processing system.<sup>52</sup> We, therefore, turn to the neural data and ask whether action-verb comprehension depends on the visual motion system.

Visual motion perception in primates engages a hierarchy of specialized brain regions. The earliest visual motion-selective brain region is MT/MST.<sup>26,27</sup> Human MT/MST is located in the posterior aspect of the inferior temporal sulcus on the border of the occipital and temporal lobes.<sup>28</sup> Studies of the rhesus macaque show that MT/MST contains a preponderance of direction- and speed-selective neurons.<sup>29</sup> In healthy humans, MT/MST is active while viewing motion,<sup>30</sup> and bilateral damage to this region results in severe modality-specific deficits in visual motion perception—akinetopsia.<sup>31,32</sup> Similarly, transient disruption of MT/MST using transcranial magnetic stimulation (TMS) induces a selective deficit in visual motion perception.<sup>33</sup>

Other brain regions further along the processing stream are also engaged in motion vision. The right posterior superior temporal sulcus (rSTS) is specifically important for perceiving human and animal motion. This brain region responds more to biological motion than to coherent but non-biological motion<sup>34,35</sup> and TMS to the rSTS selectively impairs visual perception of biological motion.<sup>36</sup> Higher order motion representations are also present in several parietal regions including the intra parietal sulcus (IPS) and the right inferior parietal lobule (IPL).<sup>37–40</sup> Unlike the lower level representations of MT/MST, parietal representations of motion are not modality specific: the IPS responds equally to visual, tactile, and auditory motion.<sup>41,42</sup> Thus, parietal representations of motion are spatiotemporal, rather than visual.

Are motion-perception brain regions engaged in action verb comprehension? If so, which motion-perception brain regions participate in word comprehension (e.g., modality-specific representations in MT/MST, and/or rSTS, or the polymodal parietal representations)?

One type of evidence that could be used to determine whether motion vision and action-verb comprehension share a common neural mechanism comes from neuropsychological studies. Are motion blind patients impaired in comprehension of motion-related words and sentences? If visual motion areas played a causal role in understanding motion language, patients with visual motion

perception deficits would be expected to also have language comprehension deficits specifically for words whose meanings include motion features. Clinical descriptions suggest that patients who suffer from akinetopsia do not present with obvious language deficits.<sup>31,33</sup> However, no formal language tests have been performed with akinetopsic patients; therefore, subtle deficits in language processing may have gone undetected. There are two studies in the literature showing that damage to left posterior lateral temporal lobe in the vicinity of MT/MST can lead to deficits in action categorization and action picture naming deficits.<sup>54,55</sup> However, no motion vision deficits are reported in those patients, raising the possibility that their lesions do not in fact affect MT/MST itself. Furthermore, inspection of lesion locations suggests that the lesions of these patients implicate posterior temporal language areas involved in verb comprehension, rather than the MT/MST.<sup>25</sup>

To overcome the shortcomings of spatial resolution of lesion studies, neuroimaging has been used to examine MT/MST activity during word comprehension tasks in healthy adults. Reville and colleagues<sup>22</sup> asked whether MT/MST is active when participants match newly learned non-word strings to visual events. Participants were trained to associate non-word strings (e.g., *biduko*) with animations such as movements of novel objects (e.g., back and forth horizontal translation) or changes in color or form of the same novel objects (e.g., *potagi*: darkening). Participants also learned labels for the novel shapes in these animations. In a subsequent neuroimaging session participants were asked to match non-word phrases like “*biduko goki*” to their corresponding visual animations (e.g., the ‘*goki*’ shape oscillating in the horizontal direction).<sup>22</sup> Reville and colleagues asked whether MT/MST becomes active when participants process the newly learned labels, before the visual motion event is presented on the screen. They reported that a left-lateralized brain region, anterior to MT/MST, was more active when participants heard motion phrases (e.g., *biduko goki*) than when they heard change of state phrases (e.g., *potagi goki*). When neural responses from multiple individuals were averaged together, this lateral temporal region overlapped to a small degree with MT/MST. It was also found that activation in the anterior region increased when participants heard change-of-state non-words that had

similar onsets (e.g., *biduka goki*) as the motion non-words.

These results suggest that a brain region anterior to MT/MST may participate in matching motion words to their motion referents. However, for a number of reasons these data do not speak to whether MT/MST is engaged in action-verb comprehension.

First, brain regions involved in understanding actual action-verbs could be quite different from those involved in matching newly learned labels to simple videos of motion animations. Second, the authors did not examine activity in each individual’s MT/MST region. Instead brain activity for novel motion words was averaged over the group of participants. This group analysis revealed a weak response anterior to MT/MST. This activation overlapped to a small extent with MT/MST at a lenient statistical threshold. Because the location of MT/MST in each individual brain varies, it is not possible to say whether for any individual subject MT/MST was engaged by the novel motion labels. If anything, the fact that the peak of MT/MST and the peak of the anterior language region were clearly separate, even in the group, suggests that distinct functional areas respond to motion words and visual motion.

A number of other studies have looked specifically at activity in MT/MST and other parts of the visual-motion system during action-verb comprehension. Kable and colleagues<sup>56</sup> presented subjects with triads of action pictures and triads of object pictures. In a separate experiment, the same participants also saw triads of written words: action-verbs, animal nouns and tool nouns. Participants judged which of two possible alternative pictures or words was most similar to the target picture or word. Consistent with prior findings, Kable and colleagues observed an increased response in MT/MST to the action pictures with implied motion.<sup>51,56</sup> In contrast, action-verbs did not produce a larger response in MT/MST than animal or tool nouns. In a follow up study, participants once again saw action-picture and action-verb triads. This time, participants judged which of two actions was more similar to the target in its manner of motion (e.g., is skipping more similar to rolling or to bouncing?).<sup>57</sup> Again, they found that MT/MST responded to action-pictures with implied motion, but not to action-verbs. Consistent with these results, Bedny and colleagues<sup>25</sup> found that MT/MST does not respond to spoken action-verbs when

participants judge how similar in meaning two action-verbs are to each other. These studies suggest that MT/MST is not automatically engaged in action-verb comprehension. The Bedny *et al.* study also found that the rSTS biological motion area does not respond to action-verbs. When making judgments about action-verbs, rSTS activity was not different from rest or from concrete object nouns.<sup>25</sup> Together, the results of these studies suggest that modality-specific visual motion representations are not automatically engaged during action-verb comprehension.

Does action-verb comprehension rely on higher-level brain regions in the parietal lobe that represent spatiotemporal motion information? No study thus far has directly examined whether action-verbs activate polymodal parietal motion representations. However, a recent study compared the effect of other motion words (in this case prepositions; e.g., up/down) on BOLD signal in low-level modality-specific motion areas and on BOLD signal in higher-level polymodal motion areas in the parietal lobe. In an elegant study, Sadaghiani and colleagues measured the behavioral and neural priming effects of motion words and non-linguistic auditory motion stimuli. While undergoing fMRI, participants saw a dot that was either unambiguously moving in one direction or predominantly moving in one direction but not clearly so. The task was to indicate whether the dot was moving left, right, up, or down. While doing the visual-motion task, participants simultaneously heard three possible auditory stimuli: sounds that appeared to move, sounds that changed in pitch, (rising and falling tones), or the words up/down/left/right. All three kinds of sounds similarly facilitated participants' ability to determine the direction of the moving dot. However, the different sound types (motion/pitch/words) differentially influenced brain activity: only moving sounds influenced activity in MT/MST itself.<sup>58</sup> These data are consistent with prior evidence that auditory motion can influence processing in visual motion areas, even though by itself auditory motion is insufficient to activate MT/MST.<sup>41</sup> In contrast, words influenced activity in the right IPS—possibly the locus of a higher-level multi-modal motion perception region, but not MT/MST. Rising and falling tones (i.e., pitch) produced an intermediate effect. That is, in MT/MST there was a linear decrease in the effect of auditory

stimuli from motion, to pitch, to speech and, unlike motion sounds, speech did not produce a measurable effect on MT/MST activity but did affect activity in the parietal cortex. These data suggest that during visual tasks, the effect of word meanings on visual motion perception may be mediated by higher-order multimodal motion regions, rather than early visual regions like MT/MST.<sup>58</sup>

No similar studies have yet been done with action verbs, but there is some indirect evidence that higher-order parietal motion areas may be engaged during action-verb comprehension. Some studies have found parietal activity when participants make semantic decisions about action verbs relative to semantic decisions about other word categories.<sup>59,60</sup> For example, van Dam<sup>60</sup> and colleagues found more inferior parietal activity for action-verbs that are associated with specific movements of the body (e.g., to wipe) than with general movement patterns (e.g., to clean; notably, neither of these studies observed activity in MT/MST). Further converging evidence for the involvement of the parietal lobe in language-relevant representations of action and motion comes from studies of tool names. Some regions within the parietal lobe are automatically engaged during comprehension of tool words,<sup>61,62</sup> perhaps because actions and motion are relevant to their meanings. Similar to studies of action-verbs, these studies of tools do not find MT/MST activity.

Further studies are needed to determine whether parietal areas engaged in action-verb and tool-noun comprehension are the same as parietal areas involved in motion perception. The parietal cortex also contains other kinds of representations that could be relevant to action: a patchwork of areas relevant to action execution and action observation.<sup>63</sup> Left parietal areas also contribute to aspects of language processing.<sup>64</sup> At present, it remains possible that distinct parietal areas support motion perception, action execution, and action-verb comprehension, respectively. However, the available data are intriguing and suggest that the polymodal representations of parietal cortex are an excellent test bed for questions regarding shared and separate circuits for language, perception, and action.

Together, the results reviewed here provide evidence that action-verb comprehension does not depend on modality-specific visual motion brain regions (i.e. MT/MST and the rSTS). Some

action-verbs may activate polymodal and spatiotemporal representations of motion (in the parietal lobe). However, more research is needed to determine whether action-verb comprehension recruits these parietal representations.

It is less clear whether richer language stimuli, like sentences might activate early modality-specific visual motion areas. A recent study by Saygin and colleagues found elevated activity in MT/MST when participants listen to sentences that describe motion.<sup>65</sup> By contrast, other studies do not find MT/MST activation for action sentences, but do find activity in biological motion area rSTS.<sup>66</sup> Still others do not find activity for motion sentences in either MT/MST or the rSTS.<sup>67</sup> Why some studies of sentences find MT/MST activation, while others do not is not yet clear. There are many differences among these experiments. One feature that distinguishes the one study that observed MT/MST activity is that participants saw videos of speakers producing language, rather than simply listening to or reading sentences.<sup>65</sup> Thus, participants were actually seeing visual motion during the comprehension task. It is possible that rich motion language can influence MT/MST activity when MT/MST is already engaged by a visual motion stimulus. This would be analogous to the priming effects of auditory motion on MT/MST activity. The sound of motion alone does not engage the MT/MST, but motion sounds can enhance the response of MT/MST to visual motion.<sup>41</sup> Note, however, that motion-words without a sentence context do not influence MT/MST activity even in the presence of visual motion.<sup>58</sup> Therefore, the combination of a concurrent visual motion stimulus and rich motion descriptions may be required to enable language to influence activity in MT/MST. Other factors, such as differences in the vividness of the motion sentences may also explain inconsistencies among different studies. More studies are needed that directly compare different kinds of motion language (single words, sentences of different vividness) and different concurrent perceptual tasks (viewing motion versus not viewing motion during the experiment).

In sum, action-verbs do not automatically activate modality-specific visual-motion areas during comprehension (MT/MST and rSTS). There is some evidence that motion words might activate higher-order spatiotemporal motion representations in the parietal lobe. However, more work is needed to es-

tablish which parietal areas are engaged in comprehension of action-verbs and what their contribution might be. A key question is whether parietal areas that are active during action-verb comprehension are the same as those active during visual motion tasks. If so, this would provide evidence that higher-order polymodal perceptual representations are involved in word comprehension.

On the other hand, visual motion areas, like MT/MST, may be activated when participants listen to sentences that describe motion and concurrently see motion in the environment. However, it remains unclear what such visual motion activation contributes to language comprehension and under what circumstances these areas are engaged. One possibility is that some sentences that describe visual motion lead to spontaneous motion imagery. The motion system might alternatively be engaged in the course of building a situation model for a sentence that describes motion, but not lexical access per se. Studies of the time-course of word and sentence comprehension may help to clarify the contribution of the visual-motion system to sentence comprehension.

### Motor control and action verbs

The role of the motor system in action verbs comprehension has received a great deal of attention in the cognitive neuroscience literature and has been reviewed elsewhere.<sup>68–70</sup> Here, we briefly highlight the evidence from neuroimaging on the role of the motor system in representing the meanings of action-verb (note that there is also a distinct debate regarding whether the motor cortex is involved in speech perception.)

The motor cortex is located in the posterior aspect of the frontal lobe anterior to the central sulcus. It consists of the primary motor cortex (M1), located along the precentral gyrus (BA 4), and several anterior premotor areas. Relative to premotor areas, M1 is more exclusively dedicated to motor-control. M1 has the largest number of direct projections to the spinal cord<sup>71</sup> and the clearest somatotopic organization by limb: muscles of the leg, arm, and face are controlled by partially distinct cortical regions within M1 (for other organizational principles in M1 see Ref. 72). In non-human primates, M1 neurons respond selectively to direction and force of movement as well as particular sequences of movements.<sup>73,74</sup> Lesions and

TMS applied to M1 cause deficits in voluntary motor control.<sup>74–76</sup>

The premotor cortex is located anterior to M1 and is often subdivided into ventral premotor cortex, dorsal premotor cortex, and the supplementary motor area on the medial wall of dorsal BA 6 (SMA and pre-SMA). These premotor areas support higher-order motor functions such as movement sequencing, movements planning, and motor learning. As in M1, one principle of organization within premotor areas is limb-specific somatotopy. However, this somatotopic map is even more overlapping and disorganized than the map of M1 and coexists with other organizational principles. Furthermore, relative to M1, premotor cortex has more abstract representations of movements. For example, activity of premotor areas is more sensitive to the behavioral context of movements and to the goal of the movement.<sup>74</sup> Furthermore, within ventral premotor cortex there are so-called mirror neurons, which respond both when a primate performs a particular action and when the primate sees another animal perform the same action. Many of these neurons are selective for the goal of the action, rather than for the particular motor sequence.<sup>77</sup> Finally, premotor cortex is involved in higher-order aspects of motor control, such as movement selection and sequencing.<sup>78</sup>

Recent research has also demonstrated that premotor areas are involved in non-motor aspects of cognition.<sup>79</sup> Premotor cortex is involved in functions such as sequencing, planning and reasoning outside of the motor domain.<sup>74</sup> For example, the ventral premotor cortex is involved in predicting actions and sequentially structured events that humans cannot perform.<sup>80–82</sup> Similarly, some premotor regions like the SMA and pre-SMA support higher cognitive control functions and are therefore not exclusively involved in motor control.<sup>83–86</sup> In this regard, the premotor cortex shares features with adjacent prefrontal cortex.<sup>87</sup>

Many studies have observed left premotor activation when participants listen to or read action-verbs: including in the SMA/pre-SMA, left ventral premotor cortex, and left dorsal premotor cortex.<sup>88,89</sup> Primary motor cortex itself (M1) is active during motor imagery, but not during action-verb comprehension, in the absence of imagery instructions.<sup>90</sup> What do left premotor areas contribute to action-verb comprehension?

While some studies observe activity in left premotor areas for action verbs, a large proportion of neuroimaging studies do not observe increased activity for action-verbs anywhere in the motor system.<sup>25,56,57,60,91</sup> Therefore, motor activity to action verbs is either task dependent, only present for some types of action-verbs, or weak relative to other kinds of category-specific effects. Furthermore, in cases where motor activity is observed, it remains unclear whether the motor system is specifically involved in the comprehension of motor aspects of action-verb meanings. Regions within the motor system participate in non-action-related aspects of language processing.<sup>92</sup> For example, the ventral premotor cortex and SMA/pre-SMA participate in general aspects of sentence processing and word retrieval.<sup>93,94</sup> A key question is whether activity in left premotor areas for action-verbs reflects such general contributions of premotor cortex to language, or specific contribution to motor aspects of action-verb meanings.

In an effort to determine whether motor-cortex activity for action-verbs specifically reflects the retrieval of motor elements of verb meanings, a number of studies have asked whether the activation of motor and premotor cortex to action-verbs is somatotopic. According to the embodied cognition hypothesis, verbs that refer to movements of the leg, for example “to run,” activate the leg area of motor cortex and verbs that refer to movements of the hand, for example “to clap,” activate the hand area. Studies on this topic have yielded conflicting results. In one of the first attempts to answer this question, Hauk and colleagues had participants passively read verbs that refer to movements of the leg, verbs that refer to movements of the arms, and verbs that refer to mouth movements. Based on their data, the authors concluded that action-verbs lead to automatic, somatotopic activation of motor areas.<sup>24</sup> However, first key analyses in the study compare different verb types to a non-language baseline rather than to each other. Therefore, this study did not clarify whether each verb category activates any motor area more than the other verb categories or instead, whether language comprehension activates the motor system more than low-level perceptual tasks. Second, in this study, BOLD signal for action-verbs was not measured in motor regions themselves, but rather in areas that responded during word comprehension. Therefore, these results do not reveal whether motor

areas themselves are activated by action-verbs in a somatotopic manner.

Several subsequent studies have also described purported somatotopic effects for action-verbs in the vicinity of motor cortex and prefrontal cortex.<sup>95</sup> Until recently, however, no study had looked directly at the responses of motor areas themselves to action-verbs.

A recent study that looked specifically at motor and premotor activity for action-verbs found that this activity is not in fact somatotopic. Postle and colleagues<sup>96</sup> looked at the response to hand, foot, and mouth verbs in primary and premotor areas and compared them to several control conditions including object nouns and non-words. As in prior studies, such as the one by Hauk and colleagues described above, participants silently read action-verbs referring to movements of the hand, foot, and tongue (e.g., move tongue from side to side). In a separate experiment, the same participants also performed movements of the hand, foot, and mouth and viewed actions performed with the hand, foot, and mouth. Consistent with prior work, the authors found a somatotopic response in premotor cortex when participants visually observed the actions of others. But the same areas did not respond somatotopically to action-verbs. Instead, premotor leg, arm, and hand areas respond to all action verbs. Several of these premotor areas also responded equally to action-verbs and object nouns and even non-words<sup>96</sup> (see also Ref. 97). These data suggest that some automatic premotor activity for action-verbs may reflect a general role of premotor cortex in language and higher-order cognition, and not its contribution to motor aspects of action-verb meanings.

The Postle *et al.* study<sup>96</sup> examined the response of somatotopic premotor areas that are engaged during simple motor tasks (e.g., side-to-side tongue movements). Therefore, their findings leave open the possibility that different, higher-order premotor areas, which do not have a somatotopic organization, and do not respond during simple motor tasks, are nevertheless specifically involved in representing the motor aspects of action-verb meanings. Some evidence for this possibility comes from recent studies of “manual” verbs. As compared to non-manual verbs, manual verbs lead to increased activity in left dorsal premotor and superior prefrontal cortex.<sup>90</sup> This dorsal premotor/prefrontal

activity for manual verbs is less left lateralized in left-handed individuals.<sup>89</sup> Such reduced left-lateralization may be due to less experience performing actions with the right hand. On the other hand, activity may be less left-lateralized in left-handers because these individuals have less left lateralization of language and cognitive functions more generally.<sup>98</sup> Further studies of this dorsal premotor area are required to determine (1) whether dorsal premotor/prefrontal cortex plays a specific role in representing motor or action-related aspects of action-verb meanings, and (2) what role, if any, this same brain region plays in motor control.

While action-verbs themselves do not somatotopically activate the premotor cortex, somatotopic activation has been reported for richer linguistic stimuli, such as sentences. Aziz-Zadeh and colleagues<sup>99</sup> found that left premotor hand, mouth, and leg areas showed a somatotopic preference for phrases describing actions by these different effectors.<sup>98,100</sup> Interestingly, while action observation led to somatotopic activity bilaterally in premotor cortex, action phrases led to somatotopic activity only in the left hemisphere. These data suggest that a subset of premotor areas engaged in action execution and action observation are also involved in thinking about actions that are described linguistically.

Further evidence that premotor cortex is activated when participants listen to sentences about actions comes from a study of expertise. Beilock and colleagues<sup>101</sup> presented hockey players, hockey fans, and hockey novices with sentences about hockey-related actions and non-hockey-related actions.<sup>101</sup> They found that when participants were listening to sentences about hockey-related actions; both hockey players and hockey fans had increased activity, relative to novices, in a part of the dorsal premotor cortex. Studies of motor control have observed similar left-lateralized dorsal activity when participants plan, sequence, and select complex movements.<sup>102,103</sup> This dorsal premotor area does not appear to be effector-specific (somatotopic). For example, activity is left lateralized irrespective of which hand is used to perform the action and activity is observed only during complex movements. Therefore, this premotor activation is likely distinct from somatotopically responsive premotor areas and perhaps contains more abstract action representations.

Further support for the idea that this language-relevant dorsal premotor area may contain abstract representations of actions comes from the Beilock study itself. It was found that activity in this premotor area is influenced by experience with actions, but not selectively by motor experience—activity in this dorsal area was increased both for hockey players and hockey fans, who did not have direct experience performing the actions described. Interestingly, the primary sensory-motor cortices were active for hockey sentences in novices only. Moreover, increased primary sensory-motor activity correlated negatively with action sentence comprehension.<sup>101</sup> These data suggest that early motor areas may be engaged in imagery when listening to language about actions, and that such imagery is neither specifically related to action knowledge nor facilitates comprehension. On the other hand, higher-order motor areas that are involved in controlling and planning complex actions may be involved in reasoning about actions described linguistically, as well as other reasoning about action. This dorsal premotor activity may also reflect spontaneous imagery during sentence comprehension.

To summarize, studies of motor involvement in action-verb comprehension present an analogous picture to studies of the visual motion system. Early motor regions such as M1 are not involved in understanding action-verbs nor is M1 activated by linguistic descriptions of actions. Further evidence is needed to determine whether single action verbs activate higher-order premotor regions. If action verbs do engage higher-order premotor representations, these effects appear to be weak and context dependent, as most studies of action verbs fail to observe them. There is however evidence that higher-order premotor areas are engaged when we understand sentences that describe actions.

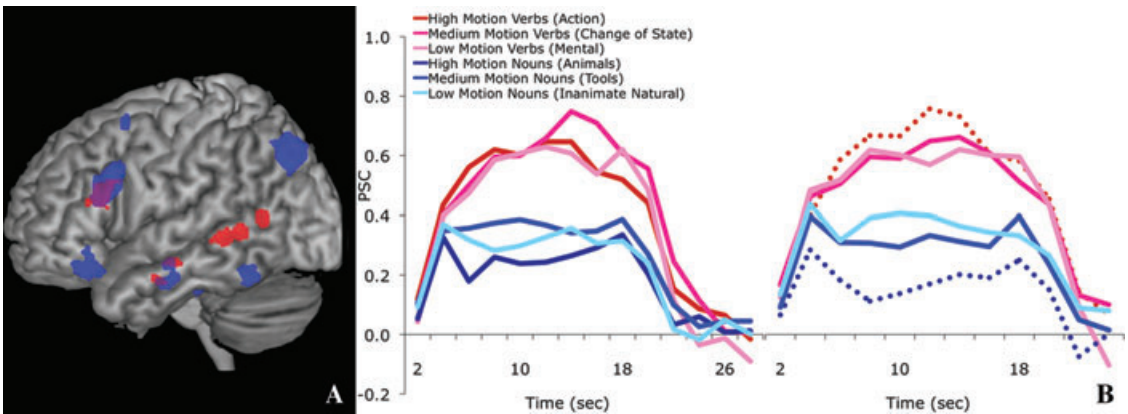
Together, the available data suggest that action-verb comprehension does not automatically engage early modality-specific cortical areas. Rather, interaction between words and perception occurs in secondary, multi-modal brain regions. These higher-order perceptual areas represent information in a more abstract format than modality-specific sensory areas. Furthermore, higher-order perceptual areas are more likely to participate during sentence comprehension than during word comprehension. This suggests that sensory-motor representations may contribute to spontaneous mental imagery dur-

ing comprehension or to the building of detailed situation models, rather than word comprehension.<sup>104</sup> Moreover, activation of sensory-motor areas during language processing is task and context dependent in ways that are not yet understood. Of course, this does not imply that sensory-motor effects observed during language tasks are uninteresting or unimportant. To the contrary, these data illustrate how language interacts with other cognitive and perceptual systems. Future studies will undoubtedly shed light on the contribution of these sensory-motor activations to language comprehension. In the section below, we attempt to put these sensory-motor effects in the context of other findings on the neural basis of word comprehension.

### Modality-independent representations of action verbs

The seminal work of early neuropsychologists showed that regions of the left temporal, parietal and prefrontal cortex contribute to word comprehension. Many patients with damage to the temporal, prefrontal or parietal cortex present with profound word comprehension deficits without deficits in locomotion or perception. These cases illustrate that a number of brain regions outside of traditional sensory-motor systems contribute to word comprehension more generally. Subsequently, neuroimaging studies have shown that a left-lateralized network of frontal, temporal, and parietal regions is active when participants listen to and read words, and action-verbs in particular (see Fig. 1).<sup>25,56,57,59,91,105,107</sup> Many of these frontal, temporal and parietal areas are not specifically involved in understanding action verbs, but are instead engaged in understanding a variety of words types including nouns, adjectives, and closed class words.<sup>108</sup>

For example, several left dorsolateral prefrontal areas are involved in retrieving and selecting word meanings.<sup>109–111</sup> There is also substantial evidence that regions within the left temporal and parietal lobes store components of word-meaning representations. For example, neuropsychological studies, neuroimaging studies, and more recently TMS experiments, have demonstrated that the anterior temporal lobe plays an important role in noun comprehension.<sup>17–21</sup> A recent study also suggests that the anterior temporal lobe may be involved in understanding verbs.<sup>112</sup> On the other hand, some brain



**Figure 1.** Brain regions involved in comprehension of action verbs. (A) Activation for action verbs and animal nouns relative to a low-level perceptual control condition. Action-verbs > backwards speech in red, animal-nouns > backwards speech in blue. (B) Activation for three categories of verbs and three categories of nouns in the IMTG region. The graph on the left depicts data from the IMTG ROI identified using the verbs > nouns comparison. The graph on the right plots data from the IMTG region identified using the action verbs > animal nouns contrast. The data illustrate that the IMTG responds more to verbs than nouns, irrespective of visual motion information. For example, the IMTG response is high for mental state verbs (which are low in motion features) and low for animal nouns (which are high in motion features).

regions within this left-lateralized network respond preferentially to particular word types.<sup>59,113</sup> One such brain region along the posterior aspect of the left middle temporal gyrus (IMTG) appears to be more important for understanding action-verbs as compared to concrete adjectives (e.g., colors) and object nouns (e.g., animals or tools). Below, we discuss some recent investigations into the contribution of this IMTG region to action-verb comprehension. In particular, we focus on whether representations in the IMTG are indeed modality independent, as compared to the modality-specific representations of sensory-motor experience.

Activity in the IMTG for action-verbs was first reported by Martin and colleagues.<sup>23</sup> Martin *et al.* observed more activity in the IMTG when participants generated action verbs than when they generated color names to visually presented nouns. A large number of subsequent studies have replicated this finding in a variety of tasks including lexical decision, semantic similarity judgments, synonym judgments and odd-man-out semantic judgments.<sup>25,56–57,105,91,114–116</sup> The IMTG is more active for action-verbs relative to various control conditions such as names of concrete objects, color adjectives, and low level controls such as false fonts and backwards speech.<sup>23,56</sup> Unlike sensory-motor effects discussed in the previous section, the IMTG responds to action-verbs in the absence of sentence context.

IMTG activity during verb comprehension was originally interpreted to reflect retrieval of visual motion information relevant to the meanings of action-verbs, consistent with embodied cognition models of word meaning.<sup>23</sup> This visual-motion hypothesis was inspired by the neuroanatomical proximity of the IMTG to visual motion brain regions (left MT/MST and the left homologue of the rSTS biological motion area). However, recent studies have demonstrated that IMTG representations are neither visual nor motion related. In one study, the same group of participants performed semantic judgments on action-verbs (how similar are “run” and “jump?”), viewed non-biological motion (concentric rings moving radially), and viewed biological motion (animations of human point-light walkers). These tasks activated distinct regions within the posterior-lateral temporal lobe. Viewing non-biological motion relative to luminance change activated MT/MST. Viewing biological motion relative to scrambled motion activated the rSTS and to a lesser extent the left STS. Making semantic judgments about action verbs activated the IMTG (relative to semantic judgments about object nouns). Crucially, these lateral temporal areas did not overlap with each other in individual participants. The left homologues of right MT/MST and the rSTS were distinct from the IMTG.<sup>25</sup> These data demonstrate that the IMTG is neuroanatomically distinct from modality-specific visual motion areas.

These results leave open the possibility that the IMTG stores modality-specific representations of visual motion that are specifically relevant to understanding action-verbs but are not engaged during visual perception. On this account (sometimes called the “anterior shift” hypothesis) the representations of the IMTG are not the same as those engaged in motion perception. Instead, the IMTG represents visual motion information specifically relevant to word meanings.<sup>23,56</sup> These representations are still modality-specific and are derived developmentally from sensory experience, but they are neuroanatomically distinct from perceptual representations.

We tested this hypothesis by studying action-verb comprehension in congenitally blind individuals. If the IMTG represents modality-specific visual-motion information derived from visual experience, its function should be altered in individuals who have never seen. Contrary to this prediction, we found that congenitally blind individuals also engage the IMTG during action verb comprehension. The IMTG of congenitally blind adults was similarly localized and similar in size to sighted individuals.<sup>117,118</sup> Moreover, the IMTG showed the same functional response profile across three types of nouns and three types of verbs in congenitally blind and sighted participants.<sup>117</sup> (For converging behavioral evidence of preserved word meanings in blind children, see Ref. 119.) This preservation of function in the IMTG stands in contrast to plasticity observed in visual areas of congenitally blind adults.<sup>120,121</sup> For example, unlike in sighted adults, in congenitally blind individuals, MT/MST responds to sound.<sup>122–124</sup> Together, these results illustrate that the IMTG neither stores visual representations of motion nor develops specifically as a result of early visual motion experience.

A further question concerns whether the IMTG represents information along the same dimensions as nearby perceptual motion areas. Specifically, one hypothesis is that the IMTG is sensitive to motion information, like MT/MST and the rSTS. By contrast, we find that unlike visual motion areas, the IMTG is not sensitive to the presence or absence of motion in any modality. The IMTG response is equally high to action-verbs like “to run” and mental state verbs such as “to think.” Similarly, the IMTG response is equally low for motion noun that are rich in motion features such as animal names (e.g.,

the tiger) and nouns that are low in motion features (e.g., the rock).<sup>25,106</sup> Therefore, unlike neighboring perceptual brain regions, the IMTG is not sensitive to perceptual features. These results argue that the IMTG stores modality-independent representations that encode conceptual rather than perceptual properties.

A crucial outstanding question concerns the specific nature of IMTG conceptual representations. For example, the IMTG might respond selectively to the conceptual category of events, which, unlike entities, are situated in time. Alternatively, the IMTG might represent information relevant to the grammatical category of verbs. There is some evidence that during sentence comprehension the IMTG is sensitive to aspects of a verb’s grammar that are intimately related to the verb’s meaning. For example, a verb like “give” requires a giver, a thing being given, and a recipient (three obligatory arguments), whereas a verb like “run” requires only the runner (one obligatory argument). IMTG responds more to sentences with verbs that have more arguments, even when the sentences are matched in overall length.<sup>125</sup> There is also evidence that lateral temporal regions, including the IMTG, are specifically sensitive to the kind of information relevant to categorizing events. Damage to these brain regions impairs the ability to categorize visual events as belonging to a particular lexical category (e.g., distinguishing between hammering and sawing). By contrast, the IMTG does not appear to be necessary for distinguishing between hammering and other versions of hammering with erroneous body posture or movement.<sup>126,127</sup> Together, these results suggest that the IMTG represents conceptual information about events or meaning-relevant grammatical information about verbs.<sup>25</sup>

In sum, the IMTG responds to action-verbs across a range of tasks with single verbs or word pairs relative to a range of control conditions. IMTG representations are modality-independent in that they are neither visual themselves nor similar to visual representations of actions (e.g., responsive to motion).

The IMTG provides an example of the kinds of representations that are automatically retrieved when we understand words. These representations are abstract and are sensitive to distinctions among categories such as events and objects, rather than sensory modalities such as vision and audition. Such

representations also reflect the structure of language itself and distinguish among words based on the way they behave in sentences. Rather than sharing neural mechanisms with motor control and visual motion perception, action-verbs appear to share neural substrates with other verbs.

## Conclusions

The neural basis of action-verbs is often argued to provide strong evidence for an embodied view of cognition. On this account, word-meanings are said to be embodied in sensory-motor systems.<sup>3,18,19,68,128,129</sup> We argue that a closer look at the neural data on action-verbs paints a different picture. There is considerable evidence that at the neural level, understanding words does not entail breaking down their meanings into a mosaic of sensory-motor experiences.<sup>130</sup> Indeed, a greater reliance on modality-independent neural circuits might be a key feature that distinguishes language comprehension from perception. When we experience “running,” we initially process our experience in modality-specific systems. Distinct neural circuits respond to visual, tactile, auditory, and motor aspects of running. By contrast, understanding the word “run” occurs in modality-independent neural systems in the left temporal, parietal, and prefrontal cortices. These brain regions parse the world into events, agents, and objects, rather than vision, audition, and touch. The functions of such brain regions may be described in terms of specific conceptual categories, grammatical categories, or computational characteristics.<sup>15</sup>

Although the neuroanatomical data suggest that word comprehension is supported by modality-independent representations, there is also ample evidence that language, perception, and action are not isolated modules, but rather interact dynamically. Both behavioral and neural data compellingly illustrate the pervasiveness, speed, and automaticity of dynamic interactions between perception and language comprehension.<sup>52,131</sup> A full account of language comprehension will need to describe the contributions of both modality-independent and modality-specific representations to language processing.

## Conflicts of interest

The authors declare no conflicts of interest.

## References

1. Miller, G.A. & P. Johnson-Laird. 1987. *Language and Perception*. Harvard University Press. Cambridge, MA.
2. Barsalou, L.W. 1999. Perceptual symbol systems. *Behav. Brain Sci.* **22**: 577–609; discussion 610–560.
3. Pulvermuller, F. 1999. Words in the brain’s language. *Behav. Brain Sci.* **22**: 253–279; discussion 280–336.
4. Gallese, V. & G. Lakoff. 2005. The brain concepts: the role of the sensorymotor system in conceptual structure. *Cogn. Neuropsychol.* **22**: 455–479.
5. Caramazza, A., A. Hillis, B. Rapp & C. Romani. 1990. The multiple semantics hypothesis: Multiple confusions? *Cogn. Neuropsychol.* **7**: 161–189.
6. Jackendoff, R. 2002. *Foundations of Language: Brain, Meaning, Grammar, Evolution*. Oxford University Press. Oxford.
7. Caramazza, A. & B.Z. Mahon. 2003. The organization of conceptual knowledge: the evidence from category-specific semantic deficits. *Trends Cogn. Sci.* **7**: 354–361.
8. Fodor, J. 1983. *The Modularity of Mind*. MIT Press. Cambridge.
9. Descartes, R. 1639. Meditations on First Philosophy in which are demonstrated the existence of God and distinction between the human soul and the body.
10. Berkeley, G. 1709/1732. *An Essay Towards a New Theory of Vision*. Dublin: Printed by Aaron Rhamés for Jeremy Pepyal.
11. Zalta, E.N., ed. 2008. *The Stanford Encyclopedia of Philosophy*. The Metaphysics Research Lab, Stanford University. Stanford, CA.
12. Paivio, A. 1971. *Imagery and Verbal Processes*. Holt, Rinehart & Winston. New York.
13. Potter, M.C. & B.A. Faulconer. 1975. Time to understand pictures and words. *Nature* **253**: 437–438.
14. Potter, M.C., V.V. Valian & B.A. Faulconer. 1977. Representation of a sentence and its pragmatic implications: verbal, imagistic, or abstract? *J. Verb. Learn. Verb. Behav.* **16**: 1–12.
15. Tyler, L.K. & H.E. Moss. 2001. Towards a distributed account of conceptual knowledge. *Trends Cogn. Sci.* **5**: 244–252.
16. Zwaan, R.A. 2003. The immersed experiencer: Toward an embodied theory of language comprehension. *Psychol. Learn. Motiv.* **44**: 35–62.
17. Patterson, K., P.J. Nestor & T.T. Rogers. 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* **8**: 976–987.
18. Kemmerer, D. 2007. How words capture visual experience: The perspective from cognitive neuroscience. In *Words and the World: How Words Capture Experience*. B. Malt & P. Wolff, Eds. Oxford University Press. Oxford.
19. Pulvermuller, F. 2001. Brain reflections of words and their meaning. *Trends Cogn. Sci.* **5**: 517–524.
20. Barsalou, L.W. 2007. Grounded cognition. *Annu. Rev. Psychol.* **59**: 617–645.
21. Rogers, T.T., M.A. Lambon Ralph, P. Garrard, et al. 2004. Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol. Rev.* **111**: 205–235.

22. Revill, K.P., R.N. Aslin, M.K. Tanenhaus & D. Bavelier. 2008. Neural correlates of partial lexical activation. *Proc. Natl. Acad. Sci. USA* **105**: 13111–13115.
23. Martin, A., J.V. Haxby, F.M. Lalonde, *et al.* 1995. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* **270**: 102–105.
24. Hauk, O., I. Johnsrude & F. Pulvermuller. 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron* **41**: 301–307.
25. Bedny, M., A. Caramazza, E. Grossman, *et al.* 2008. Concepts are more than percepts: the case of action verbs. *J. Neurosci.* **28**: 11347–11353.
26. Snowden, R.J. & T.C. Freeman. 2004. The visual perception of motion. *Curr. Biol.* **14**: R828–831.
27. Born, R.T. & D.C. Bradley. 2005. Structure and function of visual area MT. *Annu. Rev. Neurosci.* **28**: 157–189.
28. Tootell, R.B., J.B. Reppas, K.K. Kwong, *et al.* 1995. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* **15**: 3215–3230.
29. Dubner, R. & S.M. Zeki. 1971. Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Res.* **35**: 528–532.
30. de Jong, B.M., S. Shipp, B. Skidmore, *et al.* 1994. The cerebral activity related to the visual perception of forward motion in depth. *Brain* **117**(Pt 5): 1039–1054.
31. Zeki, S. 1991. Cerebral akinetopsia (visual motion blindness). A review. *Brain* **114**(Pt 2): 811–824.
32. Zihl, J., D. von Cramon & N. Mai. 1983. Selective disturbance of movement vision after bilateral brain damage. *Brain* **106**(Pt 2): 313–340.
33. Beckers, G. & V. Homberg. 1992. Cerebral visual motion blindness: transitory akinetopsia induced by transcranial magnetic stimulation of human area V5. *Proc. Biol. Sci.* **249**: 173–178.
34. Grossman, E.D., M. Donnelly, R. Price, *et al.* 2000. Brain areas involved in perception of biological motion. *J. Cogn. Neurosci.* **12**: 711–720.
35. Grossman, E.D. & R. Blake. 2002. Brain areas active during visual perception of biological motion. *Neuron* **35**: 1167–1175.
36. Grossman, E.D., L. Battelli & A. Pascual-Leone. 2005. Repetitive, T.M.S over posterior STS disrupts perception of biological motion. *Vision Res.* **45**: 2847–2853.
37. Sunaert, S., P. Van Hecke, G. Marchal & G.A. Orban. 1999. Motion-responsive regions of the human brain. *Exp. Brain Res.* **127**: 355–370.
38. Vanduffel, W., D. Fize, H. Peuskens, *et al.* 2002. Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Science* **298**: 413–415.
39. Claeys, K.G., D.T. Lindsey, E. De Schutter & G.A. Orban. 2003. A higher order motion region in human inferior parietal lobule: evidence from fMRI. *Neuron* **40**: 631–642.
40. Martinez-Trujillo, J.C., D. Cheyne, W. Gaetz, *et al.* 2007. Activation of area MT/V5 and the right inferior parietal cortex during the discrimination of transient direction changes in translational motion. *Cereb. Cortex* **17**: 1733–1739.
41. Lewis, J.W., M.S. Beauchamp & E.A. DeYoe. 2000. A comparison of visual and auditory motion processing in human cerebral cortex. *Cereb. Cortex* **10**: 873–888.
42. Bremner, F., A. Schlack, N.J. Shah, *et al.* 2001. Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* **29**: 287–296.
43. Zwaan, R.A., C.J. Madden, R.H. Yaxley & M.E. Aveyard. 2004. Moving words: Dynamic mental representations in language comprehension. *Cogn. Sci.* **28**: 611–619.
44. Kaschak, M.P., C.J. Madden, D.J. Theriault, *et al.* 2005. Perception of motion affects language processing. *Cognition* **94**: B79–89.
45. Meteyard, L., N. Zokaci, B. Bahrami & G. Vigliocco. 2008. Visual motion interferes with lexical decision on motion words. *Curr. Biol.* **18**: R732–R733.
46. Meteyard, L., B. Bahrami & G. Vigliocco. 2007. Motion detection and motion verbs: language affects low-level visual perception. *Psychol. Sci.* **18**: 1007–1013.
47. Zwaan, R.A. & L.J. Taylor. 2006. Seeing, acting, understanding: motor resonance in language comprehension. *J. Exp. Psychol. Gen.* **135**: 1–11.
48. Yaxley, R.H., Zwaan, R.A. 2007. Simulating visibility during language comprehension. *Cognition* **105**: 229–236.
49. Winawer, J., N. Witthoft, M.C. Frank, *et al.* 2007. Russian blues reveal effects of language on color discrimination. *Proc. Natl. Acad. Sci. USA* **104**: 7780–7785.
50. Vaina, L.M., A. Cowey, R.T. Eskew Jr., *et al.* 2001. Regional cerebral correlates of global motion perception: evidence from unilateral cerebral brain damage. *Brain* **124**: 310–321.
51. Kourtzi, Z. & N. Kanwisher. 2000. Activation in human MT/MST by static images with implied motion. *J. Cogn. Neurosci.* **12**: 48–55.
52. Mahon, B.Z. & A. Caramazza. 2008. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol. Paris* **102**: 59–70.
53. Maeda, F., R. Kanai & S. Shimojo. 2004. Changing pitch induced visual motion illusion. *Curr. Biol.* **14**: R990–991.
54. Tranel, D., R. Adolphs, H. Damasio & A.R. Damasio. 2001. A neural basis for the retrieval of words for actions. *Cogn. Neuropsychol.* **18**: 655–674.
55. Tranel, D., D. Kemmerer, R. Adolphs, *et al.* 2003. Neural correlates of conceptual knowledge for actions. *Cogn. Neuropsychol.* **20**: 409–432.
56. Kable, J.W., J. Lease-Spellmeyer & A. Chatterjee. 2002. Neural substrates of action event knowledge. *J. Cogn. Neurosci.* **14**: 795–805.
57. Kable, J.W., I.P. Kan, A. Wilson, *et al.* 2005. Conceptual representations of action in the lateral temporal cortex. *J. Cogn. Neurosci.* **17**: 1855–1870.
58. Sadaghiani, S., J.X. Maier & U. Noppeney. 2009. Natural, metaphoric, and linguistic auditory direction signals have distinct influences on visual motion processing. *J. Neurosci.* **29**: 6490–6499.
59. Noppeney, U., O. Josephs, S. Kiebel, *et al.* 2005a. Action selectivity in parietal and temporal cortex. *Brain Res. Cogn. Brain Res.* **25**: 641–649.
60. van Dam, W.O., S.A. Rueschemeyer & H. Bekkering. 2010. How specifically are action verbs represented in the neural

- motor system: An fMRI study. *Neuroimage* **53**(4): 1318–1325.
61. Mahon, B.Z., S.C. Milleville, G.A. Negri, *et al.* 2007. Action-related properties shape object representations in the ventral stream. *Neuron* **55**: 507–520.
  62. Pobric, G., E. Jefferies & M.A. Lambon Ralph. 2010. Category-specific versus category-general semantic impairment induced by transcranial magnetic stimulation. *Curr. Biol.* **20**: 964–968.
  63. Culham, J.C. & K.F. Valyear. 2006. Human parietal cortex in action. *Curr. Opin. Neurobiol.* **16**: 205–212.
  64. Price, C.J. 2010. The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann. N. Y. Acad. Sci.* **1191**: 62–88.
  65. Saygin, A.P., S. McCullough, M. Alac & K. Emmorey. 2009. Modulation of BOLD response in motion-sensitive lateral temporal cortex by real and fictive motion sentences. *J. Cogn. Neurosci.* **22**(11): 2480–2490.
  66. Deen, B. & G. McCarthy. 2010. Reading about the actions of others: Biological motion imagery and action congruency influence brain activity. *Neuropsychologia* **48**(6): 1607–1615.
  67. Wallentin, M., T.E. Lund, S. Ostergaard, *et al.* 2005. Motion verb sentences activate left posterior middle temporal cortex despite static context. *Neuroreport* **16**: 649–652.
  68. Pulvermuller, F. & L. Fadiga. 2010. Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* **11**: 351–360.
  69. Willems, R.M. & P. Hagoort. 2007. Neural evidence for the interplay between language, gesture, and action: a review. *Brain Lang.* **101**: 278–289.
  70. Kemmerer, D. & J. Gonzalez-Castillo. 2008. The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain Lang.* **112**(1): 54–76.
  71. Dum, R.P. & P.L. Strick. 1991. The origin of corticospinal projections from the premotor areas in the frontal lobe. *J. Neurosci.* **11**: 667–689.
  72. Sanes, J.N. & M.H. Schieber. 2001. Orderly somatotopy in primary motor cortex: does it exist? *Neuroimage* **13**: 968–974.
  73. Riehle, A. & J. Requin. 1989. Monkey primary motor and premotor cortex: single-cell activity related to prior information about direction and extent of an intended movement. *J. Neurophysiol.* **61**: 534–549.
  74. Graziano, M. 2006. The organization of behavioral repertoire in motor cortex. *Annu. Rev. Neurosci.* **29**: 105–134.
  75. Pascual-Leone, A., D. Nguyet, L.G. Cohen, *et al.* 1995. Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *J. Neurophysiol.* **74**: 1037–1045.
  76. Feydy, A., R. Carlier, A. Roby-Brami, *et al.* 2002. Longitudinal study of motor recovery after stroke: recruitment and focusing of brain activation. *Stroke* **33**: 1610–1617.
  77. Rizzolatti, G. & C. Sinigaglia. 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.* **11**: 264–274.
  78. Schluter, N.D., M.F. Rushworth, R.E. Passingham & K.R. Mills. 1998. Temporary interference in human lateral pre-motor cortex suggests dominance for the selection of movements. A study using transcranial magnetic stimulation. *Brain* **121**(Pt 5): 785–799.
  79. Schubotz, R.I. & D.Y. von Cramon. 2003. Functional-anatomical concepts of human premotor cortex: evidence from fMRI and PET studies. *Neuroimage* **20**(Suppl 1): S120–S131.
  80. Schubotz, R.I. & D.Y. von Cramon. 2004. Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *J. Neurosci.* **24**: 5467–5474.
  81. Schubotz, R.I. 2007. Prediction of external events with our motor system: towards a new framework. *Trends Cogn. Sci.* **11**: 211–218.
  82. Wolfensteller, U., R.I. Schubotz & D.Y. von Cramon. 2007. Understanding non-biological dynamics with your own premotor system. *Neuroimage* **36**(Suppl 2): T33–43.
  83. Chouinard, P.A. & T. Paus. 2006. The primary motor and premotor areas of the human cerebral cortex. *Neuroscientist* **12**: 143–152.
  84. Forstmann, B.U., G. Dutilh, S. Brown, *et al.* 2008. Striatum and pre-SMA facilitate decision-making under time pressure. *Proc. Natl. Acad. Sci. USA* **105**: 17538–17542.
  85. Nachev, P., C. Kennard & M. Husain. 2008. Functional role of the supplementary and pre-supplementary motor areas. *Nat. Rev. Neurosci.* **9**: 856–869.
  86. Leek, E.C. & S.J. Johnston. 2009. Functional specialization in the supplementary motor complex. *Nat. Rev. Neurosci.* **10**: 78; author reply 78.
  87. Miller, E.K. & J.D. Cohen. 2001. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* **24**: 167–202.
  88. Ruschemeyer, S.A., M. Brass & A.D. Friederici. 2007. Comprehending prehending: neural correlates of processing verbs with motor stems. *J. Cogn. Neurosci.* **19**: 855–865.
  89. Willems, R.M., P. Hagoort & D. Casasanto. 2010. Body-specific representations of action verbs: neural evidence from right- and left-handers. *Psychol. Sci.* **21**: 67–74.
  90. Willems, R.M., I. Toni, P. Hagoort & D. Casasanto. 2009b. Neural dissociations between action verb understanding and motor imagery. *J. Cogn. Neurosci.* **21**(1): 67–74.
  91. Davis, M.H., F. Meunier & W.D. Marslen-Wilson. 2004. Neural responses to morphological, syntactic, and semantic properties of single words: an fMRI study. *Brain Lang.* **89**: 439–449.
  92. Duffau, H., L. Capelle, D. Denvil, *et al.* 2003. The role of dominant premotor cortex in language: a study using intraoperative functional mapping in awake patients. *Neuroimage* **20**: 1903–1914.
  93. Ullman, M.T. 2004. Contributions of memory circuits to language: the declarative/procedural model. *Cognition* **92**: 231–270.
  94. van Heuven, W.J., H. Schriefers, T. Dijkstra & P. Hagoort. 2008. Language conflict in the bilingual brain. *Cereb. Cortex* **18**: 2706–2716.
  95. Pulvermuller, F., Y. Shtyrov & R. Ilmoniemi. 2005. Brain signatures of meaning access in action word recognition. *J. Cogn. Neurosci.* **17**: 884–892.

96. Postle, N., K.L. McMahon, R. Ashton, *et al.* 2008. Action word meaning representations in cytoarchitecturally defined primary and premotor cortices. *Neuroimage* **43**: 634–644.
97. de Zubicaray, G., N. Postle, K. McMahon, *et al.* 2008. Mirror neurons, the representation of word meaning, and the foot of the third left frontal convolution. *Brain Lang.* **112**(1): 77–84.
98. Willems, R.M., I. Toni, P. Hagoort & D. Casasanto. 2009a. Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. *Front Hum. Neurosci.* **3**: 39.
99. Aziz-Zadeh, L., S.M. Wilson, G. Rizzolatti & M. Iacoboni. 2006. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Curr. Biol.* **16**: 1818–1823.
100. Buccino, G., L. Riggio, G. Melli, *et al.* 2005. Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Res. Cogn. Brain Res.* **24**: 355–363.
101. Beilock, S.L., I.M. Lyons, A. Mattarella-Micke, *et al.* 2008. Sports experience changes the neural processing of action language. *Proc. Natl. Acad. Sci. USA* **105**: 13269–13273.
102. Haaland, K.Y., C.L. Elsinger, A.R. Mayer, *et al.* 2004. Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *J. Cogn. Neurosci.* **16**: 621–636.
103. Grafton, S.T. & A.F. Hamilton. 2007. Evidence for a distributed hierarchy of action representation in the brain. *Hum. Mov. Sci.* **26**: 590–616.
104. Zwaan, R.A. & G.A. Radvansky. 1998. Situation models in language comprehension and memory. *Psychol. Bull.* **123**: 162–185.
105. Perani, D., S.F. Cappa, T. Schnur, *et al.* 1999. The neural correlates of verb and noun processing: A PET study. *Brain* **122**: 2337–2344.
106. Grossman, M., P. Koenig, C. DeVita, *et al.* 2002. Neural representation of verb meaning: An fMRI study. *Hum. Brain Mapp.* **15**: 124–134.
107. Bedny, M. & S.L. Thompson-Schill. 2006. Neuroanatomically separable effects of imageability and grammatical class during single-word comprehension. *Brain Lang.* **98**: 127–139.
108. Price, C.J. 1998. The functional anatomy of word comprehension. *Trends Cogn. Sci.* **2**(8): 281–288.
109. Thompson-Schill, S.L., M. D'Esposito, G.K. Aguirre & M.J. Farah. 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. USA* **94**: 14792–14797.
110. Swaab, T.Y., C. Brown & P. Hagoort. 1998. Understanding ambiguous words in sentence contexts: electrophysiological evidence for delayed contextual selection in Broca's aphasia. *Neuropsychologia* **36**: 737–761.
111. Bedny, M., M. McGill & S.L. Thompson-Schill. 2008b. Semantic adaptation and competition during word comprehension. *Cereb. Cortex* **18**: 2574–2585.
112. Holland, R. & M.A. Ralph. 2010. The anterior temporal lobe semantic hub is a part of the language neural network: Selective disruption of irregular past tense verbs by rTMS. *Cereb. Cortex* **20**(12): 2771–2775.
113. Martin, A. 2007. The representation of object concepts in the brain. *Annu. Rev. Psychol.* **58**: 25–45.
114. Yokoyama, S., T. Miyamoto, J. Riera, *et al.* 2006. Cortical mechanisms involved in the processing of verbs: an fMRI study. *J. Cogn. Neurosci.* **18**: 1304–1313.
115. Shapiro, K.A., L.R. Moo & A. Caramazza. 2006. Cortical signatures of noun and verb production. *Proc. Natl. Acad. Sci. USA* **103**: 1644–1649.
116. Kemmerer, D., J.G. Castillo, T. Talavage, *et al.* 2008. Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain Lang.* **107**: 16–43.
117. Bedny, M., A. Caramazza, A. Pascual-Leone & R. Saxe. (in press). Typical neural representations of action verbs develop without vision. *Cerebral Cortex*.
118. Noppeney, U., K.J. Friston & C.J. Price. 2003. Effects of visual deprivation on the organization of the semantic system. *Brain* **126**: 1620–1627.
119. Landau, B. & L. Gleitman. 1985. Language and experience: evidence from the blind child. Harvard University Press. Cambridge, MA.
120. Sadato, N., A. Pascual-Leone, J. Grafman, *et al.* 1996. Activation of the primary visual cortex by Braille reading in blind subjects. *Nature* **380**: 526–528.
121. Amedi, A., A. Floel, S. Knecht, *et al.* 2004. Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nat. Neurosci.* **7**: 1266–1270.
122. Saenz, M., L.B. Lewis, A.G. Huth, *et al.* 2008. Visual motion area MT+/V5 responds to auditory motion in human sight-recovery subjects. *J. Neurosci.* **28**: 5141–5148.
123. Wolbers, T., P. Zahorik & N.A. Giudice. 2010. Decoding the direction of auditory motion in blind humans. *Neuroimage*. May 5. [Epub ahead of print].
124. Bedny, M., T. Konkler, K.A. Pelphrey, *et al.* 2010. Sensitive period for a multi-modal response in human visual motion area MT/MST. *Curr. Biol.* **20**(21): 1900–1906.
125. Shetreet, E., D. Palti, N. Friedmann & U. Hadar. 2007. Cortical representation of verb processing in sentence comprehension: number of complements, subcategorization, and thematic frames. *Cereb. Cortex* **17**: 1958–1969.
126. Kalenine, S., L.J. Buxbaum & H.B. Coslett. 2010. Critical brain regions for action recognition: lesion symptom mapping in left hemisphere stroke. *Brain* **133**: 3269–3280.
127. Kemmerer, D., D. Rudrauf, K. Manzel & D. Tranel. 2010. Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex*. Nov 18. [Epub ahead of print].
128. Barsalou, L.W., W. Kyle Simmons, A.K. Barbey & C.D. Wilson. 2003. Grounding conceptual knowledge in modality-specific systems. *Trends Cogn. Sci.* **7**: 84–91.
129. Zwaan, R.A. & M.P. Kaschak. 2008. Language in the brain, body, and world. In *The Cambridge Handbook of Situated Cognition*. P. Robbins & M. Aydede, Eds. Cambridge University Press. New York, NY.
130. Chatterjee, A. 2010. Disembodying cognition. *Lang. Cogn.* **2**: 79–116.
131. Tanenhaus, M.K. & S. Brown-Schmidt. 2008. Language processing in the natural world. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **363**: 1105–1122.