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Motor and Nonmotor Language Representations in the Brain

Nira Mashal, Michael Andric, and Steven Small

Introduction

Typical face-to-face conversation involves an elaborate arrangement of movements. Both a speaker and his or her conversational partner exchange information about articulated speech via perception of mouth and lip movements. Virtually all face-to-face speech is also accompanied by spontaneously produced hand gestures. The brain coordinates all of these movements in various networks of regions, including some typically associated with language processing and others sometimes referred to as the "motor system." An important question is to what extent this motor system, beyond its role in producing actions, is also involved in perceiving them. The presence of motor system involvement in both producing and perceiving actions leads to a further line of inquiry seeking to discern the extent of its role in coding actions for comprehension. That is, might the motor system, via its regular responsibility in helping to produce and perceive actions, provide a basis for how the brain represents meaning more generally?

In this chapter, we discuss the motor regions of the cerebral cortex and their participation in a number of functions related to human language, i.e., producing and perceiving speech and language and representing the meaning of words and sentences. We first elaborate on motor system involvement in articulate speech, continue to characterize its involvement in manual gesture, and, lastly, discuss its more general role in interpreting a message's content.

Recent anatomical and physiological findings in the nonhuman primate brain have profoundly impacted our understanding of how actions are processed and

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understood neurobiologically. The cortical motor system of the primate is a collage of many anatomically and functionally distinguishable areas (Rizzolatti & Luppino, 2001). Single neuron recording studies have shown that in one of these areas of the macaque monkey, area F5 in the rostral part of the ventral premotor cortex, there exist neurons that code specific actions, possibly providing a "vocabulary" of motor action representations (Rizzolatti et al., 1988). Some of the neurons in F5 are active either when the monkey performs a specific mouth or hand action, or when it observes another monkey (or human) performing the same or a similar action. Such identified "mirror neurons" have also subsequently been found in the inferior parietal area PF (Fogassi, Gallese, Fadiga, & Rizzolatti, 1998). Mirror neurons have been proposed as the basis for a mechanism that transforms specific sensory information into a motor format, giving an immediate understanding of an observed motor act (Fabbri-Destro & Rizzolatti, 2008). A mirror mechanism is proposed to exist in humans as well, and similarly to mediate our understanding of actions (Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Arbib, 1998; Rizzolatti & Fabbri-Destro, 2008; Skipper, van Wassenhove, Nusbaum, & Small, 2007).

Does such a mechanism play a role in language comprehension via an observer's visual perceptions of a speaker's mouth and hand actions? Indeed, accumulating evidence suggests that areas of our own cortical motor system become active when we interpret spoken language (e.g., Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007; Skipper et al., 2007; Wilson, Saygin, Sereno, & Iacoboni, 2004). The specific function of this motor activity, however, is still under considerable debate. Some have suggested that perceiving speech may incorporate a mechanism of simulating its production (Halle & Stevens, 1962; Liberman & Whalen, 2000). Existing data also admit alternate plausible theories emphasizing integration of motor and sensory information in perception (Hickok & Poeppel, 2004, 2007; Skipper, Nusbaum, & Small, 2006). Similarly, emerging data suggest that activity in motor regions is also present when we observe the hand gestures that accompany spoken language ("co-speech gestures"; e.g., Green et al., 2009; Skipper, Goldin-Meadow, Nusbaum, & Small, 2009; Willems, Ozyurek, & Hagoort, 2007), as well as the salient gestures that convey propositional meaning independent of speech ("emblems"; e.g., Villarreal et al., 2008). Moreover, cortical motor activity in language settings does not appear to be present just when perceiving the actions of its expression.

The question about the role of the motor system in language comprehension leads naturally to the more specific question about whether neurally instantiated motor programs are used in representing meaning more generally. Several studies of word and sentence processing have postulated that brain activity in primary and premotor cortices is used to represent the meaning of words and sentences. These studies have generally described such activity during the processing of action-related language, and not during processing of linguistic content unrelated to actions. Examples include activity in motor regions for processing action-related words (e.g., Hauk, Johnsrude, & Pulvermüller, 2004) and for sentences that describe oral, manual, and foot actions (e.g., Tettamanti et al., 2005). Thus, while we still lack a complete, systematic explanation of the role of the motor system in language, its involvement appears indisputable.

Speech Perception

When we observe someone speaking to us, we integrate auditory information from the speech stream with visual information from (especially) the lips and mouth to come up with the intended message. Evidence obtained from transcranial magnetic stimulation (TMS) and functional magnetic resonance imaging (fMRI) studies have suggested that a hearer might perceive speech in part (e.g., Skipper et al., 2006) or entirely (e.g., Liberman & Whalen, 2000) by simulating the articulatory gestures of the talker. This implies that some sort of motor mechanism – and by inference some motor regions of the brain – plays an important role in speech perception (e.g., Halle & Stevens, 1962; Massaro & Cohen, 1995; for review see Galantucci, Fowler, & Turvey, 2006). Thus, to find support for the notion that motor regions are involved in speech perception, a growing number of studies have used advanced brain imaging techniques to show similar brain regions activated during both speech perception and speech production tasks.

A large body of evidence obtained from fMRI has shown that audiovisual perception of monosyllables activates brain areas dedicated to speech production. A recent fMRI study showed that passive listening to meaningless monosyllables activates the ventral premotor cortex (PMv), an area also activated during production of the same syllables (Wilson et al., 2004). In a theoretical paper (Skipper et al., 2006), we have postulated that PMv integrates visual information from the face of the speaker with auditory information from the speech stream using motor commands that could have generated those movements. In this model, the flow of sensory information (backward model) maps and integrates the sensory information onto articulatory motor representations in the frontal lobe (forward model).

Subsequent work has been conducted with "illusory" audiovisual syllables, artificial audiovisual stimuli in which visual and auditory information are inconsistent, leading to a percept that is neither the auditory nor the visual component (McGurk & McDonald, 1976). These studies showed that observation and production overlap in multiple brain areas including premotor cortices and primary motor cortex (Skipper et al., 2007). When participants perceived an "illusory" incongruent /ta/ consisting of a visual image of the mouth producing /ka/ while hearing the audio /pa/, the activity in the motor area resembled the activity patterns evoked by the congruent audiovisual /ta/ more than /ka/ or /pa/. Interestingly, activity patterns in the visual cortex resembled the activity evoked by audiovisual /ka/, particularly early in the process, and activity patterns in auditory areas resembled the activity evoked by audiovisual /pa/, with similarly evolving time course.

A recent TMS study demonstrated neural activity in speech motor regions during passive speech perception, suggesting that activity in motor areas is causally linked to the perception of speech (Meister et al., 2007). That study used both fMRI and

TMS, first to localize premotor regions activated during both speech production and speech perception and then to apply slow (inhibitory) repetitive TMS (rTMS) over one of the previously identified premotor sites while participants heard a consonant–vowel syllable in noise. The subject had to identify it as pa, ta, or ka by pressing one of three keys. The results showed a decrease in the rate of correct responses for the speech perception task after applying TMS over the left premotor cortex as compared to baseline (no TMS). The authors concluded that the premotor area plays an essential role in speech perception, and that sensory regions are not in themselves sufficient for human perception. This suggests that a mechanism such as simulation, that couples action and perception, is critical for speech perception.

If motor brain regions are associated with speech perception, then listening to speech should lead to excitability of certain muscles, measured by motor-evoked potentials. Watkins et al. (2003) applied TMS over the face area of primary motor cortex to elicit motor-evoked potentials (MEPs) in the lip muscles. The MEPs were measured while participants listened to speech (continuous prose), listened to nonverbal sounds (e.g., glass breaking, bells ringing), viewed speech-related lip movements, and viewed eye and brow movements. The results indicated that either listening to speech or viewing speech-related actions enhanced the amplitude of motor-evoked potentials in the lip muscles compared to baseline. This effect was seen in response to stimulation of the left hemisphere but not the right hemisphere. This result provides evidence that speech perception of both auditory and visual information increases the excitability of the motor system involved in speech production.

Thus, neural systems for speech perception and speech production, traditionally localized in a dissociated way to the left posterior temporal and inferior frontal areas, respectively, seem to interact functionally during language comprehension (at least). Of course, it is well known since the nineteenth century that these systems are anatomically interconnected. Since Déjérine (1891, 1892), Broca's area, classically considered a motor speech production area, (e.g., Bookheimer, 2002; Broca, 1861) has been thought to be connected to Wernicke's area (Wernicke, 1874) by the arcuate fasciculus, although the original data on this connectivity came from gross anatomical inspection without physiological support. Neuroanatomical studies in monkeys (Yeterian & Pandya, 1985) support this connectivity in a homologous situation, and diffusion tensor imaging data from humans (Catani & Mesulam, 2008) have further elaborated the veracity of the original anatomical postulate (Déjérine, 1891). Geschwind (1966) built on these original concepts, and articulated a connectionist approach, summarizing what is now considered the classic Broca-Wernicke-Geschwind model of brain language relationships. According to his model, Broca's area is the center of expressive language, Wernicke's area is the center of receptive language, and the arcuate fasciculus serves as the connecting pathway between the two. The model predicts that lesions to Broca's area would cause Broca's aphasia, lesions to Wernicke's area would cause Wernicke's aphasia, and lesions to the arcuate fasciculus would cause conduction aphasia (Geschwind, 1971).

Since Geschwind, considerable research using the lesion analysis method, as well as research using newer technologies for studying brain–behavior relationships, are proving problematic for Geschwind's model. For example, it has become clear that the behavioral syndrome of Broca's aphasia is not caused by a lesion restricted to Broca's area, and can be caused by many other types of lesions (Feinberg & Farah, 1997). The same is true for Wernicke's aphasia (Ojemann, Ojemann, Lettich, & Berger, 1989). Conduction aphasia is more likely caused by a lesion to Wernicke's area than to the arcuate fasciculus (Anderson et al., 1999; Damasio & Damasio, 1980). Direct cortical stimulation of perisylvian areas that are associated with specific aphasic symptoms does not cause these symptoms as predicated by the model (Ojemann et al., 1989). Finally, a host of imaging studies, such as those reviewed here, suggest considerable integration of the neural mechanisms for production and perception of language.

The most recent connectionist model incorporates a connection between the rostral part of the inferior parietal lobule and the ventral premotor cortex and pars opercularis of the inferior frontal gyrus (IFGOp) via the superior longitudinal fasciculus, subcomponent III, and not through the arcuate fasciculus (Schmahmann et al., 2007). Spoken language areas, including auditory areas of the superior temporal gyrus, are also connected to frontal-motor areas through cortico-cortical connections (Makris et al., 1999; Rizzolatti & Luppino, 2001). These connections suggest that different cortical systems may interact functionally during language performance.

In summary, during the period since the original proposal of the connectionist model of Geschwind, particularly in the recent period of research with physiological and imaging techniques, researchers have greatly advanced their understanding of how speech production and perception are processed in the brain. Instead of referring to speech production and speech perception as two dissociated processes located in segregated yet connected brain "centers," its now known that speech perception and speech production interact during language performance and that speech perception integrally includes access to the speech motor system. After discussing the role of speech-associated gesture in language comprehension, which also involves direct involvement of the motor system, we will discuss the evidence that motor areas active during language comprehension in fact contribute to both comprehension and the representation of meaning.

Gesture Perception: Gestures Accompanying Speech

Co-speech gestures are those hand and arm movements that unknowingly accompany most spoken language (Kendon, 1994; McNeill, 1992, 2005). While a gesture is simply a "motion that embodies a meaning reliable to the accompanying speech" (McNeill, 2005), these actions vary in the types of information they contribute. For example, whereas *beat* gestures provide rhythmic "temporal highlighting" (McNeill, 1992) to their accompanying speech (e.g., using the hand like a baton and matching down motions with spoken intonations), representational *iconic* gestures depict semantic content in the context of accompanying speech (e.g., using downward directed wiggling fingers while describing someone walking). Such iconic gestures are thought to contribute to a message's meaning and interpretation (Goldin-Meadow, 2006; Kendon, 1994; McNeill, 2005). In pursuing a stronger appreciation for how the brain represents meaning, researchers are increasingly investigating the biology associated with processing these motor acts.

At a basic visual level, co-speech gestures are one class (among many) of biological movements. Thus, brain areas responsive to visually presented biological motion, e.g., portions of the superior temporal sulcus (STS) and adjoining middle occipital gyrus and anterior occipital sulcus (approximating V5/MT+), respond when observing such gestures (Dick, Goldin-Meadow, Hasson, Skipper, & Small, 2009; Kircher et al., 2009; Willems et al., 2007; Wilson, Molnar-Szakacs, & Iacoboni, 2008). More interesting, however, is that motor regions also appear to play a prominent role in interpreting these actions. As we just discussed in the context of mouth actions, neurophysiological data from monkeys suggest that understanding purposeful actions appears to be mediated by premotor and parietal responses similar to those involved in performing the actions (for reviews see Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Craighero, 2004). Brain imaging studies suggest similar mechanisms might operate in humans (Buccino et al., 2001). Does this include interpreting co-speech gestures? Although an entirely systematic profile of responses is not yet evident, generally, the research so far suggests yes.

Premotor and parietal activity when observing co-speech gestures

Significant neural responses in premotor and parietal cortices appear to be involved in the biology of observing co-speech gestures. For example, reliable premotor cortex activity is found when people view iconic co-speech gestures, either when compared to simple grooming movements (Holle, Gunter, Ruschemeyer, Hennenlotter, & Iacoboni, 2008), or when they are mismatched with a verb in a sentence (e.g., seeing someone say "hit" while performing a "writing" gesture; Willems et al., 2007). Premotor sensitivity is also evident in discourse settings when meaningful gestures (e.g., iconic, metaphoric, deictic) accompany continuous audiovisual story presentation (Skipper et al., 2009). In contrast, movements such as adjusting the collar and touching the cuff ("self-adaptive" movements) do *not* result in differential hemodynamic signal fluctuation (Skipper et al., 2009). Suggesting such responses extend to viewing co-speech gestures more generally, other studies also indicate premotor activity when people observe beat (Hubbard, Wilson, Callan, & Dapretto, 2009) and metaphoric (Kircher et al., 2009) gestures.

Further supporting the notion that premotor-parietal responses mediate action understanding is the finding that inferior parietal lobe activity occurs when people observe co-speech gestures (Dick et al., 2009; Green et al., 2009; Holle et al., 2008; Kircher et al., 2009; Skipper et al., 2009). The supramarginal gyrus (SMG), particularly, appears to play an important role. Differential hemodynamic signal fluctuation occurs in the SMG during story comprehension when meaningful co-speech gestures are presented compared to when they are not (Skipper et al., 2009). There is also strong effective connectivity between SMG and premotor cortices during co-speech gesture observation (Skipper et al., 2007, 2009). Interestingly, while Skipper et al. (2007, 2009) did not delineate right and left SMG, other work indicates functional differences between the two; for example, finding significant right SMG responses when gestures conveyed information unrelated to accompanying speech (Green et al., 2009).

Co-speech gesture processing also leads to differential functional activity across left and right intraparietal (IP) regions. For example, left IP activity dominates when a co-speech gesture is mismatched with a spoken verb in context (Willems et al., 2007), whereas right IP activity is prominent when observing co-speech gestures compared to grooming movements (Holle et al., 2008). Right IP activity is also found for observing beat gestures, but only when they are not accompanied by speech (Hubbard et al., 2009). It appears then that these IP responses reflect its involvement in action recognition, more generally, rather than reactivity to the message content per se.

Overall, co-speech gesture processing includes patterns of premotor and parietal activity similar to observing other purposeful actions such as grasping. However, co-speech gestures notably differ from grasping, often contributing semantic information pertinent to a speaker's message. Beyond extensive behavioral research (see McNeill, 1992, 2005), this idea is supported by results from event-related potential (ERP) studies documenting N400 effects – believed to reflect difficult integration of semantic information in context – pertaining to incongruence between words and gestures (Kelly, Kravitz, & Hopkins, 2004). Other studies dealing with the semantic relation between speech and gesture also find an N400 effect (Holle & Gunter, 2007; Kelly, Ward, Creigh, & Bartolotti, 2007; Ozyurek, Willems, Kita, & Hagoort, 2007; Wu & Coulson, 2005). Further, activity during co-speech gesture processing is often found in brain areas that are classically considered as integral to language interpretation, but, as with premotor and parietal responses, a wholly consistent pattern is still lacking.

Inferior frontal and temporal lobe activity when observing co-speech gestures

Co-speech gestures often add supplementary semantic information to a verbal message, and brain regions associated with processing such information respond when people perceive these gestures. For example, significant activity in the anterior left IFG, particularly the pars triangularis (IFGTr), is found when observing mismatches between an iconic gesture and a verb during sentence processing (Willems et al., 2007). Thus, left IFGTr may be particularly involved in interpreting meaning regardless of its expression in motor (e.g., as gesture) or verbal form. Similar findings in this region are apparent when people observe speech with gestures compared to speech alone (Dick et al., 2009; Kircher et al., 2009). Diverging from Willems et al. (2007), though, Dick et al. (2009) find this activation to be independent of the informativeness of the manual gesture, as the right IFGTr demonstrates stronger activity during observation of "self-adaptive" movements compared to meaningful co-speech gestures, and Green et al. (2009) find stronger bilateral IFGTr responses during observation of unrelated co-speech gestures compared to related ones Furthermore, IFGTr connectivity in a network including inferior parietal, temporal, and frontal motor regions appears to be strongest when observing "self-adaptive" movements and weakest when observing relevant gestures (Skipper et al., 2007). Perhaps when information from co-speech gestures appears to reduplicate that in speech, IFGTr involvement in interpretation is lower than when it does not. By this analysis, since self-adaptive movements do not contribute meaningful information, they would increase semantic retrieval and/or selection demands. Such an account fits with the Willems et al. (2007) finding of differential IFGTr activity when the gesture was "mismatched" to the verb since the hand information was no longer germane to the message, leaving relatively higher need for semantic retrieval.

Besides the frontal lobe, the temporal lobe has also been associated with processing meaning in language studies (Hickok & Poeppel, 2004; Martin & Chao, 2001; Wise et al., 2001), and temporal lobe activity does appear to be prominent during observation of co-speech gestures, as well. When gestures correspond to the semantics in a speaker's message, the anterior superior temporal region has strong connectivity with premotor regions (Skipper et al., 2007). Activity in this area also occurs when observing metaphoric gestures in isolation (Kircher et al., 2009). In the left posterior middle temporal gyrus (MTG), activity is greater for observing metaphoric (Kircher et al., 2009) or iconic (Green et al., 2009) gestures accompanying speech than for observing either speech or gesture alone. Existing theories associate anterior temporal lobe activity with the incorporation of semantic and syntactic structures into propositional representations of meaning, e.g., in sentence processing (Humphries, Binder, Medler, & Liebenthal, 2006; Noppeney & Price, 2004), and posterior activity with recognizing word meanings (Binder et al., 1997; Chao, Haxby, & Martin, 1999; Gold et al., 2006). These regions may be functioning in similar capacities in co-speech gesture processing, although it remains to be elaborated if their primary role in semantics is to interface sensory and conceptual representations (Hickok & Poeppel, 2004), to perform semantic recognition (Martin & Chao, 2001), and/or something else entirely.

Gesture Perception: Symbolic Hand Gestures (Emblems)

Another class of hand gestures, emblematic gestures or *emblems*, convey meaning independent of speech (Goldin-Meadow, 1999). Emblems are conventionalized manual actions that communicate symbolic meaning and can substitute for speech (e.g., giving a "thumbs up" to express "It's good"). With emblems, the hand action itself delivers an intended message. Unlike conventional sign languages, however, they are not combinatorial and lack the linguistic structures found in human language (McNeill, 2005). Rather, using a single hand position and movement, such gestures convey semantic, propositional information. Emblems thus have a unique combination of properties as both a single purposeful hand action and symbolic expression.

Premotor and parietal activity when observing symbolic gestures

Similar to co-speech gestures, perception of emblems leads to activation both in brain areas that are sensitive to biological movements (e.g., V5/MT and STSp) and in areas of the premotor and parietal cortex. Specifically, left ventral premotor cortex is regularly active during emblem observation (Lotze et al., 2006; Villarreal et al., 2008). Additionally, the intraparietal sulcus and inferior parietal lobule (SMG in particular) are also consistently active (Lotze et al., 2006; Nakamura et al., 2004; Villarreal et al., 2008). While localization of these parietal responses using fMRI has been either left-lateralized (Lotze et al., 2006) or bilateral (Nakamura et al., 2004; Villarreal et al., 2008), regional electrophysiological recordings during recognition of static pictures of emblems suggest right laterality (Nakamura et al., 2004). This lack of overall systematic lateralization suggests that emblem recognition may be associated with diffuse neural activity patterns across premotor and parietal cortices.

Inferior frontal and temporal lobe activity when observing symbolic gestures

Unlike co-speech gestures, emblems are typically used without accompanying speech, yet activation during emblem interpretation includes regions commonly associated with language interpretation. For example, left IFGOp, proximally marking the posterior part of Broca's area, is functionally responsive when observing emblems. This effect has been shown comparing activity for observing emblems versus rest (Lotze et al., 2006; Villarreal et al., 2008) and versus observing object-directed hand actions (Villarreal et al., 2008). Pars triangularis of the IFG is also responsive during emblem observation, whether on the right (Lotze et al., 2006; Nakamura et al., 2004) or bilaterally (Villarreal et al., 2008), and both IFGTr activity (Lotze et al., 2006; Villarreal et al., 2008) and activity of the pars orbitalis of the left IFG (Lotze et al., 2006) are greater for emblems than for pantomimed transitive hand actions.

In the temporal lobes, activity in the posterior portion of the MTG, associated previously with recognizing word meaning (Binder et al., 1997; Gold et al., 2006), is also present during emblem observation, and this activity is greater than for observing hand actions that do not directly convey meaning (Villarreal et al., 2008).

Significant activity when observing emblems is also present in the anterior temporal lobes (Lotze et al., 2006), in regions previously associated with semantic integration (Nopenney & Price, 2004; Stowe, Haverkort, & Zwarts, 2005), and sentence processing (Friederici, Opitz, & von Cramon, 2000; Humphries, Love, Swinney, & Hickok, 2005; Nopenney & Price, 2004).

Recall that unlike co-speech gestures or sign language, emblems are single expressions of meaning communicated in the absence of speech, and thus activation of these regions classically associated with language are responding to nonspeech expressions of meaning. Overall, it appears that emblem processing involves coordination of visual, premotor, and parietal activity with inferior frontal and temporal activity. One interpretation of these data is that the two inherent properties of emblems – as purposeful hand actions and expressions of semantic meaning – lead to integrated processing by two related neural networks in the brain. More generally, this pattern of responses suggests that the brain may be organized at one level by perceptual recognition (e.g., of a visually presented hand action), but at another level by the type of relevant information (e.g., semantic meaning) required for orchestrating functional response patterns.

Action Language

Thus far, we have discussed the role of the motor system in speech perception and language comprehension. Specifically, we have reviewed work on perception of the lips and mouth and how this might enhance speech perception, and perception of manual gestures – both those that accompany speech (co-speech gestures) and those that communicate meaning independent of speech (emblems) – and how they relate to language understanding. At this juncture, we will address the research on the more general role of the motor system in representing meaning related to action. What role might the motor system play in the processing of words or sentences describing actions, apart from their role during direct observation of such actions? One hypothesis that has been explored is that the motor system of the brain becomes active when processing language about actions, even when no related actions can be explicitly seen. A further hypothesis has been that not only does such activity exist, but it forms the basis of the neural representation of meaning, for language but also more generally. These hypotheses stand in direct contrast to the notion that words and sentences are understood through amodal mental representations (e.g., Fodor, 2001).

Reading, Listening, and the Motor System

Based on convergent findings from a number of neuroimaging studies, there is strong evidence that motor areas of the human brain are active during language comprehension, and good reason to believe that such motor activation does indeed contribute to comprehension (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk et al., 2004; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Tettamanti et al., 2005). For example, in one fMRI study subjects were asked to read words referring to arm, leg, or face actions (e.g., to pick, kick, lick, respectively) or to actually perform those movements by the fingers, leg, or tongue (Hauk et al., 2004). Since primary motor and premotor cortices both have a degree of somatotopic organization, it was possible to test whether areas in the motor cortex activated while reading action words were also active when actually performing the actions. Indeed, motor cortical activation elicited by an action word overlapped with the cortical representation of the action to which it referred. (Left inferior temporal and left inferior frontal activation were also present on word reading, as expected.) More specifically, activation for finger movements overlapped with activation produced by arm words in left precentral gyrus and in right middle frontal gyrus, and for foot movements and leg words in dorsal premotor areas and left dorsal pre- and post-central gyri. This study remarkably suggests that processing action words, like performing the actions themselves, activates motor and premotor cortices in a somatotopic fashion.

These data have been corroborated by a study using TMS. If the motor system is involved in understanding action-related sentences, then their presentation should modulate the listener's motor cortex activity. To test the hypothesis, motor evoked potentials (MEPs) were recorded from the hand and foot muscles while subjects listened to hand-action-related sentences (e.g., "He turned the key"), foot-action-related sentences (e.g., "He kicked the ball"), and sentences with abstract content (e.g., "He loved his country") serving as the control condition (Buccino et al., 2005). The MEPs of the hand and the foot muscles were recorded during single-pulse TMS of the subjects' hand and foot motor areas, respectively. The results revealed a decrease in the MEP amplitude recorded from the hand muscles during listening to hand-action-related sentences as compared to listening to both foot-related and abstract sentences. Also, a decrease in the MEP amplitude recorded from the foot muscles during listening to foot-action-related sentences was found as compared to listening to both hand-related and abstract sentences. These results support the view that motor areas are involved in understanding action-related sentences.

Using fMRI, Tettamanti et al. (2005) tested the hypothesis that the homologous human regions of the macaque mirror neuron system would be active when listening to descriptions of actions. Previous fMRI research suggested that observation of mouth actions induces activation in IFGOp, extending to the rostral-most sector of the ventral premotor cortex; that observation of hand actions induces activation in the ventral premotor cortex; and that observation of foot actions induces activation in the dorsal premotor cortex (Buccino et al., 2001; Buccino, Binkofski, & Riggio, 2004; Grezes, Armony, Rowe, & Passingham, 2003; Nishitani & Hari, 2002; Rizzolatti et al., 1996). Tettamanti et al. (2005) investigated the possibility that comprehension of actions relies on the observation–execution matching system not only when a person observes an action but also when the actions are verbally described by sentences. Subjects passively listened to sentences describing actions performed with the mouth (e.g., “I bite an apple”), the hand (e.g., “I grasp a knife”), and the leg (e.g., “I kick the ball”), and control sentences with abstract content (e.g., “I appreciate sincerity”). The results indicated that listening to mouth-related sentences, hand-related sentences, and foot-related sentences induces activation of different sectors of the left premotor cortex, depending on the effector used in the heard action-related sentence. Interestingly, IFGOp was the only brain region activated by action language but not abstract language, independent of body part. This suggests that during listening to action-related sentences, the IFGOp of Broca’s area plays some more general role in processing action language. However, it should be noted that only partially overlapping activations were found for sentences describing mouth, hand, and leg actions in the left inferior parietal lobe, a region that is engaged in observing actions (e.g., Buccino et al., 2001). The authors concluded that listening to action-related sentences involving different effectors activates a left-lateralized fronto-parieto-temporal system that largely overlaps with the network activated during action execution and action observation.

Some evidence suggests that not only reading action words or listening to action-related sentences activates motor areas, but so does listening to sounds associated with actions. In a TMS study (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004), participants listened to sounds associated with bimanual actions (e.g., typing or tearing a paper), actions related to leg movement (e.g., walking), or control sounds (e.g., thunder). The results showed that during stimulation of the left hemisphere M1, sounds associated with bimanual actions produced greater motor corticospinal excitability than sounds of leg movements or control sounds. During stimulation of the right hemisphere M1, however, there was no difference in MEPs between manual and leg action sounds, suggesting a possible left hemisphere dominance in recognizing actions presented in the auditory modality. Thus, the available evidence reviewed so far is favorable to the account that a mirror mechanism plays a role in understanding the meaning of actions during reading word-actions (Hauk et al., 2004), action-related sentences (Tettamanti et al., 2005), and listening to action sounds (Aziz-Zadeh et al., 2004).

Nonetheless, one gap in our knowledge at present is the demonstration of a causal link between motor cortical activations and comprehension, i.e., the degree to which motor cortical activation during action language processing is necessary for comprehension. Certainly, the motor cortex plays a role in representing the meaning of action-related words and sentences. Nevertheless, although we have demonstration that understanding these words and sentences modulates the motor system (e.g., Buccino et al., 2005), we do not yet have demonstration that the motor system modulates the understanding of these words and sentences. Thus, while we can conclude with confidence that the motor cortex plays a role in representing the meaning of action-related language, we cannot yet absolutely characterize this role nor quantify its importance.

Motor imagery and the motor system

The accumulated data thus suggest that the motor regions involved in executing an action are active when a reader or hearer processes language about that action. Some researchers who believe that this motor cortex activity plays an integral role in comprehension propose a simulation account of the mechanism. One possible way of simulating action is to perform motor imagery, and there are several types of such imagery involving different brain networks (Solodkin, Hlustik, Chen, & Small, 2004). According to Gallese and Lakoff (2005), imagining the performance of an action and understanding the meaning of an action verb should be associated with the same neural activation. Willems, Toni, Hagoort, and Casasanto (2010) used fMRI to investigate this hypothesis with respect to action verbs. Neural activity was measured while subjects performed kinetic motor imagery of specific actions and an action-verb understanding task. In the imagery task, subjects had to explicitly imagine themselves performing the action verbs, which were either manual (e.g., "to throw") or nonmanual (e.g., "to kneel"). In the understanding task, subjects had to perform a lexical decision task to the written verbs. For each task, analysis was performed of areas more active for manual actions compared to nonmanual actions. There were no brain areas showing activity for both the imagery comparison and the language comparison. These results indicate that imagery may be a process distinct from understanding action verbs: whereas mental imagery is an effortful and explicit process, language understanding is fast and effortless. Furthermore, these results point to a double dissociation in motor areas between motor imagery and understanding of action verbs.

Summary

Speech, co-speech hand gestures, and emblems are all different ways to communicate and convey meaning: speech syllables are basic units from which words are composed, co-speech hand gestures are meaningful hand movements, contributing to the message the speaker wants to convey, and emblems are used to convey meaning independently of speech. Syllables and manual gestures require mouth and hand movements, respectively, and their use in communication involves an interaction between the "sender" (the speaker) of a message and its "receiver" (the hearer). The present chapter reviewed studies suggesting that the motor system may enhance language understanding when observing mouth and hand movements by representing the intended gesture within the motor system.

Furthermore, the motor system appears to play an important role in the understanding of action words, independently of the presence of observable lip and mouth movements. We have reviewed findings that may indicate a specific functional connection between motor and language networks of the human cerebral cortex. The macaque mirror neuron system has been suggested as a possible neural substrate in humans to account for the common brain regions that are activated not only during the perception of syllables, co-speech hand gestures, and emblems, but also in the motor aspects of performing the same communication acts. It is also possible that a human mirror mechanism plays a role in understanding the meaning of action words during reading and listening to action sounds. In other words, the involvement of motor regions in both perception and production of communicative actions could be based on activity in the mirror neurons of the frontal and parietal lobes, which play a role in both action execution and action observation. Future studies should unravel the more precise relation between action perception and action execution in humans and the mechanisms underlying their interaction in processing language.

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