Spoken language and arm gestures are controlled by the same motor control system

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Spoken language and arm gestures are controlled by the same motor control system

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Arm movements can influence language comprehension much as semantics can influence arm movement planning. Arm movement itself can be used as a linguistic signal. We reviewed neurophysiological and behavioural evidence that manual gestures and vocal language share the same control system. Studies of primate premotor cortex and, in particular, of the so-called "mirror system", including humans, suggest the existence of a dual hand/mouth motor command system involved in ingestion activities. This may be the platform on which a combined manual and vocal communication system was constructed. In humans, speech is typically accompanied by manual gesture, speech production itself is influenced by executing or observing transitive hand actions, and manual actions play an important role in the development of speech, from the babbling stage onwards. Behavioural data also show reciprocal influence between word and symbolic gestures. Neuroimaging and repetitive transcranial magnetic stimulation (rTMS) data suggest that the system governing both speech and gesture is located in Broca's area. In general, the presented data support the hypothesis that the hand motor-control system is involved in higher order cognition.

Keywords: Broca's area; Gesture; Hand and mouth kinematics; Mirror system; Spoken language; Voice spectra.

There is strong empirical evidence for the involvement of the motor-control system in supporting higher order cognition such as language comprehension. Action-grounded cognition treats motor control in terms of affordance processing. Since affordances—that is, the perceived availability of objects for certain kinds of interaction—are interpretations of the environment based on activations of motor patterns, this opens the possibility that the motor control system is also a primitive meaning processor. This would offer one explanation for how it is even possible for leverage motor control to support and constrain higher order processes like language comprehension and production. In support of this idea, behavioural experiments have shown that sentence comprehension is affected by arm motor responses (Glenberg & Kaschak, 2002; Zwaan & Taylor, 2006). On the other hand, even semantics can influence movement planning (Fischer, 2003; Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Gentilucci & Gangitano,

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1998; Glover, Rosenbaum, Graham, & Dixon, 2004). Above all, arm movement itself can be a communication signal and, more generally, a term of language different from speech. Indeed, the sign languages of the deaf are entirely manual and facial, but display most, if not all, of the essential linguistic properties of spoken language (Emmorey, 2002; Neidle, Kegl, MacLaughlin, Bahan, & Lee, 2000; Stokoe, 1960). On the one hand, signs are fundamentally different from iconic or indexical everyday gestures, which operate independently of any linguistic function. On the other hand, they can be considered similar to another set of gestures executed in everyday life, which are symbolic (Ekman & Friesen, 1972; Kendon, 1983; Krauss & Hadar, 2000; McNeill, 2000; Ricci Bitti & Poggi, 1991). Symbolic gestures are produced in every culture, although to different extents and with different typologies. For some types of gesture, execution is frequently associated with speech production (see Goldin-Meadow, 1999; McNeill, 1992, 2000). For example, the speaker pronounces words while she or he executes gestures expressing the same meaning as the word. Consider expressing approbation. While pronouncing "OK", one often forms a circle with the forefinger and thumb in contact at their tips, while the rest of the fingers extend outward.

There are two competing views of the relationship between gesture and speech. The first posits that gesture and speech are separate communication systems (Hadar, Wenkert-Olenik, Krauss, & Soroker, 1998; Krauss & Hadar, 1999; Levelt, Richardson, & La Heij, 1985). According to this view, gesture functions as an auxiliary support when verbal expression is temporally disrupted or word retrieval is difficult. The second view (McNeill, 1992) posits that gesture and speech form a single system of communication, because they are linked to the same thought processes even if the expression modality differs. We review neurophysiological and behavioural data in order to determine which of the two points of view is correct and more generally whether language expressed either by words or by gestures is controlled by systems that were primarily involved in the control of arm movements. This could support the theory that the motor control system is a primitive meaning processor, according to the action-grounded cognition theory.

Neurophysiological data in monkey premotor cortex

In humans speech and gesture seem, at first glance, to be controlled by separate, though adjacent, systems. Indeed, Brodmann's area (BA) 44, a part of Broca's area, is involved in encoding phonological representations in terms of mouth articulation gestures (Demonet et al., 1992; Paulesu, Frith, & Frackowiak, 1993; Zatorre, Evans, Meyer, & Gjedde, 1992). It is separate from, but adjacent to premotor BA 6, which is well known to code arm and face movements (Figure 1b). On cytoarchitectonics and functional bases Rizzolatti and Arbib (1998) proposed that the homologue of the monkey premotor area F5 is BA 44, whereas the homologue of the monkey premotor area F4 is the human lateral BA 6 (Figure 1a). Area F5 is involved in controlling hand and mouth movements, and, in particular, two classes of neurons may be the base on which the system integrating arm gestures with speech was constructed.

The first class of F5 neurons, called "mirror" neurons, becomes active when the animal executes a hand action and when it observes the same action performed by another individual. According to Rizzolatti and colleagues (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) the mirror system can be involved in understanding the meaning of the action by matching observation with execution. It might therefore have provided the link between actor and observer that also exists between the sender and receiver of messages. Since this system is able to receive (and to understand) as well as send messages with the arm, Rizzolatti and Arbib (1998) proposed that it was used as an initial communication system in language evolution.

Mirror neurons in monkey have also been recorded in the rostral part of the inferior parietal
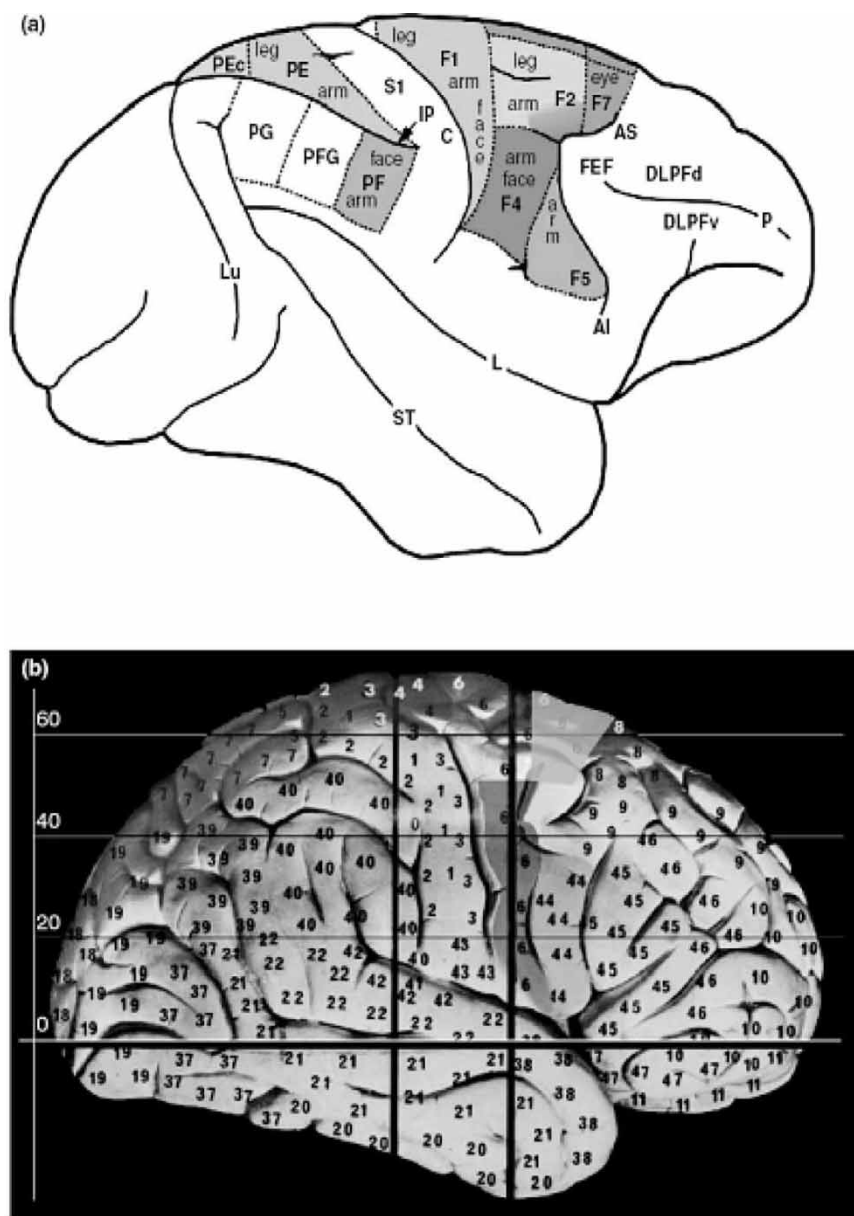
Figure 1. *Lateral view of the (a) monkey and (b) human cortex. According to Rizzolatti and Arbib (1998), Brodmann's area 44 corresponds phylogenetically to the monkey premotor area F5, whereas lateral Brodmann's area 6 corresponds to the monkey premotor area F4.*

lobule (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002), and neurons activated only by the observation of movements of different body effectors were recorded in the superior temporal sulcus

(STS) region (Perrett, Mistlin, Harries, & Chitty, 1990). In humans the observation of actions done by others especially activates the rostral part of the inferior parietal lobule and

the lower part of the precentral gyrus as well as the posterior part of the inferior frontal gyrus (IFG; Buccino et al., 2001). The observation of transitive actions (i.e., directed to an object) and intransitive actions (i.e., internally generated) activates the frontal regions, whereas the observation of only transitive actions activates the parietal regions (Buccino et al., 2001). In other words, a larger representation of arm movements including arm gestures is coded in the human mirror system located in the frontal regions (see below). Conversely, a more restricted representation of hand movements alone, including transitive action, is coded in the frontal mirror system in monkeys.

The second class of neurons commands grasp actions with the hand and the mouth (Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino, & Matelli, 1988). A typical neuron of this class discharges when the animal grasps a piece of food with its mouth or when the animal grasps the same piece of food with the hand contralateral or ipsilateral to the recorded cortical side. Frequently, the discharge of this class of neurons is selective for the specific type of grasp used (for example, a neuron discharges when a precision grasp, but not a power grasp, is used), and it is even elicited by the visual presentation of a graspable object, provided that its size is congruent with the type of grasp coded by the neuron. Fischer, Prinz, and Lotz (2008 this issue) showed that when presented with a hand with a particular grasp posture, human observers spontaneously shifted their attention to simultaneously presented objects whose size was congruent with the grasp posture. In other words, using the mirror system the observer could implicitly imitate the posture of the presented hand and, consequently to activation of a similar class of neurons present also in humans, was attracted towards the congruent object with the implicit intention to grasp it. Rizzolatti and colleagues (1988) proposed that these neurons are involved in coding the aim of the grasp action—that is, to take possession of an object. From a functional point of view, these neurons can be involved in planning

successive grasp actions. For example, they can command the grasp of an object with the hand while preparing the mouth to grasp the same object with the mouth. From an evolutionary point of view, this circuit of commands to both hand and mouth might have been used by humans to transfer an initial gesture communication system from hand to mouth. Indeed, many authors have proposed that language evolved from manual gestures rather than from vocalizations, since manual actions can provide more obvious iconic links with objects and actions in the physical world (e.g., Arbib, 2005; Armstrong, 1999; Armstrong, Stokoe, & Wilcox, 1995; Corballis, 1992, 2002; Donald, 1991; Gentilucci & Corballis, 2006; Givòn, 1995; Hewes, 1973; Rizzolatti & Arbib, 1998; Ruben, 2005).

Observation/execution of transitive actions and speech

Humans, by using the mirror system, might understand action meaning by covertly imitating the observed actions and initially might have used this gestural repertoire to exchange information about food and predatory activities. Using the hand−mouth dual-command system, this arm gestural repertoire could be shared and transferred to the mouth when the phonatory organs were completely developed (Gentilucci & Corballis, 2006).

This sharing mechanism is observable in humans. Observing and executing the grasp of small and large objects influence the simultaneous pronunciation of syllables (Gentilucci, 2003; Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001; Gentilucci, Stefanini, Roy, & Santunione, 2004b) and in particular the vocal spectra of the vowels. The vocal spectra are characterized by typical frequencies called formants: Formant 1 (F1) and Formant 2 (F2) define each vowel from an acoustical point of view (Leoni & Maturi, 2002). The experiments by Gentilucci and colleagues showed that, when observing the grasping of large as compared to small objects the lip opening and F1 of the voice spectra were greater,
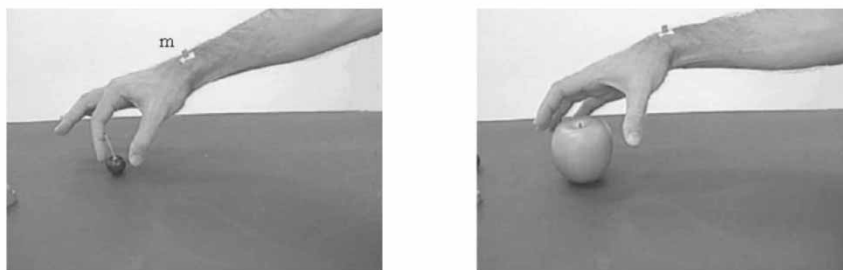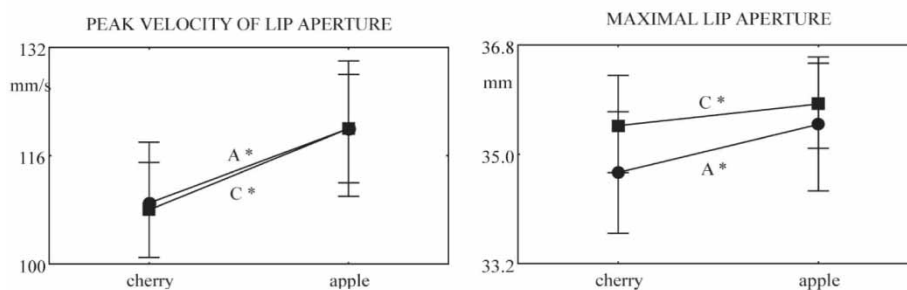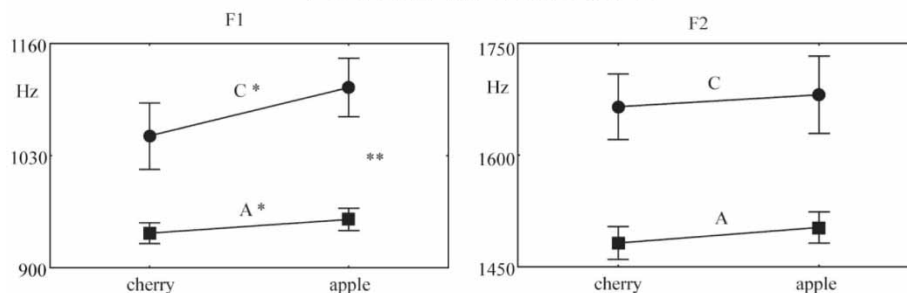
Figure 2. *Voice spectra and lip kinematics parameters when observing grasping actions and pronouncing the syllable BA /ba/. Adults (A) and children (C) observed the grasp of a cherry (small fruit) and of an apple (large fruit) and pronounced the syllable BA when the actor touched the fruit. Middle and lower panels: mean values of lip kinematics and voice spectra parameters, respectively. Squares and circles refer to the values recorded in adults and children, respectively. F1: Formant 1; F2: Formant 2. Note the increase in Formant 1 (F1) when observing the grasp of the large fruit. It was more evident in children than in adults. Bars are standard errors. Asterisks indicate statistical significance.*

corresponding to variation in the actor's finger shaping during these grasp movements (Gentilucci et al., 2004b; see also Figure 2). Comparable effects were observed when the same actions were executed while pronouncing syllables (Gentilucci et al., 2001).

The observation of the action of bringing large and small fruits to the mouth affected the simultaneous pronunciation of syllables. The observation of the action guided by the large fruit induced an increase in F2 in the voice spectra in comparison with the observation of the action

BRINGING-TO-THE-MOUTH OBSERVATION

A

B

C
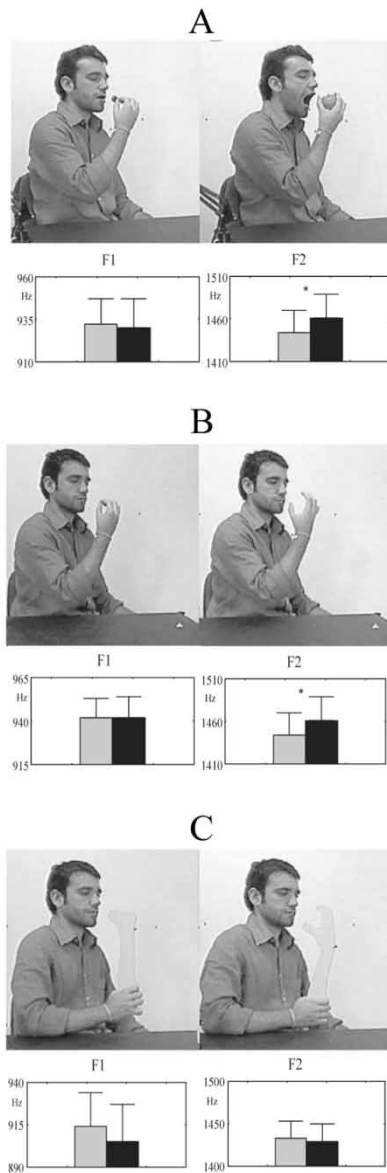
Figure 3. *Mean values of voice parameters when pronouncing the syllable BA /ba/ and simultaneously observing (A) the act of bringing a cherry (grey bars) or an apple (black bars) to the mouth, (B) a pantomime of the act, and (C) a pantomime 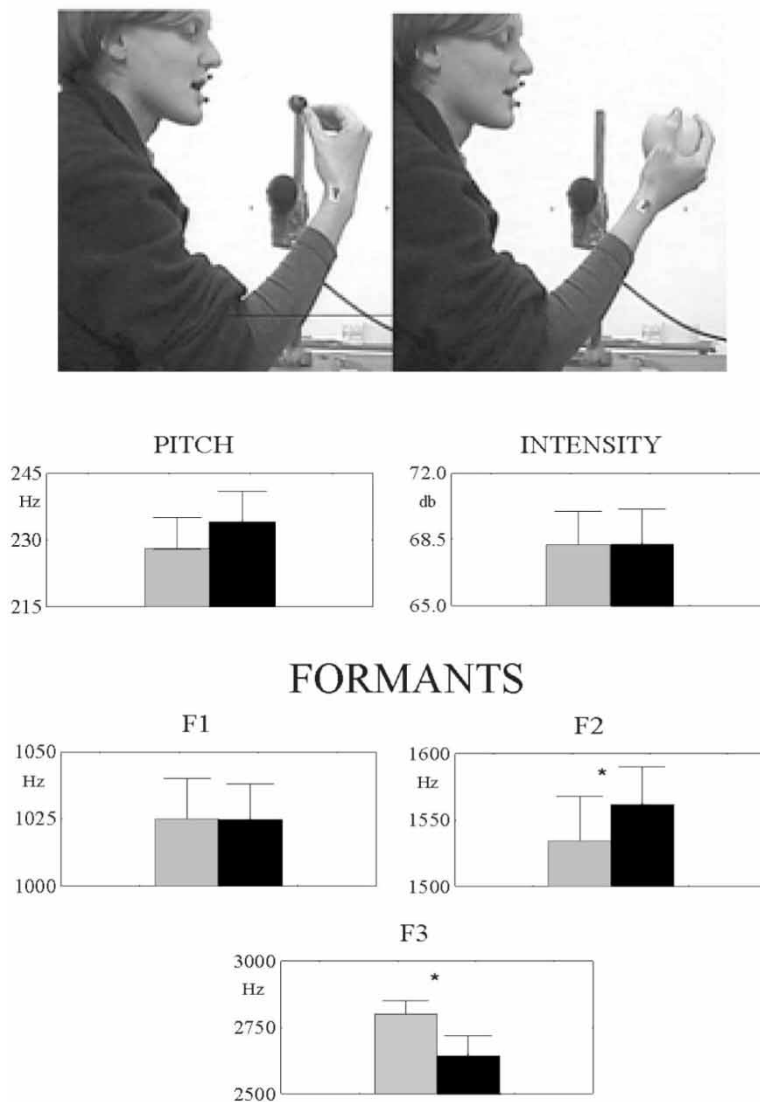of the act using a nonbiological hand. F1: Formant 1; F2: Formant 2. Note the increase in F2 (like when the act was executed, see Figure 4) in the conditions A and B. Bars are standard errors. Asterisks indicate statistical significance.*

guided by the small fruit (Gentilucci, Santunione, Roy, & Stefanini, 2004a; see also Figure 3A). The observation of the pantomime of the action affected F2 as much as the observation of the action did (Figure 3B). In other words, neither the presence of the fruit nor the opening of the mouth was responsible for the effect. The same execution of bringing fruits of different sizes to the mouth modified F2 of syllables pronounced simultaneously with action execution (Gentilucci et al., 2004a; see also Figure 4). This effect was selective for speech. In fact, no increase in F2 was observed when a vocalization unrelated to the native language of the participants was emitted simultaneously with bringing-to-the-mouth execution (Gentilucci et al., 2004a). In sum, the action observation affected the voice much as the action execution did.

The execution/observation of the grasp with the hand activated a command to grasp with the mouth, which modified the posture of the anterior mouth articulation during syllable pronunciation, according to the hand shape used to grasp the object. This, in turn, affected F1 in the voice spectra (Gentilucci, 2003; Gentilucci et al., 2001; Gentilucci et al., 2004b), which depends on mouth aperture (Leoni & Maturi, 2002). Conversely, the execution/observation of the bringing-to-the-mouth action probably induced an internal mouth movement (in order to prepare actions such as chewing or swallowing), which affected tongue displacement according to the size of the object being brought to the mouth. This, in turn, modified speech F2 (Gentilucci et al., 2004a, 2004b), which depends on tongue position (Leoni & Maturi, 2002). On the basis of these results we proposed that communication signals related to the meaning of actions (e.g., taking possession of an object by grasping, or bringing an edible object to the mouth) might be associated with the activity of particular articulatory organs of the mouth co-opted for speaking (Gentilucci & Corballis, 2006).

The matching system of observation/execution of actions directed to targets was found to be more effective in children than in adults (Gentilucci et al., 2004b; see also Figure 2). On the basis of

Figure 4. *Voice parameters when bringing a fruit to the mouth and pronouncing the syllable BA /ba/. Participants brought a cherry (small fruit) or an apple (large fruit) to the mouth, and when it was near the mouth they pronounced BA. Middle and lower panels show mean values of voice parameters when pronouncing BA during bringing to the mouth the cherry (grey bars) and the apple (black bars). F1: Formant 1; F2: Formant 2. Note the increase in F2 when bringing the apple to the mouth. Bars are standard errors. Asterisks indicate statistical significance.*

these results, Gentilucci and colleagues proposed that it could be involved in children's language acquisition (Gentilucci et al., 2004b). This is in accordance with the notion that a strict relationship exists between early speech development in children and several aspects of manual activity, such as communicative and symbolic gestures (Bates & Dick, 2002; Volterra, Caselli, Capirci, & Pizzuto, 2005). For example, canonical babbling in children aged from 6–8 months is accompanied by rhythmic hand movements (Masataka, 2001). Manual gestures predate the early development of speech in children and predict later success even up to the two-word stage (Iverson & Goldin-Meadow, 2005). Word comprehension in children between 8 and 10 months and word productions between 11 and 13 months are accompanied by deictic and declarative gestures, respectively (Bates & Snyder, 1987; Volterra, Bates, Benigni, Bretherton, & Campioni, 1979).

Relations between symbolic gestures and words

We hypothesized that the same system, which relates transitive actions to phonemes (i.e., mouth articulation postures) is also involved in the integration of symbolic gestures with words. According to this point of view, gesture and word share the same communication system. If this is true, meaningful but not meaningless gestures should affect words when the two communication signals are simultaneously emitted. Conversely, words but not pseudowords should affect gestures. Bernardis and Gentilucci (2006) presented subjects with the words CIAO, NO, and STOP printed on a PC display. The viewers responded to the stimuli with different modalities: repeating aloud the word, executing the corresponding gesture, repeating aloud the word, and executing the gesture simultaneously. In two further control conditions they pronounced the word and executed a meaningless gesture executed with the upper arm or pronounced a pseudoword (LAO) and executed the symbolic gesture. F2 and pitch in the word voice spectra increased

with the simultaneous execution of the corresponding arm gesture as compared with the sole word pronunciation. This effect was not observed when the gesture was meaningless. In order to explain the functional meaning of the increase in F2, Bernardis and Gentilucci (2006) argued that placing the tongue further forward in the mouth induces an increase in F2 (Leoni & Maturi, 2002). In nonhumans, both mouth aperture and tongue protrusion accompany gestures typical of approaching relationships (for example, lip-smacking and protruding lips that precede grooming actions among monkeys; Van Hooff, 1962, 1967). When a visible interlocutor emitting communicative signals is observed, the responder is induced to a more direct relation with her or him. Consequently, the responder may configure the mouth articulation in such a way that reflects his intention to interact directly with other individuals. In other words, tongue-brought-forward-in-the-mouth/increase-in-F2 is related to the social intention coded by the communicative signal.

In the experiment by Bernardis and Gentilucci (2006) the three gestures differed for both hand configuration and hand kinematics. This led the authors to suggest that these parameters are functionally related to the gesture meaning. The execution of the three gestures slowed down when they were executed simultaneously with word pronunciation in comparison with the execution of the gesture alone. Comparable effects were not observed when the gesture was executed simultaneously with pronunciation of the pseudoword. In accordance with these results, Nazir and colleagues (Boulenger et al., 2006) found that the processing of words, but not pseudowords, can interfere with arm movement execution when the two tasks are simultaneously executed. Summing up, we hypothesized that the gesture controller transmits aspects of the gesture, such as the intention to interact directly with the interlocutor (Bernardis & Gentilucci, 2006; Gentilucci, Bernardis, Crisi, & Dalla Volta, 2006) to the controller of the mouth pronouncing the corresponding words. This induces an increase in specific

parameters of the vocal spectra. The mouth controller, having received the signal, sends back a block command to the arm controller. The effects found in the experiment by Bernardis and Gentilucci (2006) could not be explained by subvocal verbalization of the gesture, which reinforced word pronunciation. If this were the case, a generalized increase in all parameters of the voice spectra should be observed. In fact, this did not occur. In sum, part of the gesture meaning might have been transferred to the word.

In a second experiment Bernardis and Gentilucci (2006) studied the verbal responses to communication signals presented with different modalities. The aim of the experiment was to determine whether the effects of observing/listening to (i.e., interpreting) communication signals follow the same rules as those for the execution. Participants were presented with a word (CIAO, NO, STOP) printed on a PC display, with a video clip showing an actor pronouncing the word, or executing the corresponding gesture or emitting simultaneously the two communication signals. They responded to the stimulus by pronouncing the corresponding word. The observation of the actor pronouncing the word or executing the gesture induced an increase in F2 in the word voice spectra in comparison with word reading. A further increase was observed when responding to the presentation of both of the two communication signals (Figure 5). Again the observation of communicative gestures like that of transitive actions induced the same effects as the execution did.

The authors (Bernardis & Gentilucci, 2006) suggested that the observer, when verbally responding to the presented gestures, automatically and covertly imitated them. The command of imitation was also sent to the mouth articulation posture inducing modification in voice spectra and, in particular, in F2. Again we interpreted that the intention to interact directly with other individuals—that is, the social intention coded by the gesture—was transferred to the mouth articulations involved in speech (Bernardis & Gentilucci, 2006; Gentilucci et al., 2006).
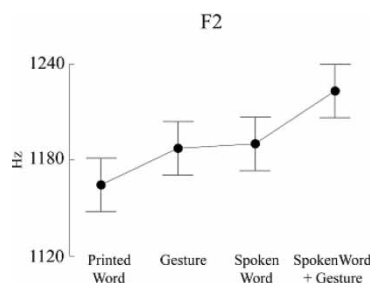
Figure 5. *Mean values of Formant 2 (F2) when responding verbally to the observation of communication signals emitted with different modalities. The presentation modalities were as follows: printed word; a video clip showing an actress executing a gesture (gesture); pronouncing the word (spoken word); executing the gesture and simultaneously pronouncing the word (spoken word + gesture). The participants responded pronouncing the word of the same meaning. Bars are standard errors.*

Gestures interact with words in Broca's area

Previous neuroimaging studies have found activation of Broca's area when representing meaningful arm gestures (Buccino et al., 2001; Decety et al., 1997; Gallagher & Frith, 2004; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Costes, & Decety, 1998) and of left ventral premotor area when observing meaningless gestures in order to imitate them (Grèzes, Costes, & Decety, 1999). Motor imagery of hand movements includes activation of both Broca's and left premotor ventral areas (Gerardin et al., 2000; Grafton et al., 1996; Hanakawa et al., 2003; Kuhtz-Buschbeck et al., 2003; Parsons et al., 1995), probably extending to the motor area (Porro et al., 1996). On the other hand, Broca's area is involved in encoding phonological representations in terms of mouth articulation gestures (Demonet et al., 1992; Paulesu et al., 1993; Zatorre et al., 1992). On the basis of these neuroimaging data we hypothesized that Broca's area is involved in transferring aspects of activated representations of arm gestures into mouth articulation gestures. These aspects may concern the goal (Buccino et al., 2001; Buccino et al., 2004) and/or the intention (Iacoboni et al., 2005) of the gesture. The transferring process of these aspects should be blocked by inactivation of the
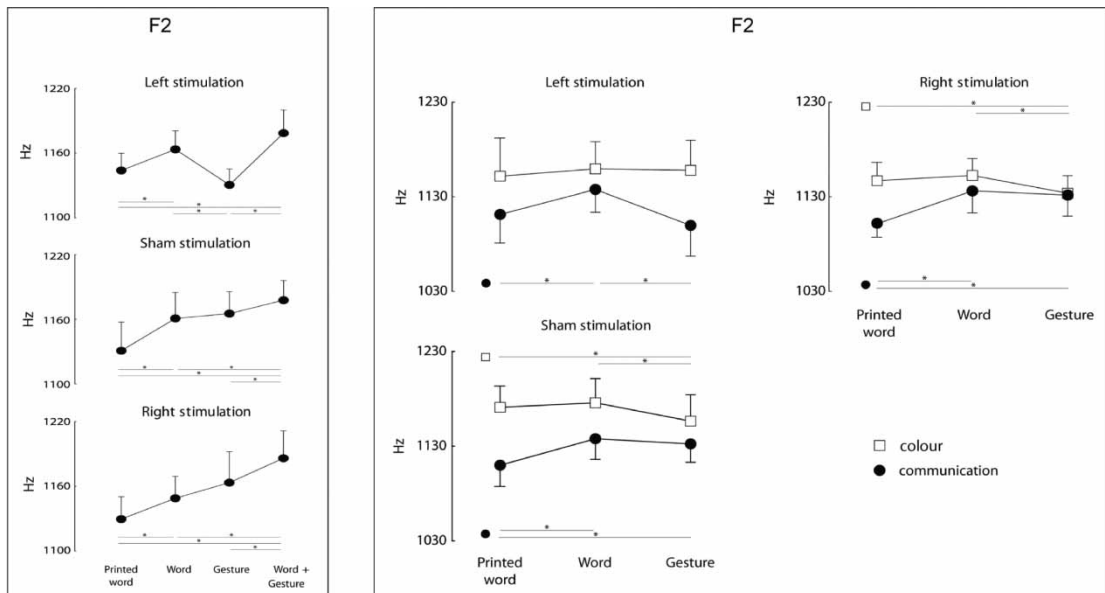
Figure 6. *Variation in mean values of Formant 2 (F2) after repetitive transcranial magnetic stimulation (rTMS) of Broca's area, of the corresponding region of the frontal right cortex, and after sham stimulation of the left cortex (Broca's area). The participants responded verbally to communication signals presented with different modalities (circles) and to colour signals in a control experiment (right panel, squares). The presentation modalities of the communication signals were as follows: printed word; a video clip showing an actress executing a gesture (gesture); pronouncing the word (spoken word); executing the gesture and simultaneously pronouncing the word (spoken word + gesture). The presentation modalities of the colour signals were the following: printed word; a video clip showing an actress pronouncing the names of colours; or executing communication gestures with a coloured spot on the hand palm. The participants responded to the communication and colour signals pronouncing, respectively, the corresponding communication word and the colour name. Bars are standard errors. Asterisks indicate statistical significance.*

area. To this end, Gentilucci and colleagues (Gentilucci et al., 2006) induced a brief inactivation of Broca's area by using the technique of repetitive transcranial magnetic stimulation (rTMS) at low frequency (1 Hz) in subjects performing the task of verbal responses to communicative signals previously described (Bernardis & Gentilucci, 2006). They stimulated Broca's area at 1 Hz—that is, that region of the left frontal cortex where a speech arrest was induced by stimulation at high frequency (5 Hz)—and the symmetrical sites of the right cortex, and performed a sham (i.e., ineffective) stimulation of the sites on the left cortex. Figure 6 shows the results of the experiment. After sham and right stimulations F2 increased when subjects were verbally responding to the actress pronouncing the word or executing the gesture as compared to word reading.

There was a further increase when subjects were responding to the actress pronouncing the word and executing the gesture simultaneously. These results were in agreement with the previous data by Bernardis and Gentilucci (2006). In contrast, the effects of gesture observation on F2 were not observed with left stimulation.

In a control experiment the authors demonstrated that the stimulation of Broca's area produced different effects when responding to communicative and noncommunicative signals. They presented the same communicative signals as those in the previous experiment (i.e., CIAO, NO, and STOP) as well as colour signals. The colours were yellow, red, and pink. The colour presentations were the following: printed words of the colours—that is, GIALLO (yellow), ROSA (pink), and ROSSO (red); video clips showing

the actress pronouncing the names of the colours; and video clips in which the actress executed the communicative gestures (i.e., CIAO, NO, and STOP), but with coloured spots on the palm of her hand. The subjects responded to the communicative signals pronouncing the corresponding words and responded to the colour signals pronouncing the names of the colours. A different pattern was observed when analysing the responses to the colour presentations as compared to the responses to the presentations of communicative signals (Figure 6, right panel). No difference in F2 was observed when reading colour words and when responding to the actress pronouncing names of colours after the sham, right, and left stimulations. Moreover, F2 decreased when pronouncing the name of the colour presented on the gesturing hand after sham and right stimulations. The left stimulation removed this effect. We explain this result as follows: Observation of the gesture automatically activated pronunciation of the corresponding word, which interfered with the verbal response to the colour. This occurred after sham and right stimulations, but not after left stimulation. Again, Broca's area seems to be involved in transferring aspects (i.e., the social intention) of the gesture in parameters of word voice spectra. The finding that only aspects of the gestures were transferred to the semantically corresponding words suggests that gesture and word can share also other neural substrates (for a review, see Gentilucci et al., 2006).

CONCLUSIONS

Neurophysiological and behavioural data are in favour of the hypothesis that language is strictly related to arm motor control according to the action-grounded cognition theory. Indeed, symbolic gestures and speech are controlled by the same communication system, which was primarily involved in arm motor control. This system is able to emit the same communicative signal using different presentation modalities—that is, as either words or gestures—and to merge the two signals into a single signal. The merged signal acquires a wider meaning if compared with the meaning of the word and gesture separately emitted.

An open question concerns the relationship between the system we have described, which merges aspects of gesture and speech at the level of arm and mouth articulation modifications, and the system involved in semantically assembling speech and gesture when the two forms of communication are intermingled (see Kendon, 1972, 1980, 2004; McNeill, 1992, 2000). Indeed, during conversation gesture and speech frequently convey different information, and even when the two signals are semantically similar, the gesture specifies aspects of information that the word is unable to provide (for example, see Goldin-Meadow, 2005; Kendon, 2004). Kendon (2004) proposed the existence of a system that temporally couples gesture and speech. Indeed, he observed precise temporization between vocal and gestural signals. In sum, the latter data suggest a different type of integration by which word and gesture do not semantically interact with each other at the level of emission, but are assembled in a precise temporal order in order to better specify the meaning of the sentence. What is common to the two systems is the fact that arm movements and speech are integrated by the same control system in order to produce a unique message.

REFERENCES

Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences. 28*, 105–168.

Armstrong, D. F. (1999). *Original signs: Gesture, sign, and the source of language.* Washington, DC: Gallaudet University Press.

Armstrong, D. F., Stokoe, W. C., & Wilcox, S. E. (1995). *Gesture and the nature of language.* Cambridge, MA: Cambridge University Press.

Bates, E., & Dick, F. (2002). Language, gesture, and the developing brain. *Developmental Psychobiology, 40*, 293–310.

Bates, E., & Snyder, L. S. (1987). The cognitive hypothesis in language development. In E. Ina, C. Uzgiris, & E. J. McVicker Hunt (Eds.), *Infant performance and experience: New findings with the ordinal scales* (pp. 168–204). Urbana, IL: University of Illinois Press.

Bernardis, P., & Gentilucci, M. (2006). Speech and gesture share the same communication system. *Neuropsychologia*, *44*, 178–190.

Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience*, *18*, 1607–1615.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.

Corballis, M. C. (1992). On the evolution of language and generativity. *Cognition*, *44*, 197–226.

Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.

Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777.

Demonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., et al. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, *115*, 1753–1768.

Donald, M. (1991). *Origins of the modern mind*. Cambridge, MA: Harvard University Press.

Ekman, P., & Friesen, W. (1972). Hand movements. *Journal of Communication*, *12*, 353–374.

Emmorey, K. (2002). *Language, cognition, and brain: Insights from sign language research*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Fischer, M. H. (2003). Spatial representations in number processing: Evidence from a pointing task. *Visual Cognition*, *10*, 493–508.

Fischer, M. H., Prinz, J., & Lotz, K. (2008). Grasp cueing shows obligatory attention to action goals.

Quarterly Journal of Experimental Psychology, *61*, 860–868.

Gallagher, H. L., & Frith, C. F. (2004). Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. *Neuropsychologia*, *42*, 1725–1736.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (Eds.), Common mechanisms in perception and action. *Attention and performance XIX: Action perception and imitation* (pp. 334–355). Oxford, UK: Oxford University Press.

Gentilucci, M. (2003). Grasp observation influences speech production. *European Journal of Neuroscience*, *17*, 179–184.

Gentilucci, M., Benuzzi, F., Bertolani, L., Daprati, E., & Gangitano, M. (2000). Language and motor control. *Experimental Brain Research*, *133*, 468–490.

Gentilucci, M., Benuzzi, F., Gangitano, M., & Grimaldi, S. (2001). Grasp with hand and mouth: A kinematic study on healthy subjects. *Journal of Neurophysiology*, *86*, 1685–1699.

Gentilucci, M., Bernardis, P., Crisi, G., & Dalla Volta, R. (2006). Repetitive transcranial magnetic stimulation of Broca's area affects verbal responses to gesture observation. *Journal of Cognitive Neuroscience*, *18*, 1059–1074.

Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews*, *30*, 949–960.

Gentilucci, M., & Gangitano, M. (1998). Influence of automatic word reading on motor control. *European Journal of Neuroscience*, *10*, 752–756.

Gentilucci, M., Santunione, P., Roy, A. C., & Stefanini, S. (2004a). Execution and observation of bringing a fruit to the mouth affect syllable pronunciation. *European Journal of Neuroscience*, *19*, 190–202.

Gentilucci, M., Stefanini, S., Roy, A. C., & Santunione, P. (2004b). Action observation and speech production: Study on children and adults. *Neuropsychologia*, *42*, 1554–1567.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., et al. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, *10*, 1093–1104.

Givòn, T. (1995). *Functionalism and grammar.* Philadelphia: Benjamins.

Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review, 3,* 558–565.

Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research, 153,* 103–108.

Goldin-Meadow, S. (1999). The role of gesture in communication and thinking. *Trends in Cognitive Sciences, 3,* 419–429.

Goldin-Meadow, S. (2005). The two faces of gesture: Language and thought. *Gesture, 5,* 241–257.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research, 112,* 103–111.

Grèzes, J., Costes, N., & Decety, J. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology, 15,* 553–582.

Grèzes, J., Costes, N., & Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain, 122,* 1875–1887.

Hadar, U. D., Wenkert-Olenik, R. K., & Soroker, N. (1998). Gesture and the processing of speech: Neuropsychological evidence. *Brain and Language, 62,* 107–126.

Hanakawa, T., Immisch, I., Toma, K.,. Dimyan, M. A, Van Gelderen, P., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology, 89,* 989–1002.

Hewes, G. W. (1973). Primate communication and the gestural origins of language. *Current Anthropology, 14,* 5–24.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology, 3,* 529–535.

Iverson, J. M., & Goldin-Meadow, S. (2005). Gesture paves the way for language development. *Psychological Science, 16,* 367–371.

Kendon, A. (1972). Some relationships between body motion and speech. An analysis of an example. In A. Siegman & B. Pope (Eds.), *Studies in dyadic communication* (pp. 177–210). Elmsford, NY: Pergamon Press.

Kendon, A. (1980). Gesticulation and speech: Two aspects of the process of utterance. In M. R. Key (Ed.), *The relationship of verbal and nonverbal communication* (pp. 207–227). The Hague, The Netherlands: Mouton and Co.

Kendon, A. (1983). Gesture and speech: How they interact. In J. M. Wiemann & R. P. Harrison (Eds.), *Nonverbal interaction* (pp. 13–43). Beverly Hills, CA: Sage Publications.

Kendon, A. (2004). *Gesture: Visible action as utterance.* New York: Cambridge University Press.

Krauss, R. M., & Hadar, U. (1999). The role of speech-related arm/hand gestures in word retrieval. In R. Campbell & L. Messing (Eds.), *Gesture, speech, and sign* (pp. 93–116). Oxford, UK: Oxford University Press.

Krauss, R. M., & Hadar, U. (2000). Lexical gestures and lexical access: A process model. In D. McNeill (Ed.), *Language and gesture* (pp. 261–283). Cambridge, UK: Cambridge University Press.

Kuhtz-Buschbeck, J. P., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., & Jansen, O. (2003). Effector-independent representations of simple and complex imagined finger movements: A combined fMRI and TMS study. *European Journal of Neuroscience, 18,* 3375–3387.

Leoni, F. A., & Maturi, P. (2002). *Manuale di fonetica* [Handbook of phonetics]. Rome: Carocci.

Levelt, W. J., Richardson, G., & La Heij, W. (1985). Pointing and voicing in deictic expressions. *Journal of Memory and Language, 24,* 133–164.

Masataka, N. (2001). Why early linguistic milestones are delayed in children with Williams syndrome: Late onset of hand banging as a possible rate-limiting constraint on the emergence of canonical babbling. *Developmental Science, 4,* 158–164.

McNeill, D. (1992). *Hand and mind: What gestures reveal about thought.* Chicago: University of Chicago Press.

McNeill, D. (2000). *Language and gesture.* Cambridge, UK: Cambridge University Press.

Neidle, C., Kegl, J., MacLaughlin, D., Bahan, B., & Lee, R. G. (2000). *The syntax of American Sign Language.* Cambridge, MA: MIT Press.

Parsons, L. M., Fox, P. T., Downs, J. H., Glass, T., Hirsch, T. B., Martin, C. C.,. et al. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature, 375,* 54–58.

Paulesu, E., Frith, C. D., & Frackowiak, R. (1993). The neural correlates of the verbal component of working memory. *Nature, 362,* 342–345.

Perrett, D. I., Mistlin, A. J., Harries, M. H., & Chitty, A. J. (1990). Understanding the visual appearance

and consequence of hand actions. In M. A. Goodale (Ed.), *Vision and action: The control of grasping* (pp. 163–242). Norwood, NJ: Ablex.

Porro, C. A., Francescano, M. P., Cettolo, V., Diamone, M. E., Baraldi, P., Zuiani, C., et al. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. *Journal of Neuroscience*, 16, 7688–7698.

Ricci Bitti, P. E., & Poggi, I. (1991). Symbolic nonverbal behavior: Talking through gestures. In R. Feldman & B. Rime (Eds.), *Fundamentals of nonverbal behavior* (pp. 433–457). New York: Cambridge University Press.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, 21, 188–194.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491–507.

Ruben, R. J. (2005). Sign language: Its history and contribution to the understanding of the biological nature of language. *Acta Oto-Laryngologica*, 125, 464–467.

Stokoe, W. C. (1960). *Sign language structure: An outline of the communicative systems of the American deaf.* Silver Spring, MD: Linstock Press.

Van Hooff, J. A. (1962). Facial expressions in higher primates. *Symposia of the Zoological Society of London*, 8, 97–125.

Van Hooff, J. A. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). London: Weidenfield & Nicolson.

Volterra, V., Bates, E., Benigni, L., Bretherton, I., & Campioni, L. (1979). First words in language and action: A qualitative look. In E. Bates (Ed.), *The emergence of symbols: Cognition and communication in infancy* (pp. 141–222). New York: Academic Press.

Volterra, V., Caselli, M. C., Capirci, O., & Pizzuto, E. (2005). Gesture and the emergence and development of language. In M. Tomasello & D. I. Slobin (Eds.), *Beyond nature–nurture: Essays in honor of Elizabeth Bates* (pp. 3–40). Mahwah, NJ: Lawrence Erlbaum Associates.

Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science*, 256, 846–849.

Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology: General*, 135, 1–11.