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Published in final edited form as:

Title: Inferior frontal oscillations reveal visuo-motor matching for actions and speech: evidence from human intracranial recordings.

Authors: Halje P, Seeck M, Blanke O, Ionta S

Journal: Neuropsychologia

Year: 2015 Dec

Volume: 79

Issue: Pt B

Pages: 206-14

DOI: 10.1016/j.neuropsychologia.2015.08.015

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Inferior frontal oscillations reveal visuo-motor matching for actions and speech: evidence from human intracranial recordings

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Abstract

The neural correspondence between the systems responsible for the execution and recognition of actions has been suggested both in humans and non-human primates. Apart from being a key region of this visuo-motor observation-execution matching (OEM) system, the human inferior frontal gyrus (IFG) is also important for speech production. The functional overlap of visuo-motor OEM and speech, together with the phylogenetic history of the IFG as a motor area, has led to the idea that speech function has evolved from pre-existing motor systems and to the hypothesis that an OEM system may exist also for speech. However, visuo-motor OEM and speech OEM have never been compared directly. We used electrocorticography to analyze oscillations recorded from intracranial electrodes in human fronto-parieto-temporal cortex during visuo-motor (executing or visually observing an action) and speech OEM tasks (verbally describing an action using the first or third person pronoun). The results show that neural activity related to visuo-motor OEM is widespread in the frontal, parietal, and temporal regions. Speech OEM also elicited widespread responses partly overlapping with visuo-motor OEM sites (bilaterally), including frontal, parietal, and temporal regions. Interestingly a more focal region, the inferior frontal gyrus (bilaterally), showed both visuo-motor OEM and speech OEM properties independent of orolingual speech-unrelated movements. Building on the methodological advantages in human invasive electrocorticography, the present findings provide highly precise spatial and temporal information to support the existence of a modality-independent action representation system in the human brain that is shared between systems for performing, interpreting and describing actions.

Keywords: movement, sensory, intracranial, mirror neuron system, imagery

Highlights

- Human electrocorticography of action-speech correspondence in inferior frontal gyrus
- Extensive neural networks show selective mirror-like properties for action and speech
- Multimodal representations of action and speech in fronto-temporo-parietal regions

Introduction

A neural population in the ventral premotor cortex of the macaque brain (area F5) labeled as “mirror neurons”, has important motor-visual-auditory properties, being characterized by similar firing patterns during the execution and observation of the same action (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Fogassi, & Gallese, 1996), as well as by listening to sounds of actions (Kohler, et al., 2002). Since the original description of the mirror system, the direct (even though partial) correspondence between the neural systems responsible for the recognition and execution of actions has been repeatedly supported by animal research (Coude, et al., 2014; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008). A similar observation-execution matching (OEM) system has been hypothesized also in humans (Blakemore & Decety, 2001), suggesting the existence of abstract and modality-independent action representations. Accordingly, electrocorticographic data showed the involvement of focally localized regions responding to observation and execution of action with comparable suppressions in the alpha band (Fecteau, et al., 2004; Tremblay, et al., 2004), encompassing the mu-rhythm as a sign of sensorimotor processing (Pineda, 2005). Conversely, a widespread set of cortical regions has been involved in visuo-motor mirror-like activity for observation and execution of actions in humans by behavioral (Brass, Bekkering, Wohlschlaeger, & Prinz, 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002), functional magnetic resonance imaging (Buccino, Lui, Canessa, Patteri, & Lagravinese, 2004; Decety, et al., 1997; Iacoboni, et al., 1999), scalp electroencephalography (Lepage & Theoret, 2006), single-cell recording (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010), transcranial magnetic stimulation (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000), and clinical studies (Frenkel-Toledo, Bentin, Perry, Liebermann, & Soroker, 2014; Mitra, Nizamie, Goyal, & Tikka, 2014; Nishitani, Avikainen, & Hari, 2004). The regions belonging to such a broad network for abstract representation of actions include the dorsal and ventral premotor cortex (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Wade & Hammond, 2015), superior and inferior parietal lobule (Buccino, et al., 2001; Gardner, Goulden, & Cross, 2015), angular gyrus (Davey, et al., 2015; Farrer, et al., 2008; Lui, et al., 2008), supramarginal gyrus (Abreu, et al., 2012; Pokorny, et al., 2015), and superior temporal sulcus (Alaerts, et al., 2015; see also Cattaneo & Rizzolatti, 2009). Based on this evidence, we hypothesized to find a widespread set of regions showing mu-rhythm

suppression during both observation and execution of actions, including temporal, parietal and frontal areas.

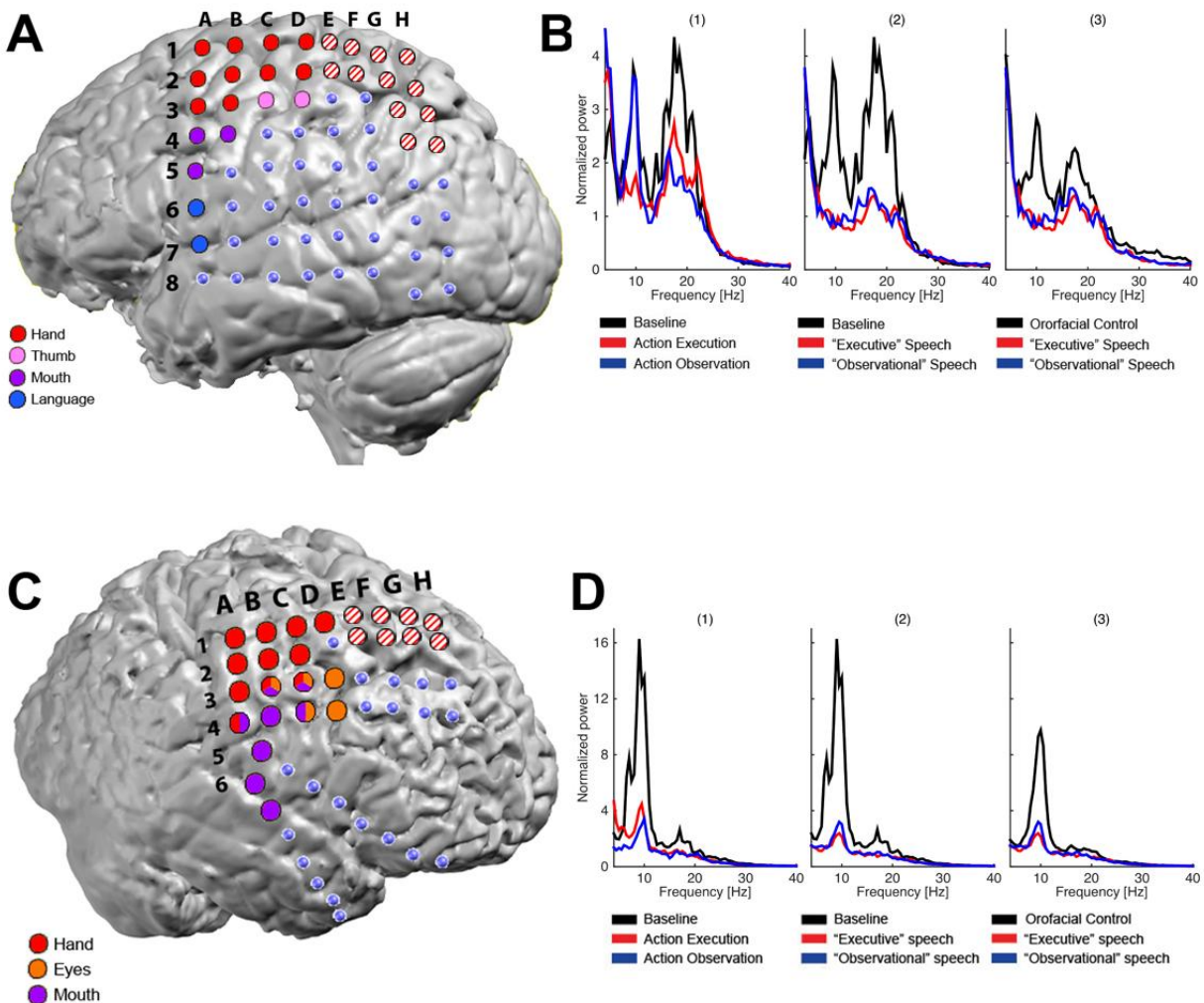
Yet, within the set of regions hypothesized to have mirror-like function, a particular focus has been posed on the inferior frontal gyrus (IFG) based on its activity during action observation and execution (Binkofski & Buccino, 2004; Binkofski, et al., 1999; Ehrsson, et al., 2000), and its supposedly cytoarchitectonically correspondence to area F5 in monkeys (Amunts, et al., 1999; Petrides & Pandya, 1999, 2002; Rizzolatti & Arbib, 1998), an area known for being involved in arm control but also in mouth and larynx movements (Corballis, 2003; Petrides, Cadoret, & Mackey, 2005). Along this line, classic and modern human intracranial electrophysiology (Gastaut & Bert, 1954; Tremblay, et al., 2004) and surface electroencephalography (Cebolla, Palmero-Soler, Dan, & Cheron, 2014; Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; Cochin, Barthelemy, Roux, & Martineau, 1999; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997; Pineda, 2005) showed that observation and execution of simple movements lead to a comparable activation (mu-rhythm suppression; 8-12 Hz) in IFG. Furthermore, beyond its well known role in speech production, the (left) IFG has been found to be involved also in a wide range of language-related activities including sign language production (Willems, Ozyurek, & Hagoort, 2007), lexical selection and retrieval (Krieger-Redwood & Jefferies, 2014), and word complexity categorization (Wright, Randall, Marslen-Wilson, & Tyler, 2011), as well as in language-unrelated activities such as semantic knowledge (Zhu, et al., 2012), motor planning (Marangolo, et al., 2011), and response inhibition (van Rooij, et al., 2015). This body of evidence supports that IFG contributes to build multimodal representations of object semantics, conveyed in various modality-independent forms of communication. On this basis, the human IFG may harbor not only an OEM system for actions (Johnson-Frey, et al., 2003), but also an OEM system for spoken speech. Here we provide evidence of comparable mu-rhythm suppression over IFG during execution, observation, and verbal description of the same action.

Methods

We recorded intracranial local field potentials (LFPs) in two patients (L and R) suffering from pharmaco-resistant epilepsy who underwent presurgical evaluation by implanted subdural electrode grids. The placement of the electrodes was determined clinically and covered the left frontal, parietal, and temporal cortex in patient L (64 electrodes; Figure 1A) and the right frontal,

parietal, and temporal cortex in patient R (48 electrodes; Figure 1C). Stimulation mapping was carried out as described previously (Blanke, Landis, & Seeck, 2000; Blanke, Perrig, Thut, Landis, & Seeck, 2000; Blanke, Spinelli, et al., 2000) and allowed us to localize the hand, mouth, and lip regions in both patients (Figure 1A and 1C), plus Broca's area in patient L.

Figure 1



LFP acquisition and analysis

We recorded LFPs from all implanted electrodes and analyzed mu-rhythm suppression separately for the high (15-22 Hz) and low (8-12.5 Hz) frequency bands with respect to spectral power and anatomo-functional distribution (Figure 1B and 1D). LFPs were recorded at 1024 Hz sampling rate from 64 subdural grid electrodes in patient L and at 512 Hz from 48 electrodes in

patient R. LFPs were recorded relative to a reference electrode located on the apex of the scalp. Each experimental 60s block was divided in 2s epochs with a 1s overlap. The power spectral density was calculated for each epoch using the Fast Fourier Transform (Matlab) with a frequency resolution of 0.5 Hz (1024 points). To minimize edge effects, the linear trend was removed and a Hann window was applied before performing the Fourier transform. For each channel, power spectra were normalized to the average power of all frequency bins between 4 and 40 Hz. The low and high mu rhythms were easily identifiable by visual inspection of the recordings as peaks in the power spectrum at ~10.5 Hz and ~18 Hz for patient L, and ~9.5 Hz and ~18 Hz for patient R (see Figure 1B and 1D), especially in electrodes over sensorimotor cortex. In both patients approximately half of the electrodes showed at least one of the two peaks. We used the peak frequencies to define two frequency bands that we used for further analysis: 8.5-12.5 Hz (low mu) and 15-22 Hz (high mu) for patient L, and 8-11 Hz (low mu) and 16-20 Hz (high mu) for patient R. Task-related modulation of band power was tested for significance ($p < 0.05$, Bonferroni corrected) with two-tailed t-tests, with each epoch being one sample. We used logarithmic values for the statistical tests, since the sample distribution of the band powers was approximately lognormal. In patient L, abnormal interictal epileptic activity was recorded in electrodes E1, E2, F1, F2, G1, G2, G3, G4, H1, H2, H3, and H4. Therefore these electrodes were excluded from further analysis. In patient R, abnormal interictal epileptic activity was recorded in electrodes E1, E2, F1, F2, G1, G2, H1, and H2. Also these electrodes were excluded from further analysis.

Conditions

We studied the OEM system and its role in action and speech by using the following conditions (compared to baseline): in the “action” conditions, patients were asked to observe (“action observation”) and perform (“action execution”) a goal-directed hand movements. In the “action execution” condition patients were asked to periodically reach, grasp and lift an orange positioned in front of them. In the “action observation” condition patients were asked to observe the experimenter performing the same action. The actions were performed by both the patients and the experimenter with either the left or the right hand in separated blocks. The total number of full action sequences was the same across all action conditions. In the “speech” conditions, patients were asked to speak out loudly and say that the patient himself (“executive speech”) or

another person (“observational speech”) were to carry out the same goal-directed hand action (as carried out physically in the action execution tasks). Thus, in the “executive speech” condition patients were asked to say: “I take the orange with my left (right) hand”. In the “observational speech” condition patients were asked to say: “He takes the orange with his left (right) hand”. In the speech conditions, “execution” and “observation” were thus only present in syntactical terms (subject and verb) for the spoken text and patients were asked to repeat the sentence at a pace that approximated the number of full action sequences carried out during the action sequence. To further control for the motor component of speech production we carried out the additional “orolingual movement control” condition, in which patients were asked to repeatedly execute mouth and tongue movements to mimic speech production but without purpose and content. All the conditions lasted for 60s and were separated by 20s of rest (fixation of the empty table). During a baseline condition (see LFP analysis) we asked the patient to look at the empty table for 60s without performing any manual or verbal action.

Results

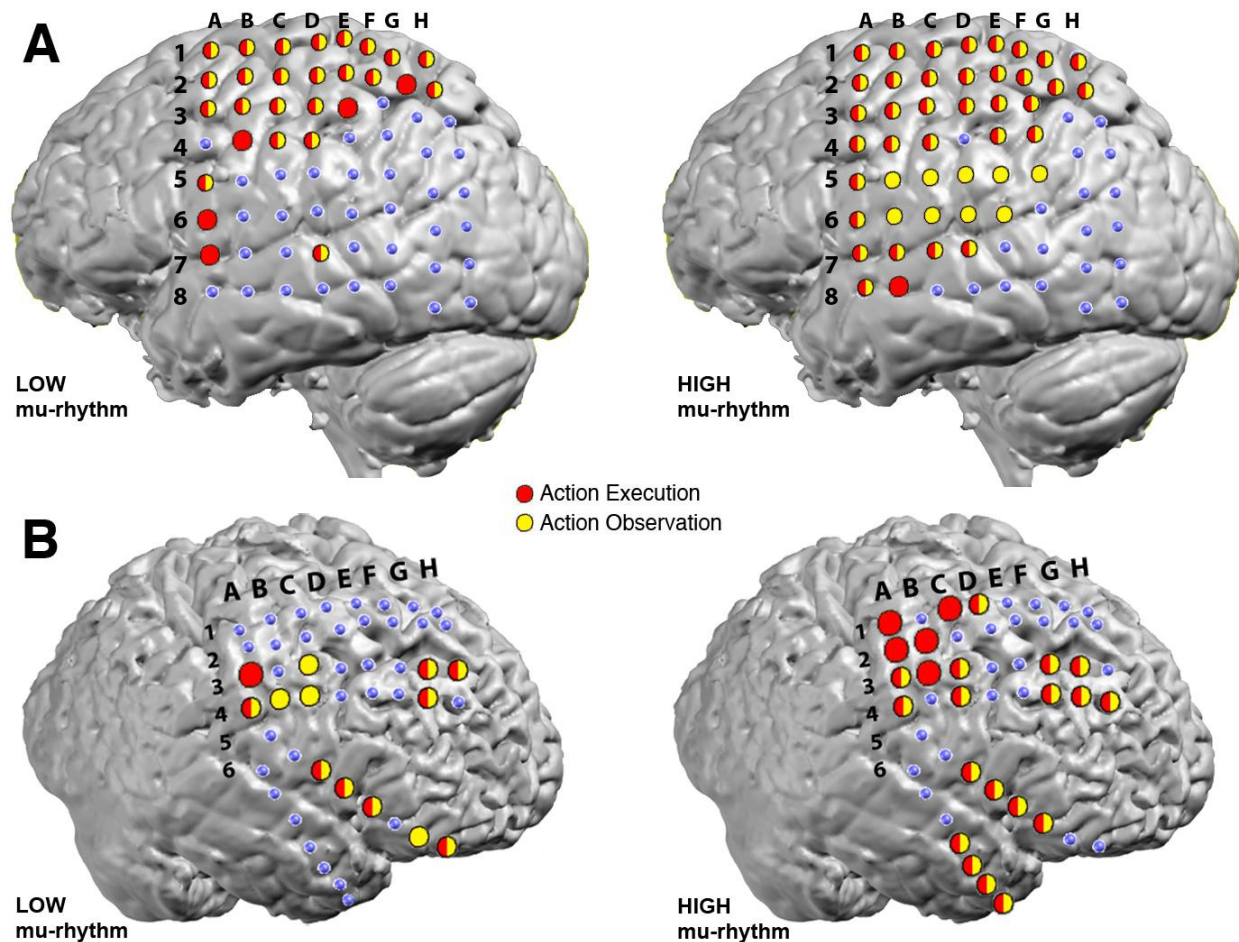
Visuo-motor OEM system

In patient L during the observation of grasping there was a significant suppression of the low mu-rhythm in 22 electrodes (42%) and of the high mu-rhythm in 43 electrodes (83%) with respect to the baseline (all $p < 0.001$). During the execution of grasping there was a significant suppression of the low mu-rhythm in 27 electrodes (52%) and of the high mu-rhythm in 35 electrodes (67%) with respect to the baseline (all $p < 0.001$). In addition, 22 (42%) and 32 (62%) electrodes showed significant suppression in the low (high) mu-rhythm relative to baseline during both action execution and observation. Compatible with the OEM hypothesis, this restricted subset of electrodes did not show significant differences when directly compared (all $p > 0.05$; Figure 2A).

In patient R during the observation of grasping there was a significant suppression of the low mu-rhythm in 25 electrodes (63%) and of the high mu-rhythm in 12 electrodes (30%), with respect to the baseline (all $p < 0.001$). During the execution of grasping there was the significant suppression of the low mu-rhythm in 23 electrodes (58%) and of the high mu-rhythm in 9 electrodes (23%), with respect to the baseline (all $p < 0.001$). In addition, 17 (43%) and 8 (20%) electrodes showed suppression in the low mu-rhythm and in the high mu-rhythm, respectively,

relative to the baseline in both “action execution” and “action observation” conditions. Compatible with the OEM hypothesis, this restricted subset of electrodes did not show differential activation when compared directly (all $p > 0.05$; Figure 2B).

Figure 2

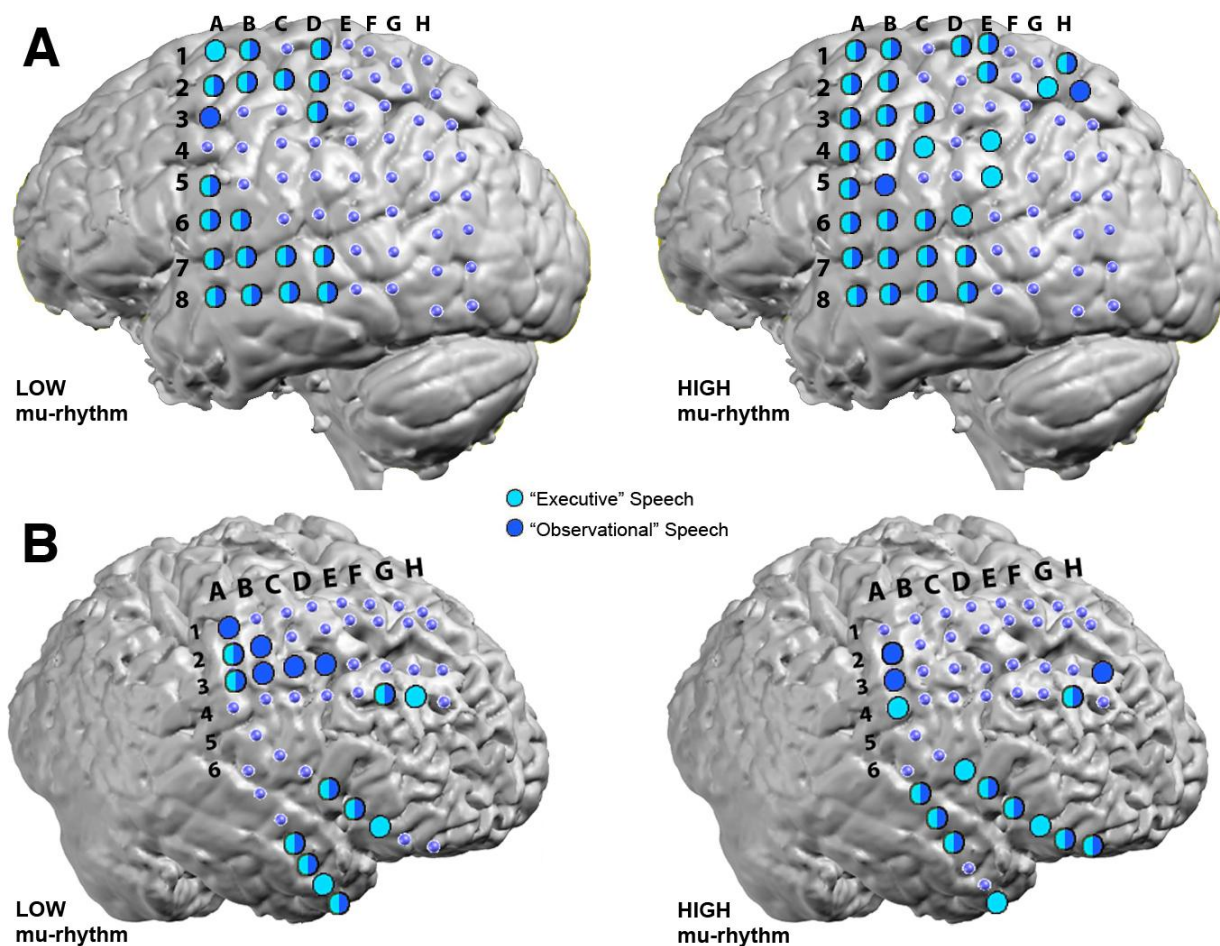


Speech OEM system

In patient L we observed low (high) mu-rhythm suppression during the “executive speech” condition at 19 (30) electrode sites, relative to baseline (all $p < 0.001$). In the “observational speech” condition we observed low (high) mu-rhythm suppression at 20 (27) electrode sites, relative to baseline (all $p < 0.001$). In addition, 18 (25) of these electrode sites were found during both executive and observational speech. Compatible with the OEM hypothesis, this restricted subset of electrodes did not show differential activation when compared directly (all $p > 0.05$; Figure 3A).

In patient R we observed low (high) mu-rhythm suppression during the “executive speech” condition at 11 (12) electrode sites relative to baseline (all $p < 0.001$). In the “observational speech” condition we observed low (high) mu-rhythm suppression at 13 (11) electrodes sites, relative to baseline (all $p < 0.001$). In addition, 7 (8) of these electrode sites were found during both executive and observational speech. Compatible with the OEM hypothesis for speech, this restricted subset of electrodes did not show differential activation when compared directly (all $p > 0.05$; Figure 3B).

Figure 3

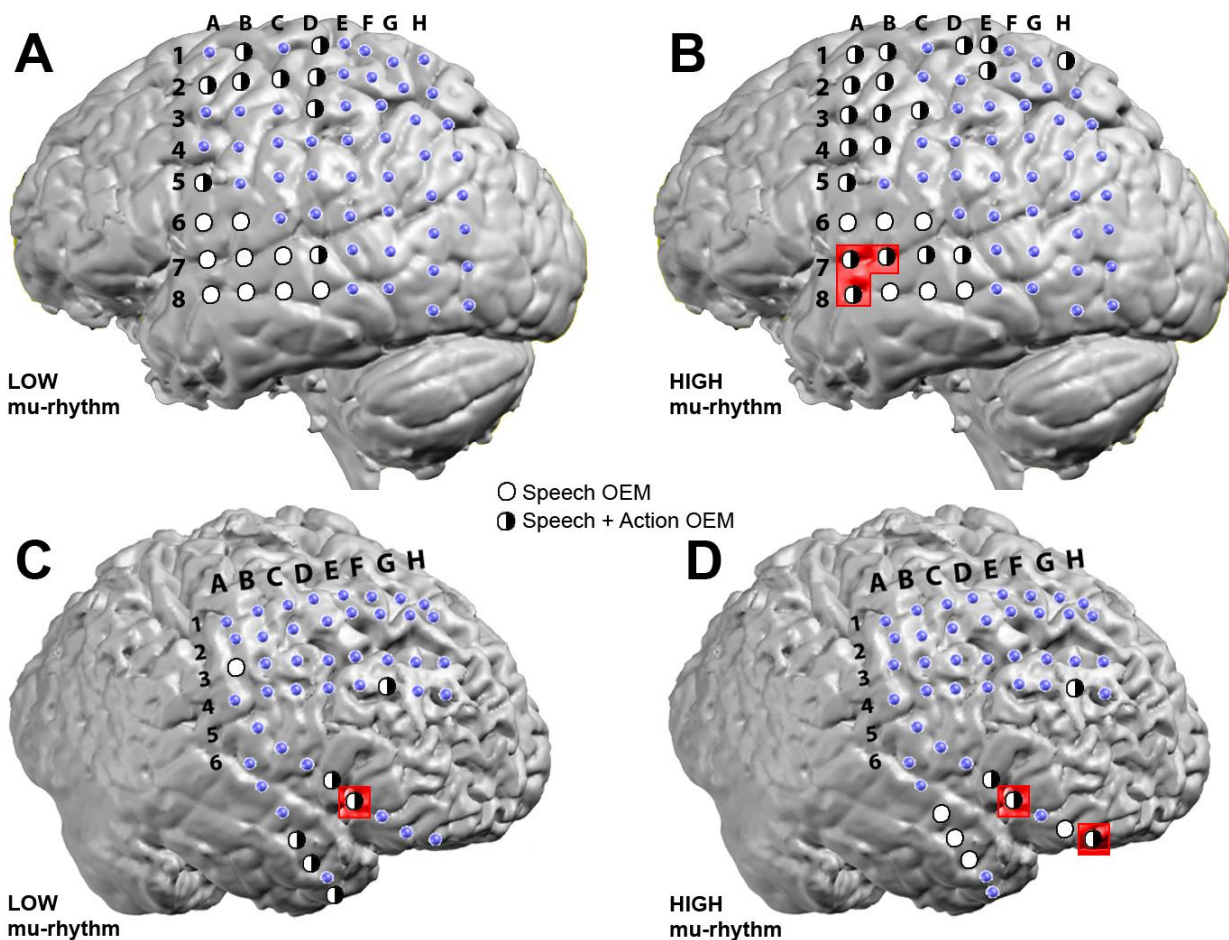


Visuo-motor OEM properties of speech OEM sites

In patient L 9 (19) speech OEM sites showed also visuo-motor OEM properties for low (high) mu-rhythm, i.e. similar suppression during executive and observational speech as in execution and observation of an action. However, 9 (6) electrode sites showed specific speech-

OEM properties for low (high) mu-rhythm suppression, i.e. did not show action-OEM properties (Figure 4A and 4B). In patient R 6 (4) speech-OEM sites showed action-OEM properties for low (high) mu-rhythm, i.e. similar suppression during executive and observational speech as in execution and observation of an action. 1 (4) electrode site(s) showed specific speech OEM properties for low (high) mu-rhythm suppression, i.e. did not show visuo-motor OEM properties (Figure 4C and 4D).

Figure 4



Localization and function of the overlapping visuo-motor and speech OEM systems

In patient L, within the speech OEM system, 9 (5) electrode sites showed significant low (high) mu-rhythm suppressions during both “executive speech” and “observational speech” conditions with respect to the “orolingual movement control” conditions. For the low mu-rhythm these electrode sites comprised: A6, A7, A8, B6, B7, B8, C7, C8 and D8. For the high mu-

rhythm these electrode sites comprised: A7, A8, B7, B8, and C8. Within these sites, only 3 adjacent electrodes (A7, A8, and B7) showed an anatomical overlap between visuo-motor OEM and speech OEM controlled for orolingual movements (Figure 4B). These three electrode sites were located in the left IFG. Electrical stimulation of electrode site A7 interfered with speech production (speech arrest) providing evidence that it was located over Broca's area as defined in stimulation mapping. Electrical stimulation of the other two sites did not reveal any overt response (Figure 1A).

In patient R, within the speech OEM system, 1 (2) electrode sites showed a significant low (high) mu-rhythm suppression during both “executive speech” and “observational speech” with respect to the “orolingual movement control”. These electrode sites comprised E5 (for the low mu-rhythm) and E5 and H5 (for the high mu-rhythm). In other words, E5 and H5 showed an anatomical overlap between visuo-motor OEM and speech OEM controlled for orolingual movements. Electrode sites E5 and H5 showed the overlap in both the low and high mu-rhythm, while the overlap in electrode H5 was specific to the high mu-rhythm (Figure 4C and 4D). All these electrode sites were located in the right IFG, with E5 in the pars triangularis and H5 in the pars orbitalis. Electrical stimulation of these sites did not reveal any overt response nor speech interference (Figure 1).

Specific sites for visuo-motor OEM

In patient L 12 (13) electrode sites showed specific visuo-motor OEM properties for low (high) mu-rhythm suppression, i.e. did not show speech OEM properties. In patient R 11 (4) electrode site(s) showed specific visuo-motor OEM properties for low (high) mu-rhythm suppression, i.e. did not show speech OEM properties.

Discussion

Overlap between visuo-motor and speech OEM systems for actions

Using the suppression of mu-rhythm signals from intracranially recorded LFPs as an indicator of cortical activity (Laufs, et al., 2003; Poulet & Petersen, 2008), we here report the presence of a speech OEM system that is partially overlapping (functionally and anatomically) with the visuo-motor OEM system. Visuo-motor and speech OEM systems were found

predominantly in the IFG bilaterally, but also in left superior temporal gyrus. In particular, we found that execution, observation, and the verbal description of the same hand action, but not orolingual movements that were not related to speech, were associated with enhanced activation in these areas. We further note that in patient R, the electrode E5 covered the pars triangularis within the IFG. It has been suggested that this region inhibits body-specific motor execution during movement observation (Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005) as well as during silent reading (Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995). Extending these previous studies, we directly compared brain activity associated with visuo-motor and speech-related accounts of action representations, showing that OEM systems for both speech and action in several bilateral frontal regions exhibit activity patterns similar to those of the mirror neuron system (i.e. comparable cortical responsiveness to the same action in different modalities). In this vein, our data support the notion of abstract and multimodal sensory-motor representations of actions (Ionta, Sforza, Funato, & Blanke, 2013), including not only visual, auditory, and motor domains (Aglioti & Pazzaglia, 2011; Glenberg & Kaschak, 2002; Keysers, et al., 2003; Kohler, et al., 2002), but also speech processes (Cerri, et al., 2015; Rizzolatti & Arbib, 1998). The stronger brain activity in the action-related speech conditions with respect to the conditions in which a speech component was absent (“meaningless” orolingual movement control condition), provides evidence that this activation pattern cannot be explained by the mere motor activation due to the movements of mouth and tongue. We suggest that the activity in the sites included in the speech OEM system (different from the ones involved in the movements of mouth and tongue) may originate from the activation of the motor representation of the verbally described action. In other words, the resulting activity in common between executive and observational speech can be ascribed to the activation of abstract and modality-independent action representations. We further note that On the basis of the present results, further investigations may clarify open questions such as the potential effect of using/observing different effectors, or the interaction with different objects and different objects’ affordances.

Supporting an anatomic-functional correspondence between visuo-motor and speech OEM systems, we found overlapping sites for speech OEM and visuo-motor OEM (in at least one frequency band) in bilateral inferior frontal cortex and the left superior temporal cortex (for discussion of the other regions see below). Within these sites the electrical stimulation of the electrodes positioned on the left hemisphere determined speech arrest, while the stimulation of

the ones positioned on the right hemisphere did not elicit an overt behavioral response. The comparable LFP activity shown on the left and right hemisphere in the present data supports a bilateral involvement in action and speech matching. It might be argued that the classical left-lateralization of speech-related processes is not compatible with the present involvement of the right inferior frontal gyrus in speech OEM. However, despite the dominance of the left hemisphere for speech, also the right hemisphere can be involved in many language tasks such as reading (Hauk, Johnsrude, & Pulvermuller, 2004), processing prosody (Gorelick & Ross, 1987; Mitchell & Crow, 2005; Sollmann, et al., 2014; Wildgruber, Ackermann, Klose, Kardatzki, & Grodd, 1996), speech automatization (Speedie, Wertman, Ta'ir, & Heilman, 1993), and meaning attribution (Taylor & Regard, 2003). Moreover, Brodmann's subdivision of Broca's area into area 44 and 45 can offer better understanding of its involvement in speech. Unlike area 44, which is usually larger on the left side, area 45 (Amunts, et al., 1999; Galaburda, 1980) and the monkey homologue area F5 (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) appear to be more symmetric. Indeed in patients not able to produce covertly generated verbs, the right (and not left) inferior frontal gyrus is underactivated (Liegeois, et al., 2003). Likewise, in patients suffering from motor neuron disease (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001), pathological changes in areas 44 and 45 bilaterally are associated with a selective impairment in processing action verbs (Bak, et al., 2006). On this basis, the present data support the involvement of the right hemisphere in different speech processes (Bottini, et al., 1994; Nishitani, Schurmann, Amunts, & Hari, 2005), with a particular role in matching agent-independent and multimodal representations of actions.

Extensive distribution of the visuo-motor and speech OEM systems

Within the visuo-motor OEM system, we observed an anatomically and functionally very widespread “mirror” type set of regions characterized by similar activity during action observation and execution. This activation pattern was found in brain regions with diverse functions (as revealed by stimulation mapping) such as hand, tongue, face, mouth, eye movements, as well as motor inhibition, speech, and somatosensory function. The involved areas comprised the inferior frontal and precentral gyri (bilaterally), the postcentral, superior temporal, and superior parietal regions (on the left hemisphere), and the (right) middle frontal gyrus. Further investigations reported also the involvement of occipito-temporal regions in mirror-like

activity (Kable & Chatterjee, 2006; Romaguere, Nazarian, Roth, Anton, & Felician, 2014). In line with the present data, previous work showed widespread activity during action imitation (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003), simulation (Ionta, Ferretti, Merla, Tartaro, & Romani, 2010), and observation/execution (Mukamel, et al., 2010). Accordingly, our data confirm mirror type mu-rhythm behavior are extremely common and distributed on both hemispheres.

Also the OEM for speech recruited a widespread set of regions with a “mirror” type activity during the pronunciation of action-related sentences both in first-person and in a third-person perspective, hinting at an abstract and modality-independent representation of actions. The direct electrical stimulation of these regions (one at a time) also determined a large panel of different functions, including speech arrest and hand, thumb, eye, lips, and mouth movements. The involved areas comprised the inferior frontal, precentral, and superior temporal gyri (bilaterally), the postcentral and superior parietal regions (on the left hemisphere), and the middle frontal and prefrontal gyrus (on the right hemisphere). Previous studies highlighted the commonalities between self and other processing and consistently reported the involvement of superior temporal, temporo-parietal, and prefrontal regions in a wide range of self-other human abilities, including emotion sharing (Singer, et al., 2004), mentalizing (Frith & Frith, 2003), interpreting gaze direction (Pelphrey, Viola, & McCarthy, 2004), and perspective taking (Aichhorn, et al., 2009; Ionta, et al., 2011), probably due to their importance in representing the body in the space (Ionta, Martuzzi, Salomon, & Blanke, 2014). In particular, Samson et al. (2005) reported that a patient presenting widespread lesions affecting the middle and inferior frontal gyrus, as well as the superior temporal gyrus, showed impairments in tasks requiring strong inhibition of self-beliefs, but not in weak self-inhibition tasks. One possible interpretation of these findings is that when IFG (and middle frontal and superior temporal gyri) are affected, self-representations take over other-representations, producing a bias towards self-beliefs. The absence of deficits in low-demanding self-inhibition tasks suggests that the relative weight of self- and other-representations changes as a function of contextual factors, and further supports the importance of IFG (and middle frontal and superior temporal gyri) in the modulation of the signals relative to these two frames of reference. In addition we note that the patient showed perspective taking impairments in different modalities, i.e. visual and social. This additional finding is in line with our data on the modality-independent representation of actions. The present data extend the role

of this widespread brain network centered on superior temporal and inferior frontal regions in processing the commonalities between self and other in terms of verbal description of actions, supporting the multimodal semantics of action representations.

Integrative and Multimodal Representations of Movements

Building on the first ground-breaking electrophysiological findings that movement observation, simulation, and execution determine proportional autonomic responses (Farrand, 1897; Lay, 1898; Stetson, 1896), muscular activity (Jacobson, 1930, 1932), and brain responses (Gastaut & Bert, 1954), the present data support the idea that conceptual knowledge encoded by the sensory-motor system can recruit a supra- or multi-modal representation of movements which may further be used as reference frame for understanding, producing, and communicating an action. Compatible with this proposal, it has been shown that properties of objects referring to actions (e.g. tools) are encoded in the motor system (Chao & Martin, 2000), and that words addressing action-related meanings activate motor areas (Aziz-Zadeh, Sheng, Liew, & Damasio, 2012; Pulvermuller, 2005). Along this line, the discovery of mirror neurons in the monkey brain area F5, active during both movement observation and execution and the supposed homology between F5 and Broca's area in the human brain (Petrides, et al., 2005), support the link between action and speech (Rizzolatti & Arbib, 1998) and inspired the "embodied cognition theory" suggesting that speech could be conceptualized as a mental simulation of the meaning content (Gallese & Lakoff, 2005; Wilson, 2013). Indeed there have been many reports about (i) the activation of sensory-motor areas during speech processes (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger, et al., 2008; Hauk, et al., 2004; Pulvermuller, 2005; Tettamanti, et al., 2005), (ii) the influence of speech processing on motor performance (Emmorey, 2013; Fischer & Zwaan, 2008; Nazir, Jeannerod, & Hauk, 2008), and (iii) the specific impairment in action-related words in patients suffering from diseases affecting the motor system (Bak, et al., 2001; Boulenger, et al., 2008). Based on these data it has been speculated that the human ability for speech may have evolved from pre-existing mechanisms dedicated to visuo-motor OEM for actions (Arbib, 2005; Cerri, et al., 2015; Corballis, 2003), proposing that multimodal action representations provide a simulation mechanism that may have evolved into representations of action goals, intentions, and language (D'Ausilio, Bartoli, & Maffongelli, 2015; Glenberg & Kaschak, 2002; Pulvermuller, 2005).

Based on the advantages of intracranial recording with respect to e.g. functional magnetic resonance imaging and electroencephalography in terms of temporal resolution and spatial precision, respectively, the present data demonstrate that the correspondence between sensory-based representations of movements performed by others and motor-based representation of self-performed movements is not limited only to e.g. visuo-motor (Mukamel, et al., 2010) and audio-motor domains (Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008) but it includes also more abstract representations, i.e. verbal description. With potential application in the development of rehabilitation technology (Pisotta, Perruchoud, & Ionta, 2015), the present findings support the existence of multimodal representations of other-performed movements and the continuous comparison with internal motor representations of self-performed movements.

Acknowledgments

This work was supported by the Swiss National Science Foundation through the Ambizione funding program to Silvio Ionta (grant PZ00P1_148186).

FIGURE LEGENDS

Figure 1 - Stimulation and Recording - Electrodes' location and electrically induced responses for patient L (panel A) and patient R (panel C). Letters indicate columns of the electrodes grid. Numbers indicate rows. Dots represent electrodes. Colored dots indicate the electrically evoked responses. Red/white striped dots indicate epileptic foci. **Local field potential power spectra** from electrode A7 in patient L (panel B) and from electrode D5 in patient R (panel D), showing the suppression of the low and high mu-rhythm during: action observation and execution (1); “executive speech” and “observational speech” with respect to baseline (2); “executive speech” and “observational speech” controlled for orolingual movements (3).

Figure 2 - Visuo-Motor Observation-Execution Matching. Low and high mu-rhythm suppression in patient L (A) and R (B). Yellow dots indicate electrode sites where the suppression occurred during the “action observation” condition. Red dots indicate electrode sites where the suppression occurred during the “action execution” condition. For red/yellow dots suppression occurred in both conditions.

Figure 3. Speech Observation-Execution Matching. Low and high mu-rhythm suppression in patient L (A) and R (B). Dark blue dots indicate electrode sites where the suppression occurred during the “observational speech” condition. Light blue dots indicate electrode sites where the suppression occurred during the “executive speech” condition. For dark/light blue dots suppression occurred in both conditions.

Figure 4. Specificity of speech observation-execution matching. Low and high mu-rhythm suppression in patient L (A and B) and R (C and D). White dots indicate electrode sites within the speech OEM showing activity only during the speech tasks. White/Black striped dots indicate electrode sites within the speech OEM also showing visuo-motor OEM. Red-highlighted regions indicate the overlap between visuo-motor OEM and speech OEM controlled for orolingual movements.

References

- Abreu, A. M., Macaluso, E., Azevedo, R. T., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012). Action anticipation beyond the action observation network: a functional magnetic resonance imaging study in expert basketball players. *Eur J Neurosci*, *35*, 1646-1654.
- Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. *Trends Cogn Sci*, *15*, 47-55.
- Aichhorn, M., Perner, J., Weiss, B., Kronbichler, M., Staffen, W., & Ladurner, G. (2009). Temporo-parietal junction activity in theory-of-mind tasks: falseness, beliefs, or attention. *J Cogn Neurosci*, *21*, 1179-1192.
- Alaerts, K., Nayar, K., Kelly, C., Raithel, J., Milham, M. P., & Di Martino, A. (2015). Age-related changes in intrinsic function of the superior temporal sulcus in autism spectrum disorders. *Soc Cogn Affect Neurosci*.
- Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *J Comp Neurol*, *412*, 319-341.
- Arbib, M. A. (2005). From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. *Behav Brain Sci*, *28*, 105-124; discussion 125-167.
- Aziz-Zadeh, L., Sheng, T., Liew, S. L., & Damasio, H. (2012). Understanding otherness: the neural bases of action comprehension and pain empathy in a congenital amputee. *Cereb Cortex*, *22*, 811-819.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Curr Biol*, *16*, 1818-1823.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, *124*, 103-120.
- Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermuller, F., & Hodges, J. R. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, *129*, 321-332.
- Binkofski, F., & Buccino, G. (2004). Motor functions of the Broca's region. *Brain and language*, *89*, 362-369.
- Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. (1999). A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur. J. Neurosci.*, *11*, 3276.
- Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nat Rev Neurosci*, *2*, 561-567.
- Blanke, O., Landis, T., & Seeck, M. (2000). Electrical cortical stimulation of the human prefrontal cortex evokes complex visual hallucinations. *Epilepsy Behav*, *1*, 356-361.
- Blanke, O., Perrig, S., Thut, G., Landis, T., & Seeck, M. (2000). Simple and complex vestibular responses induced by electrical cortical stimulation of the parietal cortex in humans. *J Neurol Neurosurg Psychiatry*, *69*, 553-556.
- Blanke, O., Spinelli, L., Thut, G., Michel, C. M., Perrig, S., Landis, T., & Seeck, M. (2000). Location of the human frontal eye field as defined by electrical cortical stimulation: anatomical, functional and electrophysiological characteristics. *Neuroreport*, *11*, 1907-1913.

- Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T., Gaillard, W., & Theodore, W. (1995). Regional cerebral blood flow during object naming and word reading. *Human Brain Mapping, 3*, 93-106.
- Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., Frackowiak, R. S., & Frith, C. D. (1994). The role of the right hemisphere in the interpretation of figurative aspects of language. A positron emission tomography activation study. *Brain, 117* (Pt 6), 1241-1253.
- Boulenger, V., Mechtouff, L., Thobois, S., Broussolle, E., Jeannerod, M., & Nazir, T. A. (2008). Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns. *Neuropsychologia, 46*, 743-756.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain Cogn., 44*, 124.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci, 13*, 400-404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., & Lagravinese, G. (2004). Neural circuits involved in the recognition of actions performed by non-conspecifics: an fMRI study. *J. Cogn. Neurosci., 16*, 1.
- Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cereb Cortex, 15*, 1243-1249.
- Cattaneo, L., & Rizzolatti, G. (2009). The mirror neuron system. *Arch Neurol, 66*, 557-560.
- Cebolla, A. M., Palmero-Soler, E., Dan, B., & Cheron, G. (2014). Modulation of the N30 generators of the somatosensory evoked potentials by the mirror neuron system. *Neuroimage, 95*, 48-60.
- Cerri, G., Cabinio, M., Blasi, V., Borroni, P., Iadanza, A., Fava, E., Forna, L., Ferpozzi, V., Riva, M., Casarotti, A., Martinelli Boneschi, F., Falini, A., & Bello, L. (2015). The mirror neuron system and the strange case of Broca's area. *Hum Brain Mapp, 36*, 1010-1027.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage, 12*, 478-484.
- Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., & Martineau, J. (1998). Perception of motion and qEEG activity in human adults. *Electroencephalogr. Clin. Neurophysiol., 107*, 287.
- Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *Eur. J. Neurosci., 11*, 1839.
- Corballis, M. C. (2003). From mouth to hand: gesture, speech, and the evolution of right-handedness. *Behav Brain Sci, 26*, 199-208; discussion 208-160.
- Coude, G., Vanderwert, R. E., Thorpe, S., Festante, F., Bimbi, M., Fox, N. A., & Ferrari, P. F. (2014). Frequency and topography in monkey electroencephalogram during action observation: possible neural correlates of the mirror neuron system. *Philos Trans R Soc Lond B Biol Sci, 369*, 20130415.
- Craigheo, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia, 40*, 492.

- D'Ausilio, A., Bartoli, E., & Maffongelli, L. (2015). Grasping synergies: A motor-control approach to the mirror neuron mechanism. *Phys Life Rev*, *12*, 91-103.
- Davey, J., Rueschemeyer, S. A., Costigan, A., Murphy, N., Krieger-Redwood, K., Hallam, G., & Jefferies, E. (2015). Shared neural processes support semantic control and action understanding. *Brain and language*, *142*, 24-35.
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., & Fazio, F. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, *120* (Pt 10), 1763-1777.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Exp. Brain Res.*, *91*, 176.
- Ehrsson, H. H., Fagergren, A., Jonsson, T., Westling, G., Johansson, R. S., & Forssberg, H. (2000). Cortical activity in precision- versus power-grip tasks: an fMRI study. *J. Neurophysiol.*, *83*, 528.
- Emmorey, K. (2013). The neurobiology of sign language and the mirror system hypothesis. *Lang Cogn*, *5*, 205-210.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.*, *73*, 2608.
- Farrand, L. (1897). Proceedings of the fifth annual meeting of the American Psychological Association, Boston, December, 1896. *Psychological Review*, *4*, 107.
- Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S., & Grafton, S. T. (2008). The angular gyrus computes action awareness representations. *Cereb Cortex*, *18*, 254-261.
- Fecteau, S., Carmant, L., Tremblay, C., Robert, M., Bouthillier, A., & Theoret, H. (2004). A motor resonance mechanism in children? Evidence from subdural electrodes in a 36-month-old child. *Neuroreport*, *15*, 2625-2627.
- Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *Eur J Neurosci*, *17*, 1703-1714.
- Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: a review of the role of the motor system in language comprehension. *Q J Exp Psychol (Hove)*, *61*, 825-850.
- Frenkel-Toledo, S., Bentin, S., Perry, A., Liebermann, D. G., & Soroker, N. (2014). Mirror-neuron system recruitment by action observation: effects of focal brain damage on mu suppression. *Neuroimage*, *87*, 127-137.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philos Trans R Soc Lond B Biol Sci*, *358*, 459-473.
- Galaburda, A. M. (1980). [Broca's region: anatomic remarks made a century after the death of its discoverer]. *Rev Neurol (Paris)*, *136*, 609-616.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593.
- Gallese, V., & Lakoff, G. (2005). The Brain's concepts: the role of the Sensory-motor system in conceptual knowledge. *Cogn Neuropsychol*, *22*, 455-479.
- Gardner, T., Goulden, N., & Cross, E. S. (2015). Dynamic modulation of the action observation network by movement familiarity. *J Neurosci*, *35*, 1561-1572.
- Gastaut, H. J., & Bert, J. (1954). EEG changes during cinematographic presentation; moving picture activation of the EEG. *Electroencephalogr Clin Neurophysiol*, *6*, 433-444.

- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychon Bull Rev*, 9, 558-565.
- Gorelick, P. B., & Ross, E. D. (1987). The aprosodias: further functional-anatomical evidence for the organisation of affective language in the right hemisphere. *J Neurol Neurosurg Psychiatry*, 50, 553-560.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41, 301-307.
- Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., & Mazziotta, J. C. (2003). The essential role of Broca's area in imitation. *Eur. J. Neurosci.*, 17, 1123.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526.
- Ionta, S., Ferretti, A., Merla, A., Tartaro, A., & Romani, G. L. (2010). Step-by-step: the effects of physical practice on the neural correlates of locomotion imagery revealed by fMRI. *Hum Brain Mapp*, 31, 694-702.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., & Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, 70, 363-374.
- Ionta, S., Martuzzi, R., Salomon, R., & Blanke, O. (2014). The brain network reflecting bodily self-consciousness: a functional connectivity study. *Soc Cogn Affect Neurosci*, 9, 1904-1913.
- Ionta, S., Sforza, A., Funato, M., & Blanke, O. (2013). Anatomically plausible illusory posture affects mental rotation of body parts. *Cogn Affect Behav Neurosci*, 13, 197-209.
- Jacobson, E. (1930). Electrical measurements of neuromuscular states during mental activities. *American Journal of Physiology*, 91, 567-608.
- Jacobson, E. (1932). Electrophysiology of mental activities. *American Journal of Psychology*, 44.
- Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron*, 39, 1053-1058.
- Kable, J. W., & Chatterjee, A. (2006). Specificity of action representations in the lateral occipitotemporal cortex. *J Cogn Neurosci*, 18, 1498-1517.
- Keysers, C., Kohler, E., Umiltà, M. A., Nanetti, L., Fogassi, L., & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Exp Brain Res*, 153, 628-636.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: action representation in mirror neurons. *Science*, 297, 846.
- Krieger-Redwood, K., & Jefferies, E. (2014). TMS interferes with lexical-semantic retrieval in left inferior frontal gyrus and posterior middle temporal gyrus: Evidence from cyclical picture naming. *Neuropsychologia*, 64C, 24-32.
- Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *Neuroimage*, 19, 1463-1476.
- Lay, W. (1898). Mental imagery: Experimentally and subjectively considered. *The Psychological Review: Monograph Supplements*, 2, i.
- Lepage, J. F., & Theoret, H. (2006). EEG evidence for the presence of an action observation-execution matching system in children. *Eur J Neurosci*, 23, 2505-2510.

- Liegeois, F., Baldeweg, T., Connelly, A., Gadian, D. G., Mishkin, M., & Vargha-Khadem, F. (2003). Language fMRI abnormalities associated with FOXP2 gene mutation. *Nat Neurosci*, *6*, 1230-1237.
- Lui, F., Buccino, G., Duzzi, D., Benuzzi, F., Crisi, G., Baraldi, P., Nichelli, P., Porro, C. A., & Rizzolatti, G. (2008). Neural substrates for observing and imagining non-object-directed actions. *Soc Neurosci*, *3*, 261-275.
- Marangolo, P., Marinelli, C. V., Bonifazi, S., Fiori, V., Ceravolo, M. G., Provinciali, L., & Tomaiuolo, F. (2011). Electrical stimulation over the left inferior frontal gyrus (IFG) determines long-term effects in the recovery of speech apraxia in three chronic aphasics. *Behav Brain Res*, *225*, 498-504.
- Mitchell, R. L., & Crow, T. J. (2005). Right hemisphere language functions and schizophrenia: the forgotten hemisphere? *Brain*, *128*, 963-978.
- Mitra, S., Nizamie, S. H., Goyal, N., & Tikka, S. K. (2014). Mu-wave Activity in Schizophrenia: Evidence of a Dysfunctional Mirror Neuron System from an Indian Study. *Indian J Psychol Med*, *36*, 276-281.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. *Cereb Cortex*, *15*, 986-994.
- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. *Curr Biol*.
- Nazir, T. A., Jeannerod, M., & Hauk, O. (2008). The role of sensory-motor systems for language understanding. Foreword. *J Physiol Paris*, *102*, 1-3.
- Nishitani, N., Avikainen, S., & Hari, R. (2004). Abnormal imitation-related cortical activation sequences in Asperger's syndrome. *Ann Neurol*, *55*, 558-562.
- Nishitani, N., Schurmann, M., Amunts, K., & Hari, R. (2005). Broca's region: from action to language. *Physiology (Bethesda)*, *20*, 60-69.
- Pazzaglia, M., Pizzamiglio, L., Pes, E., & Aglioti, S. M. (2008). The sound of actions in apraxia. *Curr Biol*, *18*, 1766-1772.
- Pelphrey, K. A., Viola, R. J., & McCarthy, G. (2004). When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. *Psychol Sci*, *15*, 598-603.
- Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, *435*, 1235-1238.
- Petrides, M., & Pandya, D. N. (1999). Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *Eur J Neurosci*, *11*, 1011-1036.
- Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *Eur J Neurosci*, *16*, 291-310.
- Pfurtscheller, G., Neuper, C., Andrew, C., & Edlinger, G. (1997). Foot and hand area mu rhythms. *International journal of psychophysiology : official journal of the International Organization of Psychophysiology*, *26*, 121-135.
- Pineda, J. A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Res Brain Res Rev*, *50*, 57-68.
- Pisotta, I., Perruchoud, D., & Ionta, S. (2015). Hand-in-hand advances in biomedical engineering and sensorimotor restoration. *Journal of neuroscience methods*, *246*, 22-29.

- Pokorny, J. J., Hatt, N. V., Colombi, C., Vivanti, G., Rogers, S. J., & Rivera, S. M. (2015). The Action Observation System when Observing Hand Actions in Autism and Typical Development. *Autism Res.*
- Poulet, J. F., & Petersen, C. C. (2008). Internal brain state regulates membrane potential synchrony in barrel cortex of behaving mice. *Nature*, *454*, 881-885.
- Pulvermuller, F. (2005). Brain mechanisms linking language and action. *Nat Rev Neurosci*, *6*, 576-582.
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends Neurosci.*, *21*, 188.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1996). Premotor cortex and the recognition of motor actions. *Cogn. Brain Res.*, *3*, 131.
- Romaiguere, P., Nazarian, B., Roth, M., Anton, J. L., & Felician, O. (2014). Lateral occipitotemporal cortex and action representation. *Neuropsychologia*, *56*, 167-177.
- Rozzi, S., Ferrari, P. F., Bonini, L., Rizzolatti, G., & Fogassi, L. (2008). Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *Eur J Neurosci*, *28*, 1569-1588.
- Samson, D., Apperly, I. A., Kathirgamanathan, U., & Humphreys, G. W. (2005). Seeing it my way: a case of a selective deficit in inhibiting self-perspective. *Brain*, *128*, 1102-1111.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, *303*, 1157-1162.
- Sollmann, N., Tanigawa, N., Ringel, F., Zimmer, C., Meyer, B., & Krieg, S. M. (2014). Language and its right-hemispheric distribution in healthy brains: an investigation by repetitive transcranial magnetic stimulation. *Neuroimage*, *102 Pt 2*, 776-788.
- Speedie, L. J., Wertman, E., Ta'ir, J., & Heilman, K. M. (1993). Disruption of automatic speech following a right basal ganglia lesion. *Neurology*, *43*, 1768-1774.
- Stetson, R. H. (1896). Types of imagination. *Psychological Review*, *3*, 398.
- Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport*, *11*, 2289.
- Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is 'mirror' only for biological actions. *Curr Biol*, *14*, 117-120.
- Taylor, K. I., & Regard, M. (2003). Language in the right cerebral hemisphere: contributions from reading studies. *News Physiol Sci*, *18*, 257-261.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci*, *17*, 273-281.
- Tremblay, C., Robert, M., Pascual-Leone, A., Lepore, F., Nguyen, D. K., Carmant, L., Bouthillier, A., & Theoret, H. (2004). Action observation and execution: intracranial recordings in a human subject. *Neurology*, *63*, 937-938.
- van Rooij, D., Hoekstra, P. J., Mennes, M., von Rhein, D., Thissen, A. J., Heslenfeld, D., Zwiers, M. P., Faraone, S. V., Oosterlaan, J., Franke, B., Rommelse, N., Buitelaar, J. K., & Hartman, C. A. (2015). Distinguishing Adolescents With ADHD From Their Unaffected Siblings and Healthy Comparison Subjects by Neural Activation Patterns During Response Inhibition. *Am J Psychiatry*, [appi.ajp.2014.13121635](https://doi.org/10.1176/appi.ajp.2014.13121635).
- Wade, S., & Hammond, G. (2015). Anodal transcranial direct current stimulation over premotor cortex facilitates observational learning of a motor sequence. *Eur J Neurosci*.

- Wildgruber, D., Ackermann, H., Klose, U., Kardatzki, B., & Grodd, W. (1996). Functional lateralization of speech production at primary motor cortex: a fMRI study. *Neuroreport*, *7*, 2791-2795.
- Willems, R. M., Ozyurek, A., & Hagoort, P. (2007). When language meets action: the neural integration of gesture and speech. *Cereb Cortex*, *17*, 2322-2333.
- Wilson, M. (2013). What do the mirror system, embodied cognition, and synaesthesia have to do with each other? *Cortex*, *49*, 2949-2950.
- Wright, P., Randall, B., Marslen-Wilson, W. D., & Tyler, L. K. (2011). Dissociating linguistic and task-related activity in the left inferior frontal gyrus. *J Cogn Neurosci*, *23*, 404-413.
- Zhu, Z., Hagoort, P., Zhang, J. X., Feng, G., Chen, H. C., Bastiaansen, M., & Wang, S. (2012). The anterior left inferior frontal gyrus contributes to semantic unification. *Neuroimage*, *60*, 2230-2237.