

Action Understanding Requires the Left Inferior Frontal Cortex

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Summary

Numerous studies have established that inferior frontal cortex is active when hand actions are planned [1], imagined [2], remembered [3], imitated [4], and even observed [5]. Furthermore, it has been proposed that these activations reflect a process of simulating the observed action to allow it to be understood [6, 7] and thus fully perceived. However, direct evidence for a perceptual role for left inferior frontal cortex is rare, and linguistic [8] or motor [9] contributions to the reported activations have not been ruled out. We used repetitive transcranial magnetic stimulation (rTMS) over inferior frontal gyrus during a perceptual weight-judgment task to test the hypothesis that this region contributes to action understanding. rTMS at this site impaired judgments of the weight of a box lifted by a person, but not judgments of the weight of a bouncing ball or of stimulus duration, and rTMS at control sites had no impact. This demonstrates that the integrity of left inferior frontal gyrus is necessary to make accurate perceptual judgments about other people's actions.

Results

The role of frontal cortex in human cognition has been debated since the 1860's, when Broca demonstrated the left inferior frontal cortex, in particular Brodman area 44 (BA44), is essential for language [10]. More recently, it has been suggested that this area is part of a mirror neuron system for action representation [6]. In the macaque, neurons in region F5 within the inferior frontal cortex fire when the monkey performs or observes an action [11, 12]. Similar neurons are believed to exist in the human inferior frontal gyrus (IFG), and studies have shown that this region is activated by both motor planning [1] and action observation [2]. However, not all studies report these effects [13], and it is not known if or how the human mirror neuron system contributes to cognitive tasks.

As with Broca's original studies, examination of patients with focal brain lesions has the potential to define the role of IFG in action understanding more clearly. However, few studies have explicitly examined action

understanding in patients with damage to left inferior frontal cortex (an exception is [14]), and interpretations are complicated by the aphasia that normally accompanies such damage. An alternative approach is to use repetitive transcranial magnetic stimulus (rTMS), which acts as a virtual lesion [15] and can impair the performance of healthy participants on specific tasks. We have used rTMS over left IFG in this way while participants performed either a task that requires action understanding or a control task. Different interpretations of the role of the human frontal mirror neuron system make different predictions for this experiment.

The most widely circulated hypothesis argues that mirror neurons provide a representation of actions that allows the observer to simulate the observed action in his own motor repertoire system and thus understand the goals or intentions of the actor [6, 7]. Variations on this hypothesis describe a "direct-matching" process between a performed and observed action [16] or suggest that mirror neurons are crucial for predicting another person's actions [17]. The central proposal is that the principal function of mirror neurons is to allow us to understand other people's actions by reference to our own, and thus we refer to all these as the action-understanding hypothesis. This hypothesis predicts that without the mirror neurons found in IFG, it would not be possible to interpret observed actions fully.

A second possibility is that mirror neurons contribute principally to motor planning or action preparation. For example, people tend to unconsciously imitate the movements of others [18], and mirror neurons may facilitate this process. Numerous fMRI experiments show that IFG is activated when participants imagine moving their hands [2], imitate finger movements [4, 19], observe hand actions with the intention of imitating them [20], or plan to make hand actions [1]. Under this motor hypothesis, activation of IFG during action-observation tasks is principally a motor phenomenon [9], and disruption of this region should impair imitation performance (as shown [21]) but not impact on perceptual or cognitive judgments about the act observed.

The third hypothesis for the role of mirror neurons in human IFG is a linguistic one. It is undisputed that left IFG has a central role in the comprehension and production of spoken language [22–24] as well as internal speech [8]. Activations reported in left IFG during action-observation tasks could therefore reflect linguistic encoding or subvocalization rather than processes specific to action understanding. This language hypothesis predicts that disruption of IFG should not have any specific impact on action understanding, but rather should impair all tasks equally.

To distinguish among these hypotheses, we applied rTMS to left IFG or to left occipital cortex (V1/V2) as a control site while participants performed a task that requires action understanding or a control task. The action-understanding task (Figure 1A) was a perceptual weight-judgment task; that is, participants observed

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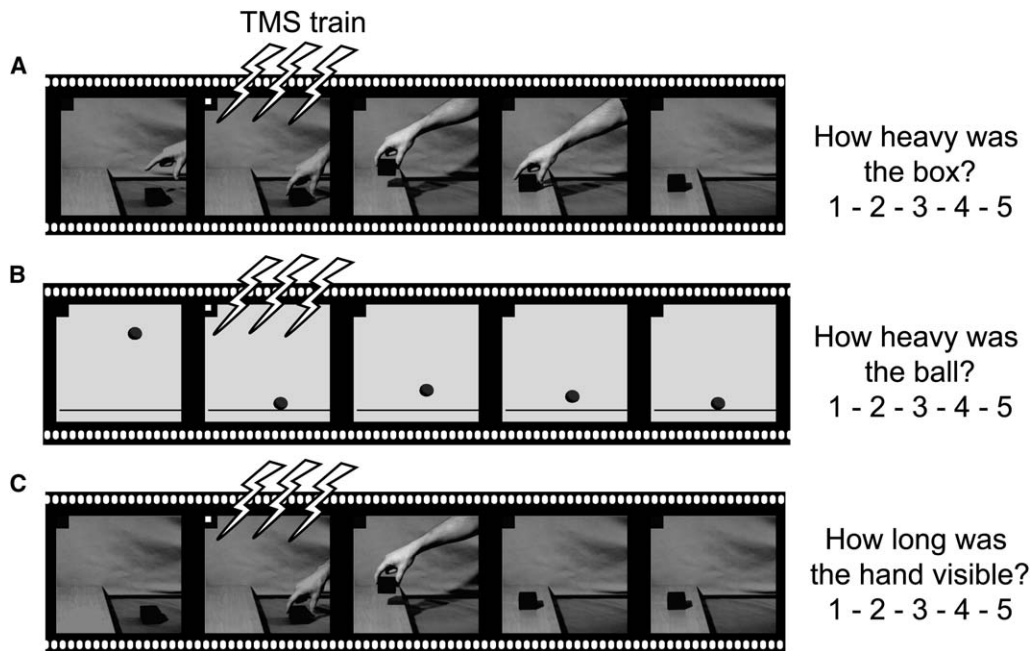


Figure 1. Stimuli

(A) Action-understanding task. Participants observed a hand lifting a box and placing it on a shelf and were required to judge the weight of the box on a scale from 1 to 5. rTMS was applied at the moment when the hand grasped the box.
(B) Ball control task. Participants observed a ball falling from the top of the screen and bouncing and were required to judge the weight of the ball. rTMS was applied at the moment when the ball bounced.
(C) Duration judgement control task. Participants observed video clips where the hand appeared near the time of grasp and disappeared near the time when the box was placed on the shelf and were required to judge how long the hand was visible for. rTMS was applied when the hand grasped the box.

a video clip of a hand lifting a box and placing it on a shelf and they were required to judge the weight of the box. This task is natural but not trivially easy [25] and requires a detailed assessment of the kinematics of the observed action [26]. Previous investigations have shown that performing weight judgment concurrently with a motor task results in systematic biases in the perceptual judgements of box weight [27], and this bias was recently localized to IFG [28]. Thus, we have reason to believe that the weight-judgement task engages the mirror neuron system and provides a sensitive test of the ability to interpret other people's actions.

We compared performance on the weight-judgment task to two control conditions in two experiments. For experiment 1, nine participants were required to judge the weight of a box by observing a video clip of a hand lifting the box and placing it on a shelf (Figure 1A), or to judge the weight of an observed bouncing ball in a control condition (Figure 1B). For experiment 2, we replicated the box weight-judgement task (Figure 1A) and compared performance to a duration-judgement task where participants observed excerpts of the video clip showing a hand lifting a box and were required to judge how long the hand was visible on the screen (Figure 1C). Thus, in experiment 1, participants perform the same task on a human and nonhuman stimulus set, while in experiment 2 participants always observed a human action, but performed a task that either did or did not require understanding of that action. During each video clip, participants received rTMS either to left IFG or to occipital cortex, or experienced sham stimulation or

no stimulation. We predicted that if IFG is necessary for action understanding, performance on the weight-judgment task when observing a lifting hand would be impaired during stimulation of this site, but not for any other site or for the bouncing ball stimuli.

Performance for each participant in each block was summarized by the r^2 of the linear regression between the correct responses and the participant's judgements, which gives a single measure incorporating both accuracy and variability. Means and standard errors over participants for each condition are shown in Figure 2. The r^2 values for all participants and all conditions in experiment 1 were submitted to a repeated measures ANOVA with factors stimulus (lifting hand or bouncing ball) and rTMS site (IFG, no TMS, occipital, or sham). A significant main effect of stimulus type was observed ($F = 50.8$, $df = 1,8$, $p < 0.001$), as well as a significant effect of stimulation site ($F = 5.52$, $df = 3,24$, $p = 0.005$). More importantly, there was a significant interaction between the stimulus type and site of stimulation ($F = 3.24$, $df = 3,24$, $p = 0.04$). Post-hoc paired t tests comparing judgments in the hand condition for all stimulation sites revealed reliably impaired performance when IFG was stimulated, [IFG versus no TMS, $t(8) = 4.3$, $p = 0.003$]; [IFG versus occipital, $t(8) = 2.565$, $p = 0.033$]; [IFG versus sham, $t(8) = 2.37$, $p = 0.046$]. None of the post-hoc tests for the ball condition were significant.

An equivalent analysis was performed for the results of experiment 2. The r^2 values for all participants and all conditions were submitted to a repeated measures ANOVA with factors task (judge weight or judge

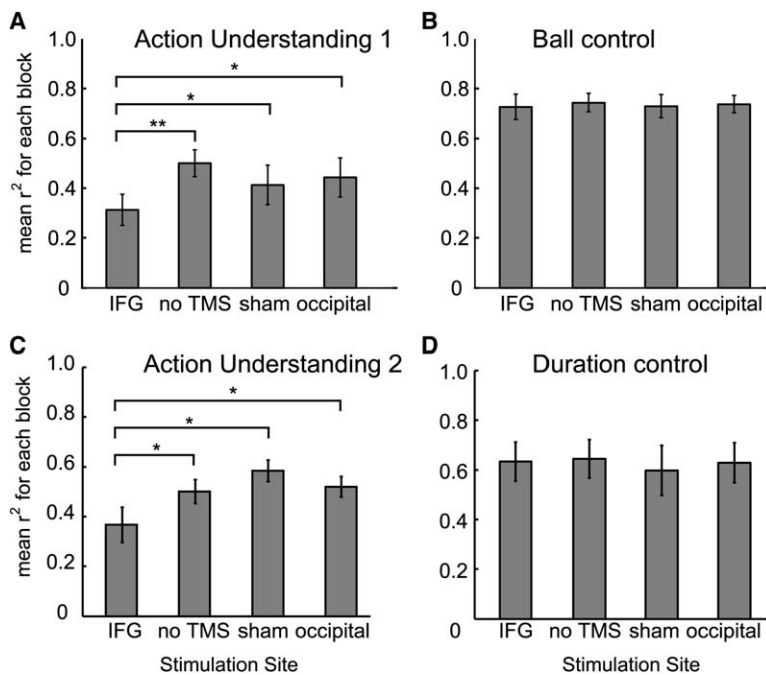


Figure 2. Results

Performance is measured by the r^2 between the participant's judgments and the correct response and is illustrated for each task.

(A) Performance on the action-understanding task (task A, experiment 1) was impaired when left IFG was stimulated compared to all other sites.

(B) Performance on the ball control task (task B, experiment 1) did not change with rTMS over any site.

(C) As before, performance on the action-understanding task (task A, experiment 2) was impaired during rTMS over left IFG but not rTMS of any other sites.

(D) Performance on the duration control task (task C, experiment 2) did not change with rTMS over any of the test sites. In all plots, ** indicates conditions differed in a t test at $p < 0.005$, and * indicates significance at $p < 0.05$. Error bars are the standard error of the mean.

duration) and rTMS site (IFG, no TMS, occipital, or sham). There was a main effect of task ($F = 9.67$, $df = 1,8$, $p = 0.014$) and a main effect of stimulation site ($F = 3.08$, $df = 3,24$, $p = 0.046$). As before, we found a significant interaction between task and site ($F = 3.61$, $df = 3,24$, $p = 0.028$). Post-hoc paired t tests were used to compare performance in each of the box weight-judgment conditions and revealed that performance was significantly impaired by stimulation of IFG [IFG versus no TMS, $t(8) = 2.74$, $p = 0.025$; IFG versus occipital, $t(8) = 3.19$, $p = 0.013$; IFG versus sham, $t(8) = 2.36$, $p = 0.046$].

As there was a main effect of task in both experiments, it could be argued that the impaired judgment of box weight during IFG stimulation was due to a general task difficulty effect, i.e., that performance on the action-understanding task dropped just because this task was difficult. If this was the case, we would expect that participants who found the control tasks difficult without TMS would show even worse performance during stimulation of IFG. Performance on the ball control task with no TMS ranged from 0.58 to 0.93, while performance on the duration judgment control task with no TMS ranged from 0.24 to 0.98, providing a sufficient range to test this possibility. We therefore calculated the correlation between performance on the ball and duration control tasks with no TMS and effect of TMS on each of these tasks, assessed as the difference between performance during IFG stimulation and occipital stimulation. We found no evidence of a correlation in any case (ball control: $r^2 = 0.02$, $p = 0.65$; duration control: $r^2 = 0.05$, $p = 0.55$). Thus, there is no evidence that a general task difficulty effect is responsible for impaired performance on the action-understanding task when IFG is stimulated.

Discussion

Overall, the data reveal that performance in judging the weight of a lifted box was impaired during stimulation

of left IFG relative to all other conditions (Figures 2A and 2C). However, judgments of the weight of a bouncing ball were not affected by rTMS (Figure 2B), nor were judgments of the duration for which the hand was visible (Figure 2D). Thus, we find that rTMS applied to IFG reduces performance on the action-understanding task only. This result is not compatible with the hypothesis that activity in IFG during action observation reflects subvocalization or language processing, because all the tasks required equivalent degrees of vocalization to make judgments on a 1–5 scale, and participants were able to perform the weight-judgment task without difficulty when the stimuli depicted a bouncing ball rather than a lifting hand. The result is also incompatible with the motor hypothesis, because we demonstrate impaired performance in a perceptual task with no imitation and no motor component beyond a simple key press. However, our result was predicted by the action-understanding hypothesis, and thus we suggest that the integrity of left IFG is critical for a perceptual judgment task that requires the understanding of human actions.

Evidence in favor of the action-understanding hypothesis has also been reported in other studies. In particular, TMS over IFG impairs the imitation of hand actions but not simple production [21], implicating this region in action understanding. A number of fMRI studies show that the IFG is activated when participants observe human actions [3, 5, 19]. In particular, it has been shown that activation of inferior frontal regions is greater when participants observed human actions than when they observed robot actions [29]. This result is coherent with our finding that the effects of rTMS were specific to the observation of a lifting hand and that judgements of ball weight were not affected.

There has been some debate over how “biological” or “human” a stimulus must be to activate IFG. Our results suggest that this is an overly simplistic question. In

experiment 2, we found that rTMS of IFG impaired performance only on the weight-judgment task, even though both tasks required close observation of a human action. However, experiment 1 demonstrated that not all weight judgment requires IFG; only the judgment of weight from human action was impaired by TMS over this site. Thus, it seems that left IFG is specifically required for tasks that involve the interpretation of a human action, and neither a weight-judgement task nor visual images of human action are in themselves sufficient to drive this region. The question of how biological a stimulus must be is therefore less important than the task that the participant is performing, and we suggest that any task that requires a detailed assessment of a human action would be likely to invoke IFG.

This interpretation is coherent with a recent action-observation study that showed that the frontal mirror neuron system is activated even when watching animal actions, if the animals perform movements that humans can also perform [30]. In addition to a role in action observation, IFG is known to contribute to motor tasks. In particular, this region is activated in fMRI when actions are imagined [2, 31] or planned [32]. However, execution of simple actions does not necessarily activate these areas. What is the common feature of all these studies that demonstrate the involvement of IFG?

We suggest that the need to simulate the observed, planned, or imaged action is found in many of the tasks that require IFG, including the weight-judgement task tested here. Such a simulation need not be conscious or explicit but would involve a detailed motoric representation of changes in kinematic parameters over the course of an action. There is evidence from previous weight-judgement studies that this task requires the ability to simulate actions. Hamilton et al. [27] demonstrated that lifting a box systematically biases your perceptual judgements of the weight of another person's box and interpreted this as evidence that a motor simulator or internal model is necessary to judge weight by observation. A recent paper that uses the weight-judgement task supports this idea. Bosbach and colleagues show that somatosensory and proprioceptive experience is needed to assess an actor's expectation of the weight of a box [33], though not to judge the physical box weight by observation. Again, the authors argue that the lack of a motor simulation in the patients tested could account for their poor performance in understanding the actor's expectation of box weight.

There is also prior evidence linking left IFG to the weight-judgment task. Inferior frontal activations in fMRI were reported when participants judged the beliefs of another actor based on their box-lifting behavior [34]. Furthermore, inferior frontal cortex was found to be a part of the network where motor processing modulates perceptual judgments of perceived human actions [28]. Taken together, these results suggest that IFG is required for perceptual weight judgment, and that perceptual weight judgement requires a motor simulation or internal model of the observed action. We do not claim that IFG is the only brain region contributing to the simulation of other people's actions. Action understanding is a complex skill and a network of brain regions is likely to be required. In particular, the inferior parietal cortex, which is part of the human mirror neuron system [6],

and regions subserving proprioceptive knowledge [33] may also play a role.

Our data demonstrate that left IFG is necessary for accurate weight-judgement performance. Thus, we provide direct evidence in support of the action-understanding hypothesis of the mirror neuron system proposed by Rizzolatti and colleagues [6, 7]. We suggest that motor simulation is a necessary component of perceptual judgements about other people's actions, and this simulation requires the integrity of left IFG.

Experimental Procedures

14 healthy naive volunteers (9 male, 5 female) aged between 21 and 35 gave their written informed consent in accordance with the requirements of the local ethics committee. Five took part in experiment 1, five in experiment 2, and four completed both experiments with at least 9 months between the two experimental sessions. For experiment 1, the nine participants saw a video clip of either a hand lifting a box and placing it on a shelf (Figure 1A) or a bouncing ball (Figure 1B). Each video was followed by the question "How heavy was the box/ball?" which was answered by pressing a key with the right hand to indicate a number from one to five. For experiment 2, the nine participants saw video clips of a hand lifting a box (Figures 1A and 1C) and judged the weight of the box or the duration for which the hand was visible on the screen. In all cases, the video stimuli were 4.4 s clips depicting either a hand lifting a box and placing it on a shelf or a bouncing ball. Trials were presented in a pseudo-random order in blocks of 80 trials of the same task. All video clips were presented by the Cogent toolbox running in Matlab 6.5 at a resolution of 512 × 480 pixels and 25 frames per s on a 17 inch CRT monitor.

Video clips of the lifting hand were generated by downsampling a single high-speed clip of a lifting hand to create "perfect" lifting movements, as previously described [26, 28]. For task A, the five clips depicted the true kinematic behavior observed when boxes of different weights are lifted, with weights ranging from approximately 50 g to 850 g. Correct responses were the numbers 1 to 5, with 1 assigned to the lightest box, and 2, 3, 4, and 5 to each remaining box in order of weight, with 5 as the heaviest. For task C, all clips depicted a hand lifting a mid-weight box. The hand appeared at the moment of grasp and disappeared when the box was placed on the shelf, so it was visible on the screen only during the lifting action. The precise duration of hand visibility was varied between 72 and 92 frames, giving five clips with different hand durations. Again, correct responses were the numbers 1 to 5, with 1 corresponding to the briefest duration and 5 to the longest. For the bouncing ball stimulus set, Matlab (<http://www.mathworks.com>) was used to generate five video clips depicting a ball falling from the top of the screen and bouncing two or three times with realistic dynamics. Correct responses were the numbers 1 to 5, with 1 corresponding to the lightest ball and 5 to the heaviest. All video clips included a white trigger signal in the corner of the 25th frame, which appeared at the point when the actor's hand grasped the box or when the ball first bounced, one second into the clip. A photodiode placed on the corner of the display monitor detected the signal and directly triggered the rTMS train, thus providing precise synchronization between the video clips and the TMS pulses.

The experiment began with a practice block of 80 trials for each stimulus set. Participants then performed blocks of 80 trials under four stimulation conditions: (1) rTMS applied to left IFG, (2) rTMS applied to left occipital cortex, (3) sham rTMS, and (4) no stimulation. Block order was counterbalanced across participants according to a latin square. Repetitive TMS was delivered at 5 Hz for 500 ms, by a Magstim Super-Rapid transcranial stimulator (Magstim Co., Whitland, UK) and a 70 mm figure-of-eight coil that produced maximum output of 2.5 Tesla. With this coil configuration, the magnetic fields generated by both halves of the coil will add up, ensuring that the induced current is strongest in the region directly beneath the center of the coil [35].

The target location for rTMS in the left inferior frontal gyrus was the pars opercularis (Talariach coordinates: -42.5, 11.6, 19.9) [36],

which is likely to include BA44. To localize this site, each participant's high-resolution anatomical MRI scan was normalized to the MNI template in SPM2, and the point (−42.5, 11.6, 19.9) was marked. All marked locations fell within the inferior frontal gyrus. The equivalent location was then found on the unnormalized scan, and frameless stereotaxy (Brainsight, <http://www.rogue-research.com>) was used to position the coil on the participant's head over the desired site. The coil was securely held against the left temple, centered over IFG, and oriented such that the maximal induced current flowed approximately in the anterolateral direction.

TMS can have nonspecific effects due to tactile or auditory sensations. The optimal control for artifacts is to have both task and site controls [37]. We controlled for site by applying TMS at different sites so that these artifacts were present over other brain areas. Particular care was taken in the placing of the IFG coil because TMS here is more uncomfortable than over occipital or parietal areas. We manipulated coil orientation (a major factor in the nature of the tactile artifact) to find an orientation that minimized the discomfort to a subjective equivalent to that of the stimulation over other sites. As detailed above, we also used two task controls, with judgments of the weight of a bouncing ball and of the duration of hand visibility, to ensure that neither TMS discomfort nor task difficulty effects could explain the observed results.

The control rTMS location was V1/V2, defined as the site located 2 cm lateral from and 2 cm below theinion, and at this site the coil was oriented such that the maximal induced current flowed downwards [37]. All participants reported seeing phosphenes when single pulses were applied at this location in a completely dark room. For both sites, the output strength of the TMS machine was set at 110% of the subject's motor threshold. A sham stimulation condition was also used to control for nonspecific effects of TMS, such as sound. The coil was held tangentially over the vertex, so that any cortical effects are unlikely to occur. Average motor threshold was 58% of the maximal stimulator output, and the average stimulation intensity during rTMS was 64%. All subjects reported similar subjective sensations during the task for all three rTMS sites.

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References

1. Johnson, S.H., and Grafton, S.T. (2003). From 'acting on' to 'acting with': the functional anatomy of object-oriented action schemata. *Prog. Brain Res.* 142, 127–139.
2. Grafton, S.T., Arbib, M.A., Fadiga, L., and Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp. Brain Res.* 112, 103–111.
3. Johnson-Frey, S.H., Maloof, F.R., Newman-Norlund, R., Farrer, C., Inati, S., and Grafton, S.T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron* 39, 1053–1058.
4. Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., and Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science* 286, 2526–2528.
5. Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., and Freund, H.J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404.
6. Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
7. Gallese, V., and Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2, 493–501.
8. Hinke, R.M., Hu, X., Stillman, A.E., Kim, S.G., Merkle, H., Salmi, R., and Ugurbil, K. (1993). Functional magnetic resonance imaging of Broca's area during internal speech. *Neuroreport* 4, 675–678.
9. Jacob, P., and Jeannerod, M. (2005). The motor theory of social cognition: a critique. *Trends Cogn. Sci.* 9, 21–25.
10. Broca, P. (1861). Perte de la parole, ramollissement chronique et destruction partielle du lobe antérieur gauche du cerveau. *Bulletin de la Société Anthropologique* 2, 235–238.
11. Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain* 119, 593–609.
12. Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G., and Orban, G.A. (2005). Observing others: multiple action representation in the frontal lobe. *Science* 310, 332–336.
13. Grezes, J., and Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum. Brain Mapp.* 12, 1–19.
14. Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., and Damasio, A.R. (2003). Neural correlates of conceptual knowledge for actions. *Cogn. Neuropsychol.* 20, 409–423.
15. Walsh, V., and Rushworth, M. (1999). A primer of magnetic stimulation as a tool for neuropsychology. *Neuropsychologia* 37, 125–135.
16. Buccino, G., Binkofski, F., and Riggio, L. (2004). The mirror neuron system and action recognition. *Brain Lang.* 89, 370–376.
17. Wilson, M., and Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychol. Bull.* 131, 460–473.
18. Chartrand, T.L., and Bargh, J.A. (1999). The chameleon effect: the perception-behavior link and social interaction. *J. Pers. Soc. Psychol.* 76, 893–910.
19. Molnar-Szakacs, I., Iacoboni, M., Koski, L., and 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.
20. Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K., Freund, H.J., and Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 42, 323–334.
21. Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., and Mazziotta, J.C. (2003). The essential role of Broca's area in imitation. *Eur. J. Neurosci.* 17, 1123–1128.
22. Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., and Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain* 114, 1803–1817.
23. Stromswold, K., Caplan, D., Alpert, N., and Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain Lang.* 52, 452–473.
24. Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu. Rev. Neurosci.* 25, 151–188.
25. Runeson, S., and Frykholm, G. (1981). Visual perception of lifted weight. *J. Exp. Psychol. Hum. Percept. Perform.* 7, 733–740.
26. de C. Hamilton, A.F., Joyce, D.W., Flanagan, J.R., Frith, C.D., and Wolpert, D.M. (2005). Kinematic cues in perceptual weight judgment and their origins in box lifting. *Psychol. Res.*, in press. Published online November 26, 2005. 10.1007/s00426-005-0032-4.
27. Hamilton, A., Wolpert, D.M., and Frith, U. (2004). Your own action influences how you perceive another person's action. *Curr. Biol.* 14, 493–498.
28. de C. Hamilton, A.F., Wolpert, D.M., Frith, U., and Grafton, S.T. (2005). Where does your own action influence your perception of another person's action in the brain? *Neuroimage*, in press. Published online August 22, 2005. 10.1016/j.neuroimage.2005.07.037.
29. Tai, Y.F., Scherfler, C., Brooks, D.J., Sawamoto, N., and Castiello, U. (2004). The human premotor cortex is 'mirror' only for biological actions. *Curr. Biol.* 14, 117–120.

30. Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C.A., and Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspicuous: an fMRI study. *J. Cogn. Neurosci.* *16*, 114–126.
31. Johnson, S.H., Rotte, M., Grafton, S.T., Hinrichs, H., Gazzaniga, M.S., and Heinze, H.J. (2002). Selective activation of a parieto-frontal circuit during implicitly imagined prehension. *Neuroimage* *17*, 1693–1704.
32. Johnson-Frey, S.H., Newman-Norlund, R., and Grafton, S.T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cereb. Cortex* *15*, 681–695.
33. Bosbach, S., Cole, J., Prinz, W., and Knoblich, G. (2005). Inferring another's expectation from action: the role of peripheral sensation. *Nat. Neurosci.* *8*, 1295–1297.
34. Grezes, J., Frith, C.D., and Passingham, R.E. (2004). Inferring false beliefs from the actions of oneself and others: an fMRI study. *Neuroimage* *21*, 744–750.
35. Jalinous, R. (1995). *Guide to Magnetic Stimulation* (Whitland, Wales: Magstim).
36. Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H.B., and Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *J. Comp. Neurol.* *412*, 319–341.
37. Walsh, V., and Pascual-Leone, A. (2003). *Transcranial Magnetic Stimulation: A Neurochronometrics of the Mind* (Cambridge, MA: The MIT Press).