

Aplasics Born without Hands Mirror the Goal of Hand Actions with Their Feet

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Summary

The premotor and parietal mirror neuron system (MNS) is thought to contribute to the understanding of observed actions by mapping them onto “corresponding” motor programs of the observer [1–24], but how would the MNS respond to the observation of hand actions if the observer never had hands? Would it not show changes of blood-oxygen-level dependent (BOLD) signal, because the observer lacks motor programs that can resonate [12, 25, 26], or would it show significant changes because the observer has motor programs for the foot or mouth with corresponding goals [15, 17, 19, 27, 28]? We scanned two aplasic subjects, born without arms or hands, while they watched hand actions and compared their brain activity with that of 16 control subjects. All subjects additionally executed actions with different effectors (feet, mouth, and, for controls, hands). The BOLD signal of aplasic individuals within the putative MNS was augmented when they watched hand actions, demonstrating the brain’s capacity to mirror actions that deviate from the embodiment of the observer by recruiting voxels involved in the execution of actions that achieve

corresponding goals by different effectors. This sheds light on the functional organization of the MNS and predominance of goals in imitation.

Results and Discussion

A detailed description of the experiments can be found in the [Supplemental Data](#) available online. In brief, two aplasic and 16 typically developed (TD) individuals participated in two functional magnetic resonance imaging (fMRI) experiments. In the first, they observed movies of hands manipulating various objects (HandAction, e.g., grasping a cocktail glass or scooping soup out of a bowl) as well as static images of the hands resting behind the same objects (HandStatic). In the second experiment, all participants were asked to manipulate an object with their lips (MouthExe), their toes (FootExe), or, for the typically developed individuals, their hands (HandExe). The execution experiment was always performed after the observation to avoid biasing visual activations toward motor areas.

We initially contrasted the brain activity resulting from viewing the hand actions against the activity resulting from viewing the static hand and object (HandAction-HandStatic; [Figure 1](#)). Both aplasic subjects and the typically developed (TD) controls activated, during action observation, a bilateral circuit composed mainly of frontal, parietal, and temporal clusters corresponding to that reported in the literature [4, 7, 10–13, 15, 18, 19, 29] ([Figure 1B](#) and [Table S1](#); all results also survived FDR correction even at 0.005 over the entire brain). No significant differences were found between the two aplasic subjects and the 16 TD participants (two-sample *t* test, voxel-by-voxel, with a very lenient threshold of $p < 0.5$ FDR corrected), suggesting that the visual activation in the aplasic subjects were in the range of normal variability. A graphical comparison of the activation patterns of the 16 TDs ([Figure S1](#)) reveals substantial variation in the location and extent of visual activations. The brain activity of the two aplasic individuals fell within the range of this variability, with some TDs showing relatively less and others more activations.

The classical definition of the MNS requires an overlap of brain activations related to the observation of an action and the execution of a similar action [1, 11, 17, 18]. For the TD group, we therefore inclusively masked the visual contrast HandAction-HandStatic with the brain activation elicited during the execution of hand actions ([Figure 2](#), lower right) and thus found a bilateral putative mirror circuit composed of frontal (BA6, SFG/MFG, preCG, and left BA44), parietal (SI, SII, SPL, and the supramarginal gyrus of the inferior parietal lobule), and temporal (MTG/ITG) cortices (see [Table S3](#)). Half of the TDs had voxels involved during observation and execution also in mesial BA6 (MNI: $x = 0$, $y = 6$, and $z = 54$) in locations considered to belong to the supplementary and presupplementary motor cortex. This supports

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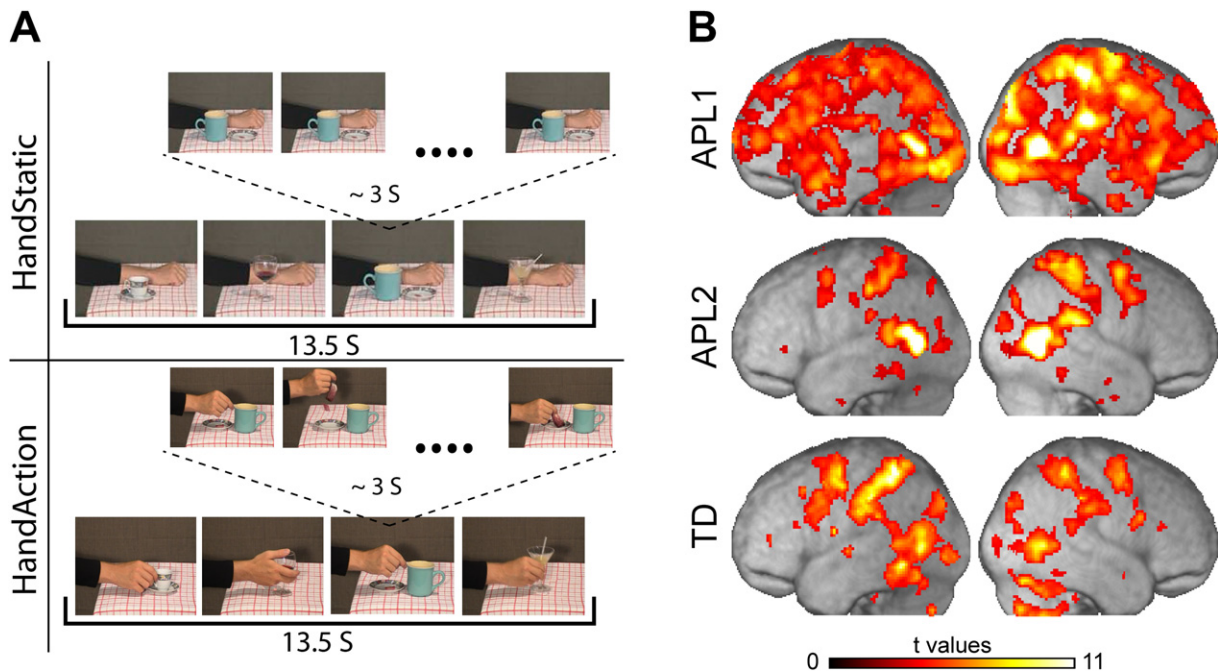


Figure 1. Design and Results of the Visual Experiment

(A) Experimental stimuli and design during action observation. Four video clips from the HandAction or the HandStatic category formed a block. (B) Activations during action observation. The upper four renders show the activations resulting from the contrast HandAction-HandStatic for the two aplastic subjects (APL1 and APL2), and the lowest two show the activations resulting from the contrast HandAction-HandStatic for the typically developed individuals (TDs). All activations are rendered on the average anatomy of all 18 subjects (16 TDs + 2 APL, $p_{unc} < 0.001$ and $p_{FDR} < 0.05$).

the idea that these regions may also be part of the human MNS [30].

In aplastic subjects, masking with activation maps related to hand execution is obviously impossible. In their seminal work, Gallese and coworkers [1] described that the most frequent subtype of mirror neurons (“broadly congruent”) often responded during the execution of an action with a particular effector (e.g., grasping with the hand) and during the observation of a similar action performed by the same or a different effector (e.g., grasping with the hand or the mouth). Voxels that are active during the observation of manipulative hand actions and during the execution of manipulative foot or mouth actions should therefore also be considered to be part of the MNS. We therefore used brain activation during foot or mouth execution (Figure 2, upper left) to examine whether the vision of hand actions recruited the putative MNS in aplastic subjects. For comparison, we also masked the data of the TD group with their brain activations during foot or mouth execution (Figure 2, lower left). In all cases, fronto-parieto-temporal areas were activated both during observation and execution, suggesting the existence of a MNS for observed hand actions also in aplastic subjects (Tables S2 and S3). In the same TD group, we also contrasted the vision of hand actions with the vision of meaningless hand movements not involving manipulations [28]. Results indicated that this fronto-parieto-temporal system responds significantly more to the observation of manipulation than other biological motion (hand movements not involving an object), supporting the interpretation of these areas as part of the MNS [28]. In addition,

to examine whether the vision of hand actions in aplastic individuals recruited regions that in TDs would respond during the execution of hand actions, we also masked the visual activations in aplastic individuals with the hand execution data of the TDs (Figure 2, upper right).

To directly compare the amplitude of mirror activations in aplics and TDs, we extracted the BOLD signal for the contrast HandAction-HandStatic in the putative mirror regions of the TDs (Figure 3). In all regions (pre-motor, parietal, and temporal) the contrast values of the two aplics fell between the first and third quartile of the TDs; i.e., in these regions at least four of the TDs showed less and four more activations than the aplastic individuals. The nonparametric Mann-Whitney U test, examining the rank order of the aplastic individual’s contrasts within the distribution of all 18 subjects, identified no evidence for hypoactivation in aplastic individuals (all $p > 0.39$). This indicates that, at least within the putative MNS, the lack of significant differences observed with the voxel-wise two-sample t test was not because of a lack of statistical power. By defining the mirror regions on the TDs, this test was systematically biased in favor of the TDs and thereby strengthened the significance of the absence of hypoactivation in the aplics.

To examine the nature of the motor programs activated by the sight of hand actions, we differentiated, in both TDs and aplics, putative mirror areas that during execution were selective for a particular effector from those that were not (see Motor Decomposition and Characterization of Visual Activations in the Supplemental Data and Figure S2). While viewing hand actions, both TDs and aplics activated a combination of

PUTATIVE MIRROR SYSTEM FOR HAND ACTIONS

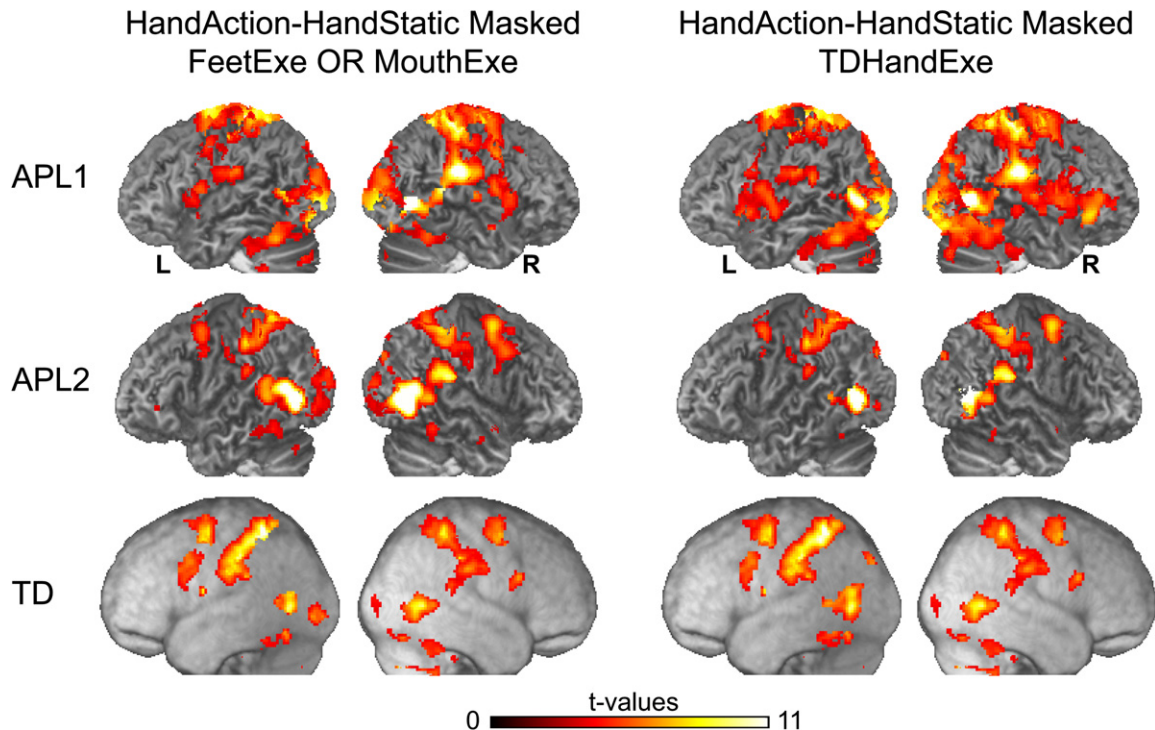


Figure 2. Putative Mirror System for Actions

The left two columns show putative hand MNS for aplastic subjects (APL1 and APL2) and typically developed individuals (TD), defined by inclusively masking the visual contrast HandAction-HandStatic with their FeetExecution or MouthExecution. The right two columns show the same but defined by masking with TD's HandExecution. For APL1-2, activations are rendered on the individual's own anatomy, and for TDs, activations are rendered on the average anatomy of the 16TDs ($p_{unc} < 0.001$ for the visual and motor contrast separately, and $p_{tdr} < 0.05$ applied after inclusively masking observation by execution).

effector-unspecific areas and regions devoted to the effector that the observer would use to perform the observed action: the hand for TDs and the foot or mouth for aplasics.

Our main finding that during the observation of hand actions both aplastic individuals robustly activated regions generally attributed to the MNS [1, 4, 6, 8–11, 15, 16, 18, 20, 21, 23] and involved in the execution of foot or mouth actions has important implications for our understanding of the MNS.

As pointed out in the introduction, the MNS is generally assumed to associate observed actions with “corresponding” motor programs of the observer [1–24]. What though is exactly meant by “corresponding”? Two aspects of actions can be distinguished: their goals and their means. If I remove the cap of a fountain pen with my mouth, my hands, or my toes, the goal of the action (i.e., what is being immediately achieved) remains the same (“removing the cap”), whereas the means (i.e., effector and kinematics) used to achieve this goal differ. This pragmatic definition of goal does not necessarily refer to a further purpose (e.g., removing the cap to write a love letter) or sense of intentionality. Distinguishing goals and means raises the question of whether the MNS associates observed actions with (1) motor programs for corresponding goals, (2) for corresponding means, or (3) a combination of (1) and (2).

In the monkey, the MNS is composed of at least two types of mirror neurons: “strictly congruent” mirror neurons (scMNs), which only respond to the sight of an action if it has the same goal and uses the same effector as the effective executed action, and “broadly congruent” mirror neurons (bcMNs), which also respond when the observed action involves a different effector—as long as it has the same goal. Such bcMNs may respond during the execution of grasping with the hand and during the observation of grasping with the hand (same goal, same effector) or the mouth (same goal, different effector) but not during the vision of placing with the hand (different goal, same effector) [1, 9]. The bcMNs are approximately twice as abundant as the scMNs in the monkey [1]. Jointly, in the monkey, bcMNs and scMNs thus associate observed actions with a combination of actions with corresponding goals and means and action with corresponding goals but dissimilar means. The human MNS literature, in contrast, seduced by the potential contribution of the MNS for imitation [4, 7, 11, 22, 31–39], has focused onto the capacity of the MNS to associate observed actions with motor programs corresponding in terms of both means and goals. Concepts such as “direct matching” [4, 7] or “motor resonance” [22] reflect this focus, and experiments that show that the sight of actions performed with different effectors specifically recruit cortex regions that are involved in

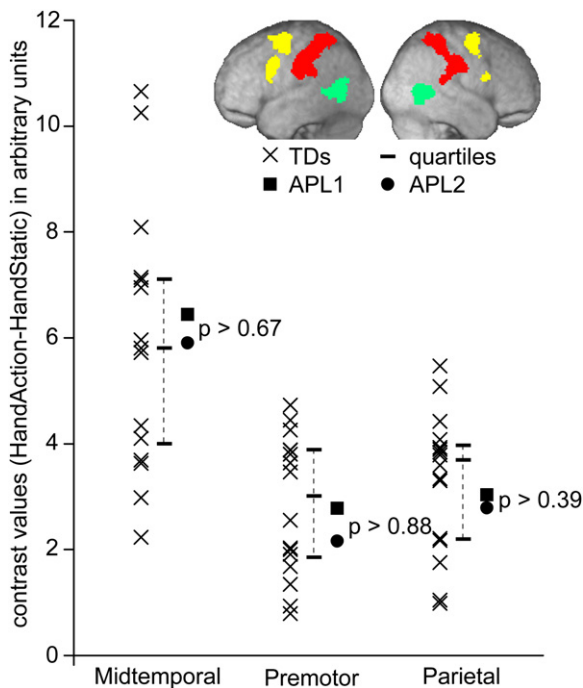


Figure 3. Visual Activations in the Putative MNS

The render shows the location of the three regions of interest derived from Figure 2 (right bottom row, HandAction-HandStatic inclusively masked with HandExe for TDs). In each case, the right and left regions of interest were combined. For each region, the graph plots the value of the observation contrast (HandAction-HandStatic) for each TD subject as a cross in the left column and for the two aphasics as a circle and a square in the right column. The dashes in the middle column represent the first, second (median), and third quartile of the TDs. Two sided, nonparametric Mann-Whitney U test comparing the contrast values of the TDs and aphasics had probabilities of $p > 0.67$, $p > 0.88$, and $p > 0.39$ for the midtemporal, premotor, and parietal cluster, respectively, showing that there is no evidence for hypoactivation of the mirror system in aphasic individuals.

the execution of actions with the same effector [6, 13, 18, 26] have fueled this focus to the point where goal matching had almost been forgotten.

Our main finding that both aphasic individuals robustly activate regions involved in mouth and foot execution provides direct evidence for the potential of goal matching to recruit the putative MNS even in the absence of a matching effector. Broadly congruent MNS similar to those found in monkeys could provide the neural substrate for this goal matching.

Evolutionary, what counts is achieving goals: If you are hungry, being capable of opening a nut matters; doing so by using your teeth or a stone does not. Indeed, young children tend to imitate the goal not the way in which an action is performed, unless the instructions clearly ask for that [27, 40–42]. In addition, when we observe other individuals, differences between the details of our bodies always introduce disparities between observed and executed actions. Overcoming such disparities, of which aphasia can be considered an extreme example, may be the evolutionary necessity that leads the MNS to also match goals of actions in an effector-independent fashion. A number of recent experiments on the mirror [5, 15, 17, 19, 28] and motor systems [43] agrees with this interpretation.

How may the brain of aphasic individuals have developed the capacity to associate motor programs of the foot or mouth with the vision of hand actions? A speculative possibility is that aphasic individuals often interact with TDs, and during joint actions, the hand actions of the TDs would often occur in synchrony with the foot and, to a lesser extent, the mouth actions of the aphasic individuals. This synchrony could have led to the enhancement of Hebbian associations between the sight of hand actions and motor programs for corresponding mouth or foot actions [20, 44].

A secondary finding of our study is that the amplitude of the putative MNS activations in the aphasic individuals during observation was within the range of normal variability in the TDs. If the activations of aphasic individuals within the putative MNS would have fallen within the lower quartile of the TDs' activations, this lack of significant differences would have been simply attributable to a lack of statistical power. Instead, the activations of both aphasic individuals fell within the center two quartiles of the TDs range, suggesting that a lack of power was not the reason for our negative finding. By itself, this negative finding, as with any negative finding, has to be interpreted with care; it does not prove that the average amplitude or spatial distribution of the visual activations within the aphasic individuals was equal to that of the TDs but simply shows that the difference between these patterns was small compared to the variance between the subjects.

In a separate experiment, the same TDs [28] were shown movies of (1) a human and (2) an industrial robot performing the same actions. During the vision of human actions, TDs have motor programs that match both in terms of means and goals, whereas during the vision of robotic actions, they only have motor programs with corresponding goals: Robotic actions differ in terms of effector (robotic claw versus human hand) and kinematics from motor programs TDs would use to perform these actions. The contrast HumanAction-RobotActions should thus quantify the amount of effector-specific motor programs that the putative MNS recruits during the vision of hand actions and be conceptually similar to the contrast between aphasic individuals and TDs in the present experiment. In agreement with the aphasic data, we found robust activations to the sight of actions for which the observer had no directly matching effector (RobotAction) in regions involved in the execution of hand actions in all our 16 TDs, and there was again no significant differences between the observation of actions with and without matching effector (Human—RoboticActions) within the putative MNS. Jointly, the lack of significant differences in both experiments indicates that when you observe actions of which you have achieved the goal yourself in the past, you will recruit your MNS to a “similar” degree whether your body includes the observed effector or not; by similar, we mean that if differences exist, they are small compared to interindividual differences within the population.

The emphasis on goals in our study is in apparent contrast with the observation of somatotopy in the MNS [6, 13, 18]. Why, if goals are so important, do we activate more dorsal sectors of the premotor cortex while listening to hand actions and more ventral sectors while

listening to mouth actions [18]? As shown in the monkey [1], the human MNS is likely to perform both goal and effector matching. In addition, goal matching does not preclude the recruitment of effector-specific motor programs. As evidenced in the case of apraxia, effector-specific motor programs (for the foot or mouth) are indeed recruited, even though the observer lacks the effector used by the observer. These recruited effector-specific programs may reflect the response of bcMNs that match the goal of observed actions onto whatever effector that the observer would use to perform these actions. What is remarkable in apraxia is that this most probable effector is not the one they most often see other people use to achieve the same goals. In this case, the activations therefore cannot be explained by a direct matching of the observed effector onto the corresponding effector (effector-effector route), and the data suggest the presence of a route mediate by the existence of other actions that achieve the same goal (effector-goal-effector route). In all experiments on somatotopy so far, this mismatch was not present [6, 13, 18]: Participants viewed or heard actions performed by the same effector that they would most probably use to perform these actions, and the proposed effector-goal-effector route would then activate the same effector-specific motor programs as a direct effector-effector route, thereby also contributing to the observed somatotopy. Experiments in which subjects observe actions performed by unusual effectors would help dissociate the contribution of the two pathways to somatotopy [18].

In the context of the role attributed to the MNS in imitation and learning [15], the idea that the observation of an action also recruits motor programs of actions with corresponding goals but differing means endows the observer with the flexibility of mapping the observed action onto the behavioral alternative that is most suited under his present circumstances. It resolves a long-standing enigma: Why do monkeys not imitate despite the presence of a mirror neuron system? If the MNS also matches goals on goals, one would expect individuals to learn to reach goals without necessarily imitating the way in which the goals are achieved. Recent primate studies demonstrate the fact that monkeys indeed learn to reach goals by observation [45]. "True imitation" then becomes a relatively rare, although sometimes important, phenomenon linked to the minority of strictly congruent neurons that closely match the details of observed and executed actions. In human infants and possibly monkeys [46], such imitation is possible but may require appropriate instructions and training [27, 40, 47]. One could thus think of motor execution following learning by observation as a competition between the motor alternatives that the combination of scMN and bcMN activate during observation. Without specific instructions, this competition will lead to execution of the most economical alternative, which might often only have the goal in common with the observed action. If infants or monkeys were instructed to imitate the details of the actions, or if detailed imitation is the only way to reach the observed goal (e.g., producing intricate stone tools), this competition would be biased toward motor programs with matching means, possibly by enhancing the response of scMN.

Finally, these findings provide direct evidence for the long-standing question of how we could comprehend actions that we never performed ourselves; contrary to what has been assumed [25], if the goal of the observed actions relate to goals that are part of our motor vocabulary, we may comprehend them through the mirror of our own actions.

Supplemental Data

Experimental Procedures, two figures, and four tables are available at <http://www.current-biology.com/cgi/content/full/17/14/1235/DC1>.

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References

1. Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain* 119, 593–609.
2. Fadiga, L., Fogassi, L., Pavesi, G., and Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *J. Neurophysiol.* 73, 2608–2611.
3. Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., and Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proc. Natl. Acad. Sci. USA* 95, 15061–15065.
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. Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., and Rizzolatti, G. (2001). I know what you are doing. A neurophysiological study. *Neuron* 31, 155–165.
6. 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.
7. Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., and Rizzolatti, G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl. Acad. Sci. USA* 98, 13995–13999.
8. Kohler, E., Keysers, C., Umiltà, M.A., Fogassi, L., Gallese, V., and Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science* 297, 846–848.
9. Keysers, C., Kohler, E., Umiltà, M.A., Nanetti, L., Fogassi, L., and Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Exp. Brain Res.* 153, 628–636.
10. Grezes, J., Armony, J.L., Rowe, J., and Passingham, R.E. (2003). Activations related to "mirror" and "canonical" neurones in the human brain: An fMRI study. *Neuroimage* 18, 928–937.
11. 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.
12. 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.
 13. Wheaton, K.J., Thompson, J.C., Syngeniotes, A., Abbott, D.F., and Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage* 22, 277–288.
 14. Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., and Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cereb. Cortex* 15, 1243–1249.
 15. Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., and Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3, e79.
 16. 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.
 17. Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science* 308, 662–667.
 18. Gazzola, V., Aziz-Zadeh, L., and Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in human. *Curr. Biol.* 16, 1824–1829.
 19. Hamilton, A.F., and Grafton, S.T. (2006). Goal representation in human anterior intraparietal sulcus. *J. Neurosci.* 26, 1133–1137.
 20. Keysers, C., and Perrett, D.I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends Cogn. Sci.* 8, 501–507.
 21. Gallese, V., Keysers, C., and Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends Cogn. Sci.* 8, 396–403.
 22. Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
 23. Keysers, C., and Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Prog. Brain Res.* 156, 383–406.
 24. Gallese, V. (2006). Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain Res.* 1079, 15–24.
 25. Jacob, P., and Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends Cogn. Sci.* 9, 21–25.
 26. 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.
 27. Bekkering, H., Wohlschlagel, A., and Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Q. J. Exp. Psychol. A* 53, 153–164.
 28. Gazzola, V., Rizzolatti, G., Wicker, B., and Keysers, C. (2007). The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *Neuroimage* 35, 1674–1684.
 29. Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., and Fazio, F. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res.* 111, 246–252.
 30. Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., and Mazziotta, J.C. (2003). Modulation of cortical activity during different imitative behaviors. *J. Neurophysiol.* 89, 460–471.
 31. Press, C., Bird, G., Flach, R., and Heyes, C. (2005). Robotic movement elicits automatic imitation. *Brain Res. Cogn. Brain Res.* 25, 632–640.
 32. Nishitani, N., and Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proc. Natl. Acad. Sci. USA* 97, 913–918.
 33. Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., and Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *J. Neurosci.* 26, 2964–2970.
 34. 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.
 35. Leslie, K.R., Johnson-Frey, S.H., and Grafton, S.T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *Neuroimage* 21, 601–607.
 36. 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.
 37. Jackson, P.L., Meltzoff, A.N., and Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *Neuroimage* 31, 429–439.
 38. Nishitani, N., and Hari, R. (2002). Viewing lip forms: Cortical dynamics. *Neuron* 36, 1211–1220.
 39. Oberman, L.M., Hubbard, E.M., McCleery, J.P., Altschuler, E.L., Ramachandran, V.S., and Pineda, J.A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Brain Res. Cogn. Brain Res.* 24, 190–198.
 40. Gergely, G., Bekkering, H., and Kiraly, I. (2002). Rational imitation in preverbal infants. *Nature* 415, 755.
 41. Thompson, D.E., and Russell, J. (2004). The ghost condition: Imitation versus emulation in young children's observational learning. *Dev. Psychol.* 40, 882–889.
 42. Nielsen, M. (2006). Copying actions and copying outcomes: Social learning through the second year. *Dev. Psychol.* 42, 555–565.
 43. Rijntjes, M., Dettmers, C., Buchel, C., Kiebel, S., Frackowiak, R.S., and Weiller, C. (1999). A blueprint for movement: Functional and anatomical representations in the human motor system. *J. Neurosci.* 19, 8043–8048.
 44. Heyes, C. (2001). Causes and consequences of imitation. *Trends Cogn. Sci.* 5, 253–261.
 45. Subiaul, F., Cantlon, J.F., Holloway, R.L., and Terrace, H.S. (2004). Cognitive imitation in rhesus macaques. *Science* 305, 407–410.
 46. Kumashiro, M., Ishibashi, H., Uchiyama, Y., Itakura, S., Murata, A., and Iriki, A. (2003). Natural imitation induced by joint attention in Japanese monkeys. *Int. J. Psychophysiol.* 50, 81–99.
 47. Wohlschlagel, A., Gattis, M., and Bekkering, H. (2003). Action generation and action perception in imitation: An instance of the ideomotor principle. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 501–515.