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Report

View-Based Encoding of Actions in Mirror Neurons of Area F5 in Macaque Premotor Cortex

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Summary

Converging experimental evidence indicates that mirror neurons in the monkey premotor area F5 encode the goals of observed motor acts [1–3]. However, it is unknown whether they also contribute to encoding the perspective from which the motor acts of others are seen. In order to address this issue, we recorded the visual responses of mirror neurons of monkey area F5 by using a novel experimental paradigm based on the presentation of movies showing grasping motor acts from different visual perspectives. We found that the majority of the tested mirror neurons (74%) exhibited view-dependent activity with responses tuned to specific points of view. A minority of the tested mirror neurons (26%) exhibited view-independent responses. We conclude that view-independent mirror neurons encode action goals irrespective of the details of the observed motor acts, whereas the view-dependent ones might either form an intermediate step in the formation of view independence or contribute to a modulation of view-dependent representations in higher-level visual areas, potentially linking the goals of observed motor acts with their pictorial aspects.

Results

Previous investigations of the visual responses of mirror neurons have been based typically on a "naturalistic testing" of their response properties. That is, the motor acts used as visual stimuli were executed in front of the monkey by an experimenter [1–3]. This method is very flexible and allowed us to discover in the past several interesting response properties of mirror neurons [1, 4–6]. However, its accuracy is limited by the trial-by-trial variability of human movements, and it makes it difficult to study the observation of actions from the monkey's own subjective perspective. In order to circumvent these problems, we used filmed actions to study the visual responses of mirror neurons.

We conducted two experiments recording the activity of mirror neurons in area F5. The first one investigated the similarity of the visual responses to the same motor act presented in movies and in a naturalistic manner. The second experiment investigated the view dependence of the visual responses of mirror neurons using movie stimuli.

In both experiments, we isolated neurons in area F5 of the ventral premotor cortex of two monkeys, and recorded their activity during the execution of goal-directed motor acts (cf. Figure 1 and Supplemental Experimental Procedures available online). Then, in the first experiment, we compared mirror neuron responses to the observation of the same motor act presented in movies and in a naturalistic way (Figure 1); in the second experiment, we studied the visual responses of mirror neurons to motor acts observed from different visual perspectives using movie stimuli. In both experiments during the presentation of movies, the monkeys had to fixate on the part of the screen where the movie was presented (see Supplemental Experimental Procedures for further methodological details).

Naturalistic versus Filmed Actions

We recorded the responses of 224 motor neurons from area F5 to the presentation of naturalistic and filmed actions. The experimental procedure is shown in Figure 1 (upper panel). The lower part of the figure shows the responses of two F5 neurons during motor execution (left column) and during visual stimulation with a naturalistic (central column) and a corresponding movie (right column) stimulus. Note that the responses to naturalistic and movie stimuli were similar. In both cases, the response peak occurred during the grasping of the object, and the strength of the discharge was virtually the same. A control experiment showed that the size of the attended region did not substantially influence the responses to movies (Supplemental Results).

Furthermore, in order to control for unspecific response components, neurons were also tested in a "nonaction condition," showing a movie of a monkey sitting in a primate chair and performing movements that were not goal directed. Figure 2A shows the responses of two mirror neurons to the presentation of the three types of stimuli. No response was present for the filmed nonaction.

The results of the quantitative analysis of the visual responses of the recorded 224 neurons showed that 123 (55%) responded to the presentation of motor acts (mirror neurons). Of them, 104 (85%) responded to naturalistic and 50 (41%) to filmed motor acts (Figure 2B). None of the tested neurons showed a significant response to filmed nonactions. A direct comparison of the responses between naturalistic and filmed motor acts revealed that 53 neurons out of 123 (43%) showed no significant preference for either type of action stimulus ($p > 0.05$, Mann-Whitney U test). The remaining 70 neurons (cf. Figure 2C) exhibited either stronger response for naturalistic motor acts ($n = 53$, 43%) or for filmed motor

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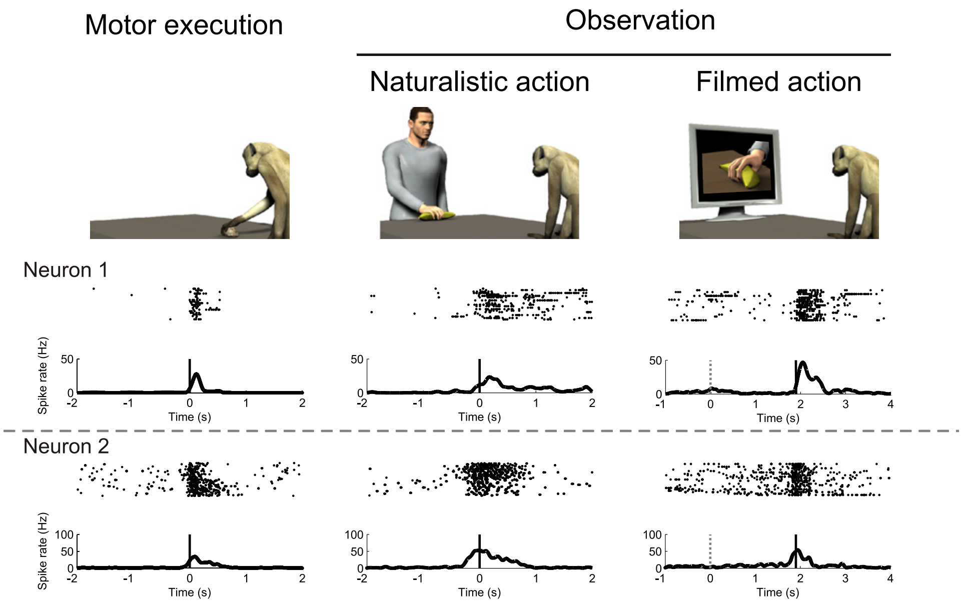

Figure 1. Illustration of the Experimental Paradigm and Example of Mirror Neuron Responses

In each session, we first tested the motor responses of neurons during active movements of the monkey (motor). The visual responses of these neurons were subsequently tested, with the experimenter executing goal-directed actions (naturalistic) and/or by presenting filmed actions (filmed action). Neurons 1 and 2 responded during the motor task to the presentation of naturalistic stimuli (alignment with the start of object touching at time 0) and to filmed actions (time 0 corresponding to the start of the filmed action, gray dashed bar; touch at 1800 ms, black continuous bar). Neuron 1 showed an increase in activity after the touch of the object during the motor task and for both types of visual stimulation. Neuron 2 showed increasing activity after object touch during the motor testing, whereas during visual stimulation it showed strong activity during all grip phases, peaking at the moment of object touch.

acts (n = 17, 14%). At the population level, the average activities computed from the response distributions for filmed and naturalistic motor acts were not significantly different ($p > 0.9$, Kolmogorov-Smirnov test).

Because the second experiment (test of view dependence) was based on filmed stimuli, we tested the correlation between the responses to movies and those to naturalistic stimuli for neurons significantly responding to movies (n = 50). These responses were highly correlated (Figure 2D), with a regression coefficient m close to 1 (average activity: $m = 1.01$, $r^2 = 0.63$, $p < 0.01$; peak activity: $m = 1.06$, $r^2 = 0.71$, $p < 0.01$). On the contrary, no significant correlation ($p > 0.5$) was observed between the visual responses to naturalistic and filmed nonaction stimuli. Also, the time courses of the responses were very similar (see Figure S2 and Supplemental Results).

Tuning with Respect to Point of View

Having established that movie stimuli activate F5 mirror neurons in a similar manner as naturalistic stimuli, we investigated the influence of the point of view on their visual responses by presenting movies that showed the same motor act (grasping) seen from three different viewpoints (Figure 3A): from the monkey's perspective (subjective point of view: 0°), from a side view (90°), and from the frontal view (180°).

We tested 389 F5 motor neurons; 201 (52%) of them exhibited significant visual responses to movie stimuli. Figure 3B shows examples of the observed types of viewpoint selectivity: neuron 1 responded selectively to the presentation of a motor act only when it was seen from the monkey's subjective perspective. Neurons 2 and 3 responded to the motor acts only when they were presented from the frontal or lateral view, respectively. Neuron 4 responded to the observation of goal-directed motor acts independent of the point of view.

Figure 4A summarizes the number and percentages of neurons that were responsive to the conditions 0°, 90°, or 180°, regardless of whether they were selective or invariant with respect to visual perspective. Figure 4B shows the results of a direct comparison between the responses to the three visual stimuli. Out of the 201 visually responsive neurons, 149 (74%) were view dependent; i.e., they showed a significant discharge preference for at least one view ($p < 0.05$, Kruskal-Wallis test). The remaining 52 neurons (26%) exhibited view-independent responses; i.e., their visual responses did not vary significantly between the three view conditions ($p > 0.05$, Kruskal-Wallis test).

The responses of the view-dependent mirror neurons were further analyzed by post-hoc comparisons ($p < 0.05$, U test, Bonferroni corrected). This analysis revealed that 60 (30%) out of all visually responsive neurons responded significantly only to one of the tested points of view. The black bars in Figure 4B indicate the numbers of neurons with a preference for a single point of view: subjective point of view (n = 27, 13%), frontal point of view (n = 15, 8%), and lateral point of view (n = 18, 9%). The percentages of neurons responding selectively to only one tested point of view were not statistically different ($p > 0.1$, binomial test).

A more detailed study of the three view-specific populations revealed a strong similarity in their tuning properties. Figure 4C shows that the normalized "tuning curves" for the three view-responsive populations were highly similar. We did not find significant differences between the activities of these populations, neither for the average nor for the peak activity ($p > 0.05$, Mann-Whitney U test, Bonferroni corrected). Very similar results were obtained when the neuronal populations with increasing and decreasing responses relative to baseline were analyzed separately (Figure S3D).

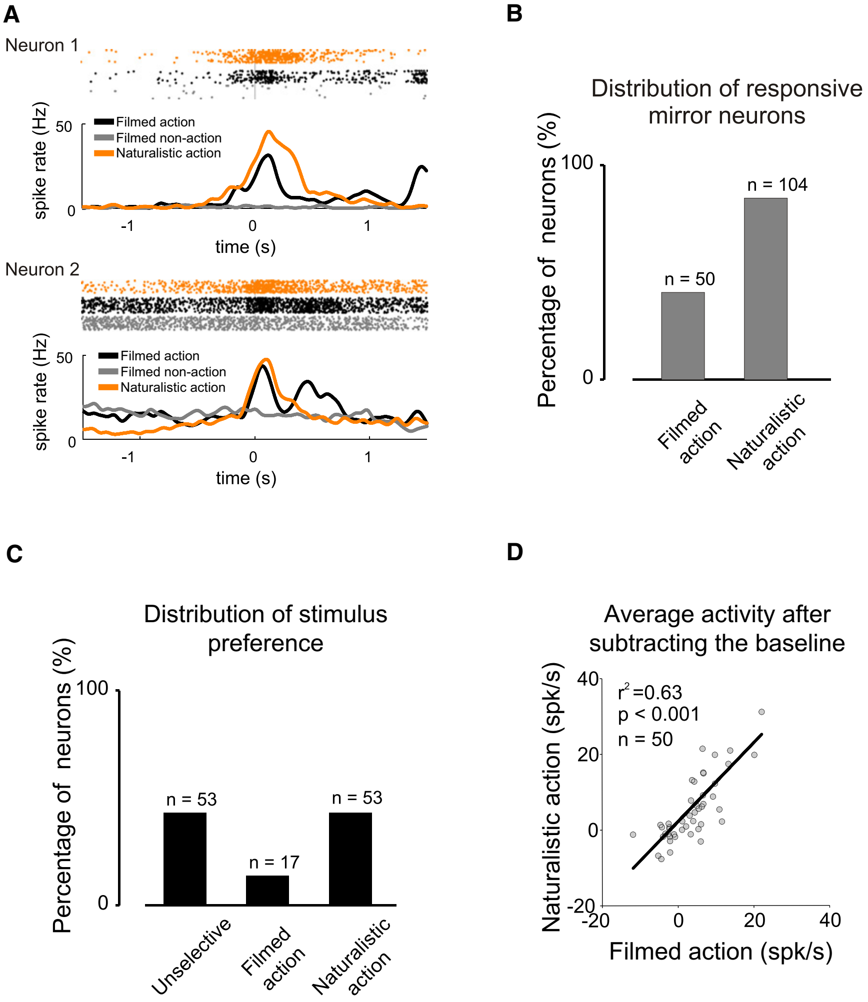

Figure 2. Comparison of the Responses of Mirror Neurons to Naturalistic Actions, Filmed Actions, and Filmed Nonactions

(A) Examples of single-unit responses of mirror neurons during the presentation of filmed actions, filmed nonactions, and naturalistic actions. Response traces are aligned with the start of object touching at time 0 (time III; see Figure S1). Neuron 1 showed an increase in activity during the grasping phase (time interval III-IV; see Supplemental Experimental Procedures), and a peak during the touching of the object. We found a similar time course of activity during testing with naturalistic visual stimuli, whereas we found no response during the presentation of the nonaction movie. Neuron 2 showed a similar modulation for filmed and naturalistic stimuli with an increase in activity when the hand reached the grasped object, peaking during the hand-object contact.

(B) Distribution of neurons selective for naturalistic and filmed actions. Bars indicate the numbers of neurons that were responding to the corresponding condition, i.e., naturalistic or filmed actions.

(C) Distribution of the preference of single neurons. Bars indicate neurons that respond preferentially to that condition ($p < 0.05$, U test).

(D) Linear regression analysis predicting the difference between the average and the baseline activities, in the grasping phase during a real action, from the corresponding responses to filmed actions (significant correlation, $r^2 = 0.63$, $m = 1.01$, $p < 0.01$).

The subjective view as compared to the other two tested views showed different amounts of the monkey's body. A separate control experiment demonstrated that the visual responses of the tested neurons did not depend on whether the monkey's body was visible or not (Figure S4).

Discussion

In the present study, we investigated the influence of the perspective from which others' motor acts are observed on the visual responses of mirror neurons in area F5. Based on a novel paradigm for studying the visual responses of mirror neurons with well-controlled filmed stimuli, we found that the majority (74%) of the tested mirror neurons were modulated by the view from which the motor acts were observed, whereas a minority of them showed view-independent responses.

In the current study, the motor acts seen from the subjective perspective showed the motor act performed within the monkey's peripersonal space, whereas the motor acts seen from the frontal and lateral views showed motor acts performed in the monkey's extrapersonal space. This might suggest an alternative explanation for our results, i.e., that the viewpoint selectivity was confounded with distance selectivity (see [5]). However, if this interpretation were correct, the selective responses to the subjective view (0°) should be associated with the animal's peripersonal space, whereas the selectivity to the other two views (90° and 180°) should be associated with the extrapersonal space. In contrast to this prediction, we found three, rather than two, equivalent subpopulations of view-dependent mirror neurons. This allows one to rule out this alternative explanation.

The results of the present study have important implications for the role of mirror neurons in action understanding. Some models of action recognition [7, 8] have assumed a hierarchy of processing steps suggesting that visual details of observed actions are mainly processed in higher-order visual areas, such as the superior temporal sulcus (STS), whereas areas containing mirror neurons (inferior parietal area PFG/anterior intraparietal area [PFG/AIP] and area F5) would mediate action understanding by matching visual and motor representations of the observed actions. This mechanism has been considered instrumental for understanding actions and intention of others [1, 2, 4, 6].

The presence of view-invariant mirror neurons in area F5 is consistent with this account. It is plausible that these neurons may implement the top level of a hierarchy that encodes observed actions, potentially in terms of their motor goals and independent of their detailed visual characteristics.

Somewhat more difficult is the interpretation of the responses of the view-dependent mirror neurons. One possible explanation is that view invariance, although already present in the STS [9, 10], is not completely obtained in this region and, thus, the view-dependent mirror neurons in area

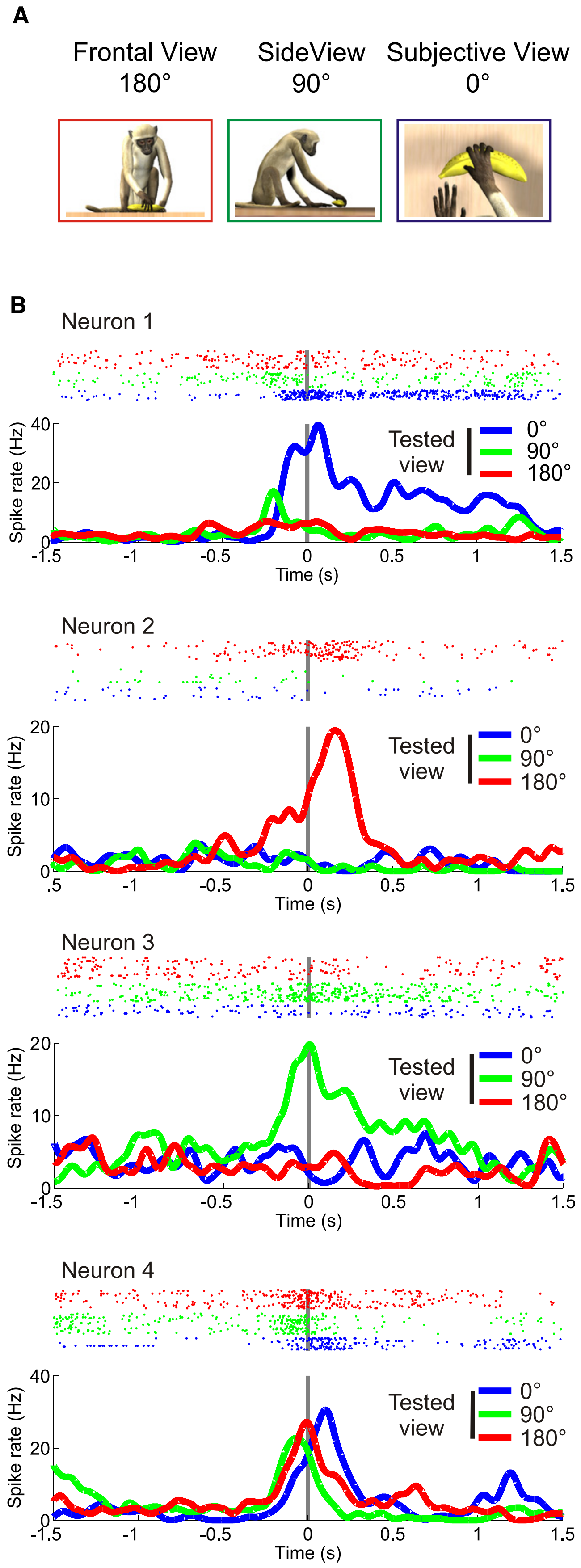

Figure 3. Comparison of Responses of Mirror Neurons to Three Points of View

(A) Experimental conditions (subjective point of view: 0°; side view: 90°; frontal point of view: 180°).

(B) Responses of three mirror neurons during observation of filmed goal-directed actions. Responses were temporally aligned with the start of the touching phase (time III; see Figure S1). Neuron 1 showed a selectivity for actions presented in the subjective point of view (0°) during the approaching phase and very weak modulation of the activity for stimuli corresponding to other points of view (90° and 180°). Neuron 2 showed a modulation for actions presented from a frontal point of view (180°), peaking during the grasping phase, and no modulation of the activity for stimuli corresponding to other points of view (0° and 90°). Neuron 3 showed a modulation for actions presented in the side view (90°) during the grasping phase, peaking at the time of contact between hand and goal object, and no modulation of the activity for stimuli corresponding to other points of view (0° and 180°). The activity of neuron 4 was modulated by actions seen from all tested points of view. The responses of this neuron were view independent.

F5 play an essential role in the formation of view-invariant representations. The generation of view invariance by pooling together the responses of view-dependent neurons is a well-established mechanism in object recognition in the ventral visual stream [11, 12] and in many computational models [13–15].

An alternative interpretation is that view-dependent mirror neurons, in spite of their motor nature, play a role in the perception of the visual perspective of the observed actions. Several anatomical studies have demonstrated that, in addition to feed-forward projections [16], the three areas that have been implicated in action recognition (F5, PFG/AIP, and STS) are also serially connected by backward projections [17, 18]. These back-projections indicate the presence of a top-down stream of information from area F5 to the inferior parietal lobule and finally to the STS. Hence, view-dependent mirror neurons might play an important role in this feedback pathway. More specifically, signals from view-dependent mirror neurons might contribute to action perception by modulating the activity of visual representations in the STS, reinforcing the processing of visual patterns that are associated with the different views of a grasping act. Consistent with this hypothesis are behavioral data demonstrating modulations of visual perception by concurrent motor behavior and motor expertise [19–21]. However, simultaneous recordings from premotor and higher-order visual areas are required to verify this hypothesis and clarify the information flow within the temporo-parieto-frontal network.

A second contribution of the present study is a novel experimental paradigm, suitable for eliciting robust visual responses of mirror neurons during the presentation of filmed actions. Although the use of filmed stimuli is well established in the study of the response properties of neurons responding to biological motion in many visual areas [22–24], previous attempts to use them for the investigation of the mirror neuron responses have not been successful [25]. Whereas in the previous studies the monkeys were not trained to fixate on the movies, the present study, consistent with a recent monkey fMRI study [26], showed that a simple fixation task, requiring the animals to fixate within a window that overlapped with the video, was sufficient to elicit visual responses in mirror neurons. This novel methodology offers many possibilities for well-controlled experiments on mirror neurons that are not possible using naturalistic stimulation.

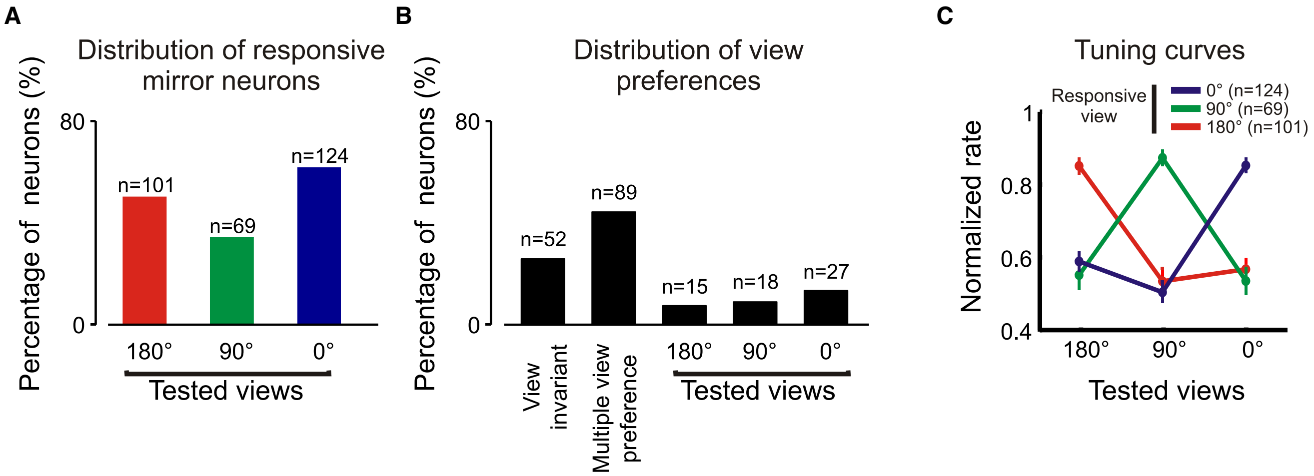

Figure 4. Population Analysis of the Neuronal Responses to the Three Tested Points of View

(A) Total number of responsive neurons for the different visual stimuli.

(B) Distribution of the preference of single neurons. Conventions are as in Figure 2.

(C) View-tuning curves computed from the neurons responding to at least one point of view. The curves are color coded as in (A) (see text). Prior to averaging, the activity of each neuron was normalized by dividing it for its absolute maximum activity over all views. Error bars represent standard errors.

Supplemental Information

Supplemental Information includes four figures, one table, Supplemental Results, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.12.022.

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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. Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. Brain Res. *3*, 131–141.
3. Rizzolatti, G., and Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. Nat. Rev. Neurosci. *11*, 264–274.
4. Bonini, L., Rozzi, S., Serventi, F.U., Simone, L., Ferrari, P.F., and Fogassi, L. (2009). Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. Cereb. Cortex *20*, 1372–1385.
5. Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., and Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. Science *324*, 403–406.
6. 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.
7. Bonaiuto, J., and Arbib, M.A. (2010). Extending the mirror neuron system model, II: What did I just do? A new role for mirror neurons. Biol. Cybern. *102*, 341–359.
8. Oztop, E., and Arbib, M.A. (2002). Schema design and implementation of the grasp-related mirror neuron system. Biol. Cybern. *87*, 116–140.
9. Oram, M.W., and Perrett, D.I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. J. Neurophysiol. *76*, 109–129.
10. Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., and Ortega, J.E. (1989). Frameworks of analysis for the neural representation of animate objects and actions. J. Exp. Biol. *146*, 87–113.
11. Logothetis, N.K., and Sheinberg, D.L. (1996). Visual object recognition. Annu. Rev. Neurosci. *19*, 577–621.
12. Tanaka, K. (1996). Inferotemporal cortex and object vision. Annu. Rev. Neurosci. *19*, 109–139.
13. Oram, M.W., and Perrett, D.I. (1994). Modeling visual recognition from neurobiological constraints. Neural Netw. *7*, 945–972.
14. Poggio, T., and Edelman, S. (1990). A network that learns to recognize three-dimensional objects. Nature *343*, 263–266.
15. Tarr, M.J., and Bulthoff, H.H. (1998). Image-based object recognition in man, monkey and machine. Cognition *67*, 1–20.
16. Petrides, M., and Pandya, D.N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. J. Comp. Neurol. *228*, 105–116.
17. Matelli, M., Camarda, R., Glickstein, M., and Rizzolatti, G. (1986). Afferent and efferent projections of the inferior area 6 in the macaque monkey. J. Comp. Neurol. *251*, 281–298.
18. Rozzi, S., Calzavara, R., Belmalih, A., Borra, E., Gregoriou, G.G., Matelli, M., and Luppino, G. (2006). Cortical connections of the inferior parietal cortical convexity of the macaque monkey. Cereb. Cortex *16*, 1389–1417.
19. Casile, A., and Giese, M.A. (2006). Nonvisual motor training influences biological motion perception. Curr. Biol. *16*, 69–74.
20. Craighero, L., Fadiga, L., Rizzolatti, G., and Umilta, C. (1999). Action for perception: A motor-visual attentional effect. J. Exp. Psychol. *25*, 1673–1692.
21. Schutz-Bosbach, S., and Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. Trends Cogn. Sci. *11*, 349–355.
22. Barraclough, N.E., Keith, R.H., Xiao, D., Oram, M.W., and Perrett, D.I. (2009). Visual adaptation to goal-directed hand actions. J. Cogn. Neurosci. *21*, 1806–1820.
23. Barraclough, N.E., Xiao, D., Oram, M.W., and Perrett, D.I. (2006). The sensitivity of primate STS neurons to walking sequences and to the degree of articulation in static images. Prog. Brain Res. *154*, 135–148.
24. Iriki, A., Tanaka, M., Obayashi, S., and Iwamura, Y. (2001). Self-images in the video monitor coded by monkey intraparietal neurons. Neurosci. Res. *40*, 163–173.
25. Ferrari, P.F., Gallese, V., Rizzolatti, G., and 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.
26. 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.