

Representation of body identity and body actions in extrastriate body area and ventral premotor cortex

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Although inherently linked, body form and body action may be represented in separate neural substrates. Using repetitive transcranial magnetic stimulation in healthy individuals, we show that interference with the extrastriate body area impairs the discrimination of bodily forms, and interference with the ventral premotor cortex impairs the discrimination of bodily actions. This double dissociation suggests that whereas extrastriate body area mainly processes actors' body identity, premotor cortex is crucial for visual discriminations of actions.

Our capacity to understand other people's behavior and to read their minds depends on the identification of agents and their actions. Viewing bodily movements activates the frontoparietal mirror system that matches action observation and execution¹. This suggests that action understanding involves the mapping of observed actions onto the onlooker's motor representations². Simulative motor mapping,

however, seems to be insensitive to the identity of the acting body³. Viewing static⁴ or dynamic⁵ images of the human body and its parts, except faces, activates a lateral occipitotemporal area (extrastriate body area, EBA). Furthermore, self-produced movements of the limbs activate EBA⁶, suggesting a functional link between body visual representations and the action observation–execution matching systems⁷. Repetitive transcranial magnetic stimulation (rTMS) of EBA interferes with the processing of static images of human bodies⁸. However, the specific functional contributions of EBA and of the motor mirror system in the processing of bodily actions are still debated^{1,9,10}. In the present study, we used rTMS to investigate the causative role of EBA and ventral premotor cortex (vPMc) in the visual discrimination of bodily forms and bodily actions.

In a two-choice matching-to-sample visual discrimination task, seventeen healthy individuals were required to decide which of two upper- or lower-limb images matched a single sample previously seen during tachistoscopic exposure (see **Supplementary Methods** online). All participants gave their written informed consent. Stimuli consisted of pictures depicting body parts and were likely to activate EBA³. However, all pictures also implied action and were likely to activate vPMc¹. The matching and nonmatching stimuli in each pair depicted the same model performing two different actions (action discrimination task) or the same action performed by two different models (form discrimination task; **Fig. 1a**). Crucially, the same match-to-sample operation was required in the two tasks. Thus, any dissociation between the tasks was likely to emerge from the implicit discrimination of differences in the action or in the morphological details of the models'

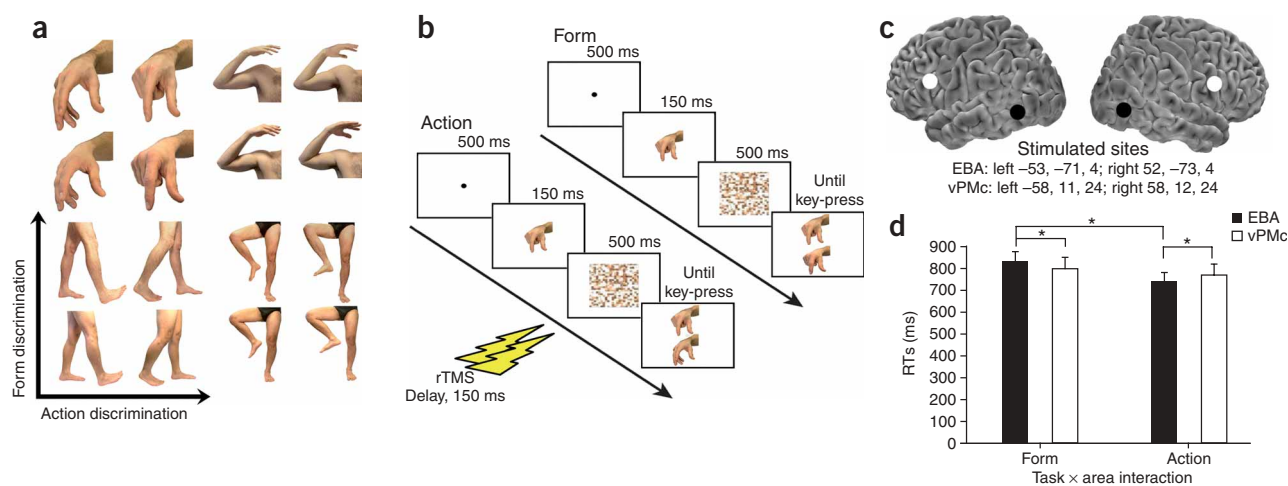


Figure 1 Experimental design and results. **(a)** Stimuli, **(b)** time line, and **(c)** stimulation sites plotted on the standard brain. **(d)** Mean (\pm s.e.m.) reaction times (RTs) for action and form discriminations after stimulation of EBA and vPMc. $*P < 0.05$.

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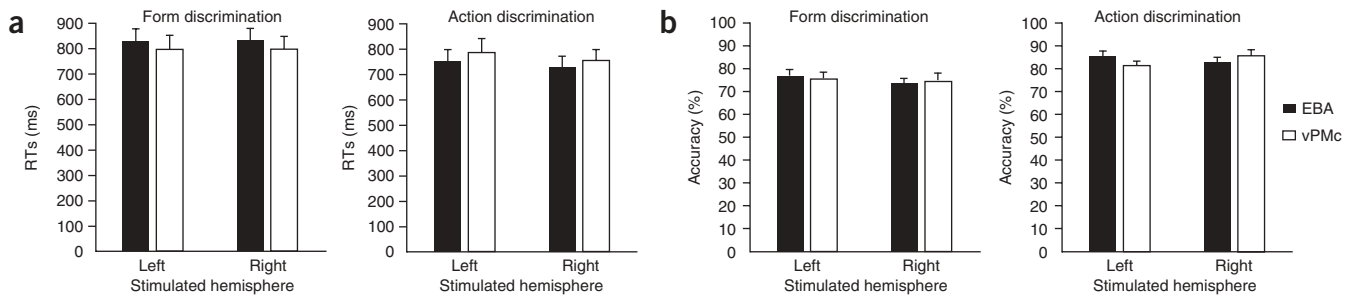


Figure 2 Absence of modulation by hemisphere stimulated. **(a)** Mean (\pm s.e.m.) reaction times (RTs) and **(b)** accuracy for action and form discrimination after stimulation of right and left EBA and vPMc.

body parts. In different blocks, we applied rTMS trains of two pulses (frequency 10 Hz, duration 200 ms, delay 150 ms; **Fig. 1b**) over the scalp in locations corresponding to EBA and vPMc in the left and right hemispheres (**Fig. 1c**) and compared performances for reaction times and accuracy (see **Supplementary Methods** online).

A three-way repeated-measures ANOVA on reaction times with task (action, form), area (EBA, vPMc) and hemisphere (left, right) as within-subject variables showed a significant interaction between task and area ($F_{1,16} = 11.84$, $P = 0.003$; **Fig. 1d**). Newman-Keuls *post hoc* comparisons demonstrated that reaction times for form discriminations were higher after rTMS of EBA ($825.88 \text{ ms} \pm 48.6 \text{ ms}$) than after rTMS of vPMc ($796.11 \text{ ms} \pm 51.19 \text{ ms}$, $P = 0.036$), showing selective interference of EBA stimulation with the discrimination of bodily forms. In marked contrast, reaction times for action discrimination were higher after rTMS of vPMc ($769.25 \text{ ms} \pm 45.49 \text{ ms}$) than after rTMS of EBA ($735.81 \text{ ms} \pm 47.37 \text{ ms}$, $P = 0.021$), showing selective interference of vPMc stimulation with the discrimination of bodily actions. As would be expected based on the significant main effect of task ($F_{1,16} = 5.69$, $P = 0.03$), action discrimination was faster than form discrimination after EBA rTMS ($P < 0.001$) and after vPMc rTMS ($P = 0.055$). No other main effects or interactions were significant. Notably, the interference caused by EBA and vPMc stimulation was independent of the hemisphere stimulated (three-way interaction $F_{1,16} < 1$; **Fig. 2a**). This suggests the absence of hemispheric dominance in purely visual discriminations of acting bodies that do not require semantic categorization of actions. Although participants were faster and more accurate (main effect task $F_{1,16} = 25.12$, $P < 0.001$) for action than for form discrimination, the differing difficulty of the tasks cannot explain the reported double dissociation. Indeed, whereas EBA rTMS selectively impaired the ability to discriminate two different forms, vPMc rTMS selectively impaired the ability to discriminate two different actions. Stimulation had no effect on accuracy of responses (task \times area $F_{1,16} < 1$; **Fig. 2b**), ruling out any speed-accuracy trade-off. Thus, the present data clearly show that EBA is crucial in processing bodily forms but not bodily actions; the opposite holds true for vPMc.

Studies showed that EBA is sensitive to the perspective from which bodies are viewed^{11,12} but is not affected by distortions of the action sequence¹⁰. Our study significantly expands previous research¹⁰ by suggesting that EBA is causatively involved in mapping morphological features of human bodies. This function may be fundamental for keeping constant the identity of others even when body configurations change enormously and at very fast rates during action. Thus, EBA may be crucial for the identification of actors, particularly when facial cues are unavailable or ambiguous. Furthermore, EBA may receive modulatory signals from sensorimotor systems⁶ and thus be involved in the multimodal representation of the actors' body identity. Studies reported that rTMS interference with vPMc impairs imitation of

observed actions¹³ as well as judgment of the weights lifted by a person¹⁴, a task that requires the rehearsal of sensorimotor signals concerning the physical effort made by the model. However, direct evidence for involvement of the motor mirror system in purely visual discriminations of actions was still lacking. The present results provide causative evidence that motor representations are necessary for visuo-perceptive action discriminations and that vPMc may represent the observed actions without taking into account the actors' identity. Importantly, the extraction of action cues occurs at a completely implicit level, suggesting that specific perceptual contexts automatically trigger body action simulation in motor areas¹⁵. In conclusion, the reported double dissociation suggests that the visual analysis of human body stimuli is based on the automatic division of labor into two cortical systems, with EBA and possibly other body-selective visual areas⁵ representing the actors' identity, and vPMc and possibly other nodes of the frontoparietal mirror system mapping the observed action in a neutral format with respect to the identity of the acting bodies.

Note: Supplementary information is available on the Nature Neuroscience website.

ACKNOWLEDGMENTS

Supported by Ministero Italiano Università e Ricerca and Fondo Investimenti per la Ricerca di Base Italy.

AUTHOR CONTRIBUTIONS

C.U. and M.C. designed and performed research, analyzed data and wrote the paper. S.I. performed research. S.M.A. designed research, supervised the project and wrote the paper.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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