Motor activation prior to observation of a predicted movement

James M Kilner[1,2], Claudia Vargas[1,3], Sylvie Duval[1,4], Sarah-Jayne Blakemore[4] & Angela Sirigu[1]

Previous research has shown that some of the same motor regions are activated both when performing and when observing a movement. Here we demonstrate in human subjects that such motor activity also occurs prior to observing someone else's action. This suggests that the mere knowledge of an upcoming movement is sufficient to excite one's own motor system, enabling people to anticipate, rather than react to, others' actions.

When we observe the actions of another person, certain areas of our brain are activated in a manner similar to that which occurs when we perform the same action[1–5]. Such a 'mirror system'[4] may facilitate our understanding of other people's actions and intentions[6]. Often, however (such as when waiting to receive a serve in tennis), we need to predict the likely actions of another person before they occur to expedite our own response to them. Here, we show that the readiness potential

(RP)[7]—an electrophysiological marker of motor preparation—is present when one is observing someone else's action. More importantly, when the nature and onset time of the upcoming action is predictable, the rise of the readiness potential precedes the observed movement's onset. This suggests that knowledge of a coming action automatically activates the motor system.

We recorded electroencephalograms (EEGs) from 22 right handed subjects while they watched a series of short video clips showing an actor's right hand and a colored object. The actor's hand was shown from an egocentric or an allocentric perspective depending on the trial (see **Supplementary Methods** online). In half the video clips, after 1.5 s, the hand moved and grasped the object; in the other half the hand remained stationary. At the beginning of each clip, the color of the object indicated whether the hand would subsequently move or not (**Supplementary Videos 1** and **2** online). Thus, the observed movements were entirely predictable from the color of object in the video. The subjects' task was to detect differences in initial hand posture between the video clips (while the hand was stationary; see **Supplementary Methods** online). As there is known to be a negative-going potential prior to a predictable stimulus, the contingent negative variability (CNV)[8], we used a Prediction Control condition to allow us to disambiguate a negative-going potential that was related to the observed movement from one related to a predictable stimulus change *per se*. In this Prediction Control condition, subjects watched a series of video of clips that showed an actor's right hand in an egocentric per-
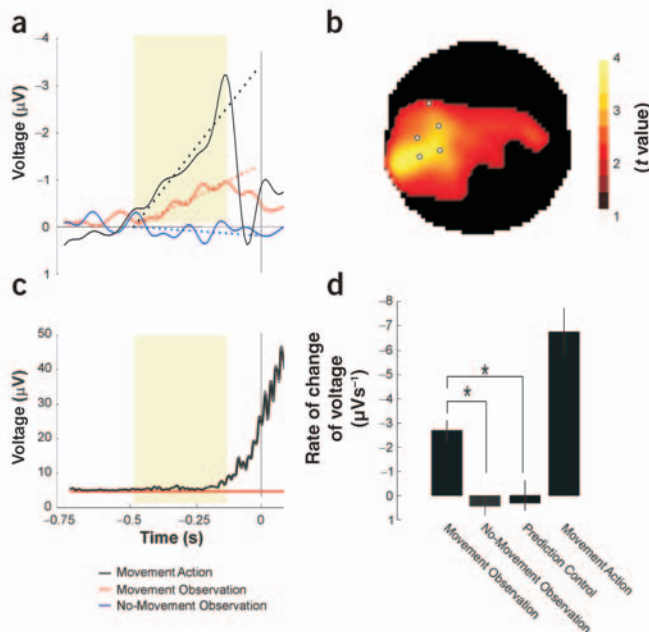
Figure 1 Readiness potentials and scalp topographies of negativity prior to the observed movement. (**a**) ERPs averaged over electrodes of interest and subjects. The different lines represent the Movement Action conditions (black line; aligned to the button press); the Movement Observation conditions (red line; aligned to the onset of movement observation); and the No-Movement conditions (blue line; aligned to the moment of no movement). Pale yellow box indicates the period over which the negativity was calculated; dashed lines indicate average line of best fit for each event-related potential (ERP) over that period. (**b**) Flattened scalp topography of the *t*-map, showing differences from zero of the gradient prior to Movement Observation for the egocentric perspective (thresholded at *P* = 0.05 uncorrected, one-tailed *t*-test). Plots are oriented such that the nose is at the top and left is left. White circles indicate our electrodes of interest, over which the ERP and negativities were calculated. (**c**) Data equivalent to that in **a** for the average rectified EMG activity for the Movement Action and Movement Observation conditions. There was no evidence of modulation in first dorsal interosseous (1DI) EMG activity when observing action (compare black to red line). (**d**) Gradient of the line of best fit averaged over subjects. Error bars, s.e.m; *, significant differences between conditions (*P* < 0.05, two-tailed paired *t*-tests).

[1]Institut des Sciences Cognitives, CNRS, 67 Boulevard Pinel, 69675 Bron, France. [2]Wellcome Department of Imaging Neuroscience, University College London, 12 Queen Square, London WC1N 3BG, UK. [3] Institute of Biophysics, Federal University of Rio de Janeiro, Ilha do Fundao, Rio de Janeiro, 21949-900, Brazil. [4]Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK. Correspondence should be addressed to A.S. (sirigu@isc.cnrs.fr).
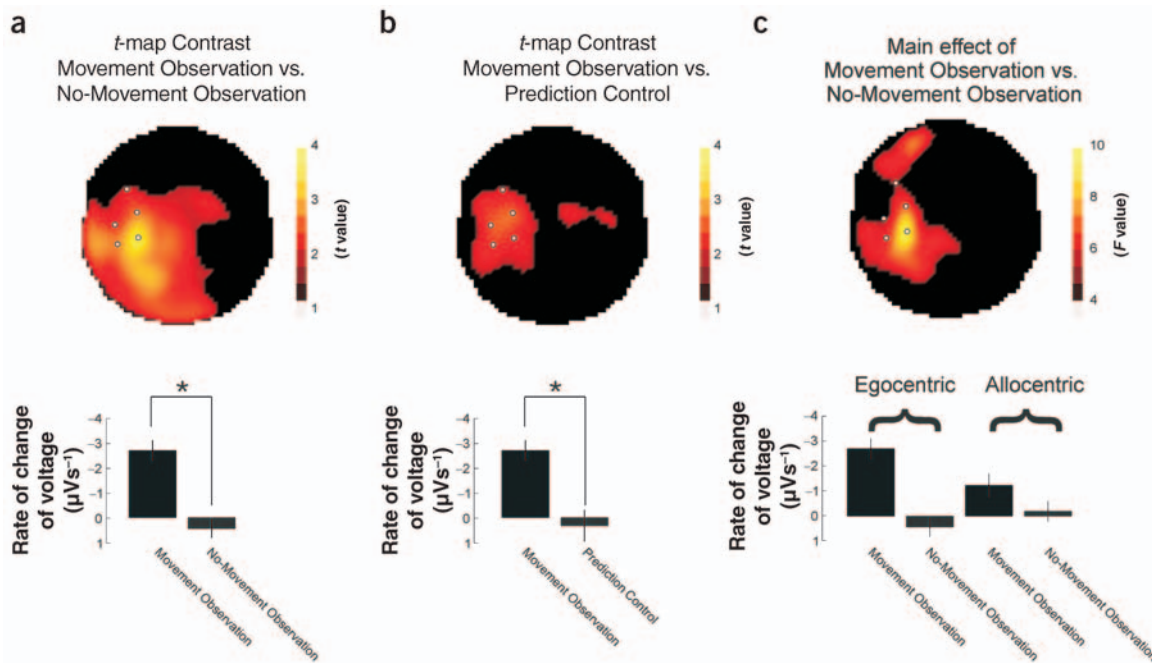
Figure 2 Statistical parametric maps of differences in the amplitude of readiness potential. (**a**) Top, scalp topography of the *t*-map for No-Movement Observation – Movement Observation (thresholded at *P* = 0.05 uncorrected, one-tailed *t*-test). Bottom, gradient of the fitted linear regression averaged over electrodes of interest and subjects for the two conditions. (**b**) Top, scalp topography of the *t*-map for Prediction Control – Movement Observation (thresholded at *P* = 0.05 uncorrected, one-tailed *t*-test). Bottom, gradient of the fitted linear regression averaged over electrodes of interest and subjects for the two conditions. (**c**) Top, scalp topography of the *F*-map for the main effect of Movement Observation compared to No-Movement Observation for the egocentric and allocentric conditions (thresholded at *P* = 0.05 uncorrected). There were no significant activations for the main effect of hand perspective nor for the interactions between hand perspective and movement. Bottom, gradient of the fitted linear regression averaged over electrodes of interest and subjects for the four conditions. In all plots: error bars, s.e.m; *, significant differences between conditions (*P* < 0.05, two-tailed paired *t*-tests).

spective and a colored object. After 1.5 s, the color of the object changed from yellow to either blue or purple and the hand remained stationary throughout. Subjects were instructed to report how many purple or blue objects they saw (**Supplementary Video 3** online). Finally, in a further Movement Action condition, subjects were required to press a button whenever the same object was presented twice in sequence, at any time between 2 and 3 s after the object appeared on the screen. EEG signals in all trials were aligned to 1.5 s after trial onset—that is, the moment when, in half the trials, the hand began to move (for details, see **Supplementary Methods** online).

The results revealed a significant negative gradient (*P* < 0.05, *t* = –3.17) that started ~500 ms before the onset of the observed hand movement when viewed from an egocentric perspective (**Fig. 1a**). This activity was comparable with the onset of the movement-related RP produced when subjects actually executed a movement with the right hand (the same hand as in the Movement Observation and No-Movement Observation Conditions; see **Supplementary Methods**). Both electrophysiological signals occurred in a similar time period, relative to movement onset, and showed commensurate scalp topography: contralateral to the observed (or moving) hand at electrodes overlying the sensorimotor cortex (**Fig. 1**). The observation-related RP occurred only in trials in which there was a predictable movement. The negative-going potential was significantly greater in trials in which there was an observed movement than in trials in which there was no observed movement (*P* < 0.05, *t* = –4.00; **Figs. 1a,d** and **2a**). Furthermore, this movement observation–related RP did not simply reflect prediction *per se*, as it was significantly different from the negativity that preceded a predictable stimulus change

(*P* < 0.05, *t* = –2.94; **Figs. 1d** and **2b**). The specificity of the observation-related RP for predictable hand actions was further demonstrated in trials in which the observed hand was either in an allocentric or egocentric perspective. Despite the fact that the location of the actor's right hand in visual space changed from the right to the left visual field, with the change from egocentric to allocentric perspective, the RP prior to the observed movement remained contralateral to the observed right hand (main effect of movement versus no movement $F_{1,15} = 10.416$, *P* < 0.05; **Fig. 2c**).

Previous research on the mirror system has mainly focused on motor activity during observation of an ongoing movement[1–6], possibly leading to a view of this mechanism as a passive, automatically triggered motor 'echo' used for action recognition. Our results suggest a more active role for this system in setting up an anticipatory model of another person's action, endowing our brain with the ability to predict his or her intentions ahead of their realization. This hypothesis is in agreement with recent findings showing that mirror neurons in the monkey premotor cortex discharge when the monkey sees only the initial portion of an action which subsequently unfolds behind an occluder[9]. The finding here, that there is an RP prior to an observed movement, suggests that mere knowledge of an upcoming movement is sufficient to excite one's own motor system, perhaps because it is more advantageous for the brain to anticipate rather than react to others' actions.

Finally, the present findings extend the functional significance of the RP to movement expectancy. This signal, which we found to be present when no movement was planned by the observer and even when no actual movement was being seen, appears to be a neural

correlate of motor prediction, and not only of motor preparation as previously thought[10].

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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