

Sensorimotor Learning Configures the Human Mirror System

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Summary

Cells in the “mirror system” fire not only when an individual performs an action but also when one observes the same action performed by another agent [1–4]. The mirror system, found in premotor and parietal cortices of human and monkey brains, is thought to provide the foundation for social understanding and to enable the development of theory of mind and language [5–9]. However, it is unclear how mirror neurons acquire their mirror properties—how they derive the information necessary to match observed with executed actions [10]. We address this by showing that it is possible to manipulate the selectivity of the human mirror system, and thereby make it operate as a counter-mirror system, by giving participants training to perform one action while observing another. Before this training, participants showed event-related muscle-specific responses to transcranial magnetic stimulation over motor cortex during observation of little- and index-finger movements [11–13]. After training, this normal mirror effect was reversed. These results indicate that the mirror properties of the mirror system are neither wholly innate [14] nor fixed once acquired; instead they develop through sensorimotor learning [15, 16]. Our findings indicate that the human mirror system is, to some extent, both a product and a process of social interaction.

Results and Discussion

If the development of the mirror system depends on sensorimotor learning, it should be possible to use sensorimotor training to change the functioning of mature mirror systems and even to give them “counter-mirror” properties. To test this prediction, we measured mirror-system functioning before and after incompatible (“counter-mirror”) sensorimotor training [17], in which human participants performed index-finger movements while observing little-finger movements and vice versa. The control group received compatible (“mirror”) sensorimotor training, in which they performed the same

finger movements as those they observed. We assessed mirror-system functioning before and 24 hr after training [17] by measuring the effects of single-pulse transcranial magnetic stimulation (TMS) on the muscle-specificity of motor-evoked potential (MEP) size during action observation. MEPs were recorded from the first dorsal interosseus (FDI) and abductor digiti minimi (ADM) muscles of the right hand during observation of single abduction movements of the index and little fingers (the movements performed by the two muscles, respectively; Figure 1). Before training, one would expect a mirror effect: MEPs in the ADM (little-finger abductor) should be greater during observation of little-finger movement than during observation of index-finger movement, and vice versa for MEPs in the FDI (index-finger abductor) [13]. If sensorimotor experience can change the functioning of the human mirror system, then incompatible training should reverse this mirror effect; for example, MEPs in the ADM (little-finger abductor) should be greater during observation of index-finger than of little-finger movement. In contrast, because compatible training involves a familiar, mirror contingency between observation and execution, the compatible group should show the same pattern of muscle-specific activation before and after training.

Figure 2 shows the pretraining MEP data from the two groups combined. The presence of a muscle-specific mirror effect was confirmed by ANOVA, which yielded a significant interaction between recorded muscle (ADM, FDI) and movement observed (little, index) ($F_{1,15} = 33.781$, $p < 0.001$): Each muscle showed greater MEPs for observation of the movement it performs than for observation of the alternative movement.

Reaction time (RT) data from the training session indicated that the compatible group responded more quickly (mean RT 275.3 ms) than the incompatible group (mean RT 449.5 ms; $t_7 = 5.096$, $p < 0.001$). This is to be expected because in the compatible group, each stimulus has been associated with the required response during the course of the participants’ previous experience. Within the incompatible group, the mean RT in the final block of training trials (414.9 ms) was faster than in the initial block (492.5 ms; $t_7 = 2.936$, $p = 0.022$), confirming that learning of the incompatible mapping occurred during training.

Figure 3 shows the two groups’ pretraining and post-training results. As predicted by the sensorimotor-learning hypothesis, incompatible training caused a reversal of muscle-specific MEP enhancement during action observation, whereas compatible training left the pretraining pattern unchanged. ANOVA with group as the between-subjects factor and session, muscle, and movement as within-subjects factors revealed a significant four-way interaction ($F_{1,14} = 7.428$, $p = 0.016$). Simple interaction analysis confirmed that there was a significant three-way interaction in the incompatible group ($F_{1,14} = 16.975$, $p = 0.001$) but not in the compatible group ($F_{1,14} = 0.071$, $p = 0.794$).

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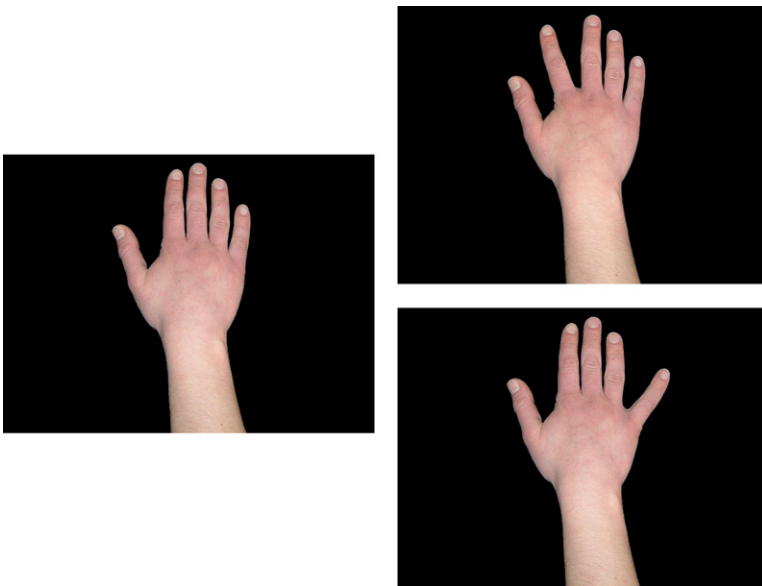


Figure 1. Finger-Movement Stimuli
The static hand (left) was followed by one of two finger-movement stimuli (top panel, index-finger movement; bottom panel, little-finger movement) or control stimuli (TMS sessions only; not shown).

During training, participants in the two groups observed and executed the two movements with equal frequency. Therefore, the countermirror reversal of MEP enhancement found in the incompatible group could not have been due to visual experience alone [18], to motor experience alone [19], or to the sum of visual and motor experience. Rather, the reversal must have been due to the observation-execution contingency experienced by the incompatible group: Sensorimotor learning reconfigured the mirror system.

These results indicate that a relatively short period of incompatible sensorimotor training is sufficient for altering mirror-system responses (as indexed by MEP enhancement) to observation of the trained actions and for replacing a muscle-specific “mirror” action observation effect [11–13] with a countermirror response. They provide strong support for the theory that the “mirror” properties of the mirror system, rather than being innate [14] or dependent on unimodal visual or motor experience, arise through correlated, sensorimotor experience of performing and observing actions [15, 16]. The design of this experiment, in which the only difference between the two experimental groups lay in the contingency between the movements that they saw and performed, allows us to distinguish between the possible roles of these different types of experience in the development of the human mirror system. Because both groups received equal exposure to the visual and motor components of the actions during training, the “countermirror” reversal of MEP enhancement seen in the incompatibly trained group must have been due to the relationship that they experienced between action observation and execution.

The sensorimotor theory [15, 17] proposes that stimulus-response learning underlies mirror-system responses. This hypothesis can explain a number of intriguing features of the mirror neuron system; an example of these features is that the system contains neurons that fire both when object grasping occurs in full view of a monkey and when movement toward the object is observed, but grasping is obscured by a screen [20]. In

the latter case, movement toward the object, which has reliably preceded grasping, activates a visual representation of grasping, and this, in turn, activates the link that exists between observation and execution of grasping and that has been acquired through sensorimotor experience [21]. Another example comes from audiomotor mirror neurons that respond to the sound of actions for which their motor properties code the appropriate action, including sounds that could not be innately specified, such as the ripping of paper [22]. In this case, the sound has become associated in the mirror neuron system with the appropriate action as a result of repeated sensorimotor pairings. In these examples, the stimuli that elicit mirror neuron firing do not “mirror” the motor responses coded for by the same neurons; the eliciting stimuli are arbitrary, in that they are not physically similar to the responses, but they have become connected to the responses through sensorimotor

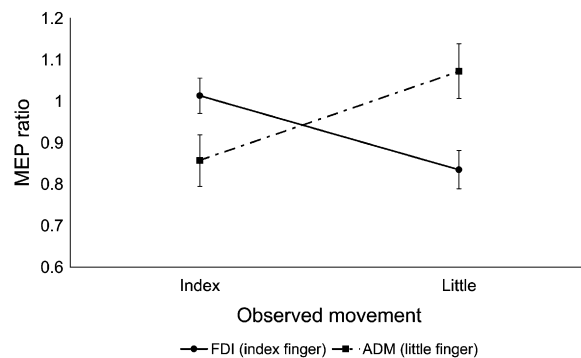


Figure 2. Mean MEP Sizes during Action Observation before Training

Normalized MEP ratios (see [Experimental Procedures](#)) are shown from both groups combined. MEPs were recorded from the two muscles during observation of index- and little-finger movements in the pretraining session. The crossover interaction indicates a “mirror” effect: For each muscle, MEPs are greater during observation of the movement performed by that muscle. Data are represented as mean \pm SEM.

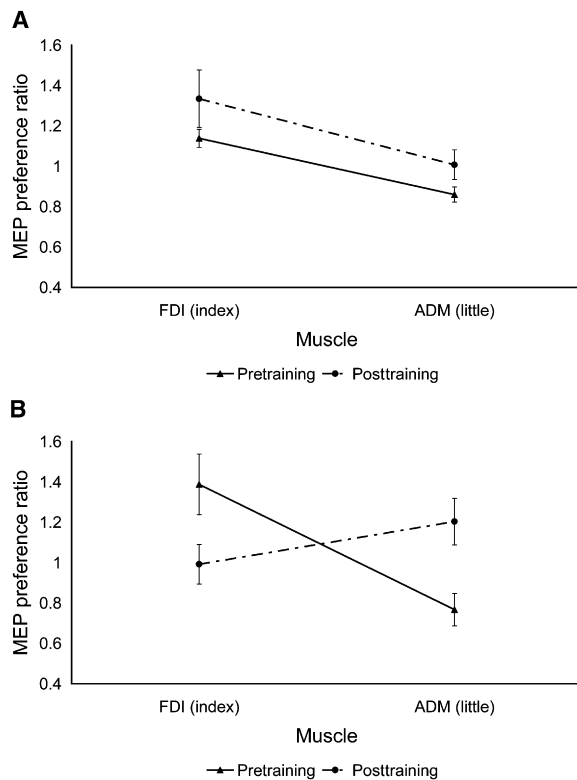


Figure 3. Effect of Sensorimotor Learning: Mean MEP Sizes during Action Observation before and after Training

(A) shows the effect of training on the compatible group, and (B) shows the effect of training on the incompatible group. For clarity of presentation, we calculated the values in these graphs by dividing MEP area during index-finger-movement observation by MEP area during little-finger-movement observation. The resulting “MEP preference ratio” indicates the degree to which the MEPs recorded in each muscle were greater during index- than little-finger movement observation: A “mirror” effect is indicated by a higher value in the FDI muscle than in the ADM, whereas a reversal of this pattern indicates a “countermirror” effect. The statistical analyses (see text) were applied to normalized MEP ratios, relative to receding hand stimuli. Data are represented as mean \pm SEM.

learning. Thus, according to the sensorimotor hypothesis, the mirror properties of the mirror system are genuine but not intrinsic—they depend on the experienced contingency, rather than the objective similarity, between stimuli and responses.

A question may arise concerning the specificity of the effects of sensorimotor training on MEP enhancement. Would MEP enhancement also be seen if participants were trained to make finger-movement responses to arbitrary nonaction visual stimuli? Such a result would be consistent with the suggestion that mirror-system responses develop as a result of general processes of sensorimotor associative learning and would imply that the nature of the stimuli that can enter into these associations is relatively unconstrained [10, 15, 23]. The alternative result—lack of MEP enhancement after training with arbitrary stimuli—would also be consistent with the operation of general processes of sensorimotor associative learning, but it would suggest that, in the case of the mirror system, these processes operate selectively on visual inputs from brain areas, such as the

superior temporal sulcus, that are specialized for the observation of body-part movements [16]. Under either outcome, mirror-system responses are a special case of sensorimotor associations. However, under the second outcome, mirror-system responses are a special subclass of sensorimotor associations in which the stimuli are visual representations of body movements.

If sensorimotor experience is, as this study suggests, crucial in the development of the mirror system, it is important to identify possible sources of this experience in everyday life. Unimodal visual and motor action experience are readily available in the course of normal development; they are provided by passive observation (visual) and simple performance (motor) of any action. In contrast, sensorimotor experience is available only from specific sources [21]. In the case of perceptually transparent actions, such as hand movements, which yield similar sensory inputs when observed and executed, watching one’s own actions gives us perfectly correlated sensorimotor experience of those actions. However, for perceptually opaque actions, such as facial expressions, which yield sensory inputs in different modalities or coordinate frames when observed and executed, social inputs are essential [24]. It is only through interaction with others (or the use of artifacts such as mirrors) that we are able to see movements of the face or trunk while performing them. We need to watch others as they do what we are doing—whether they are deliberately imitating our movements, as adults imitate infants, or simply reacting in the same way to on-going events, like fellow spectators at a sports match. Therefore, the sensorimotor-learning theory implies that the human mirror system is to some extent both a product and a process of social interaction [15]: It contributes, via its roles in language acquisition [8, 9] and theory of mind [5, 6], to our capacity for complex social interaction and also depends for its development on the availability of correlated sensorimotor experience in the sociocultural environment.

Our findings have relevance to developmental disorders. If sensorimotor experience is necessary for configuration of the human mirror system, and social interaction is an important source of this experience, then developmental problems in social interaction would be expected to have an impact on mirror-system functioning. Autism is a developmental disorder characterized primarily by abnormalities in social interaction. From an early age, children with autism show reduced orienting to social stimuli [25], and, even in adulthood, individuals with autism spectrum disorders show reduced attentional modulation of neural responses to social stimuli [26]. Impairments in attention to social stimuli are likely to limit the opportunity to learn sensorimotor links between observed and executed actions, and therefore recent reports of reduced mirror-system activation in autism spectrum disorders [27] may be explained by the sensorimotor-learning hypothesis.

In summary, we have shown that incompatible sensorimotor experience can reverse human mirror-system responses at the neurophysiological level, as indexed by MEP enhancement. The comparison with the compatibly trained group allows us to conclude that it is specifically the training’s sensorimotor nature that affects mirror-system responses, suggesting a mechanism

whereby sensory and motor representations of an action, experienced in a correlated manner during development as a result of social interaction, configure the human mirror system to match perceived and performed actions.

Experimental Procedures

Participants

Participants were screened according to a strict physiological inclusion criterion for ensuring that there was an effect of action observation on MEP size present before training. The initial effect was measured and found to be significant in a group of 44 participants ($F_{1,43} = 12.579$, $p = 0.001$). We then selected the 16 participants (11 male, five female) who showed the clearest effect, with substantial muscle-specific enhancement of MEPs in both muscles, or a crossover interaction between the two muscles, during the pre-training session and assigned them randomly to the two training groups (compatible and incompatible). None of the participants had any contraindications to TMS, all gave written informed consent prior to taking part, and they were paid for participation. The study was approved by the local ethics committee and conducted in accordance with the 1964 Declaration of Helsinki.

TMS and MEP Recording Procedure

MEPs (TMS sessions) or movements (training session) were recorded from right FDI and ADM for all trials with disposable Ag-AgCl electrodes placed in a belly-tendon montage on each muscle, with further ground electrodes on the right wrist. The electromyograph (EMG) signal was amplified by a CED 1902 (Cambridge Electronic Design, Cambridge, UK) at a gain of 10,000 \times (TMS sessions) or 1000 \times (training session). Signals were sampled at 3 kHz and band-pass filtered between 20 Hz and 3 kHz with a mains hum notch filter at 50 Hz. TMS was performed with a 70 mm figure-of-eight coil connected to a Magstim Rapid (Magstim, Dyfed, UK) and positioned over the optimum scalp location of the left motor cortex, with the handle pointing backward at 45 $^\circ$ from the midline. The optimum scalp location was that at which maximum amplitude MEPs were produced in both muscles. Pulse intensity was set at 110% of the resting motor threshold (rMT), defined as the lowest level of stimulation that produced MEPs of at least 50 μ V in both muscles in at least five out of ten trials [28]. Thus, the higher threshold muscle (the ADM) determined rMT [13]. The EMG signal was recorded from 500 ms before to 100 ms after the TMS pulse (TMS sessions) or from 100 ms before to 1900 ms after the onset of the end-posture stimulus (training session). EMG data were stored for offline analysis.

Procedure and Stimuli: TMS Sessions

Participants were seated in a darkened room with their head supported by a chinrest 50 cm from the presentation monitor. Their right arm was placed across the body and supported by an armrest such that the hand was orthogonal to the images on the screen. All participants wore a tight-fitting swimming cap on which the optimum scalp location was marked. This allowed the experimenter to confirm in each trial that the TMS coil was in the correct location. Each trial consisted of a 2000 ms black screen followed by the stimulus video and a further 1000 ms black screen. Stimuli were video files of two images of a hand, subtending approximately 14 $^\circ$ \times 23 $^\circ$ of visual angle. Each video consisted of an image of the dorsal view of a static hand, presented for a variable time interval (800, 1600, or 2400 ms), and this was followed by an image of one of the four end postures: index-finger abduction, little-finger abduction, receding hand, and static hand, which was presented for 960 ms (thus stimulus video length varied from 1760–3360 ms). This succession of images produced apparent motion and allowed the timing of movement stimulus presentation (the end posture) to be identified precisely. At a variable interval (0, 320, or 640 ms) from the onset of the end-posture stimulus, the TMS pulse was triggered by a photodiode on the stimulus presentation monitor, via a small white square on the frame of the video corresponding to the desired pulse time. This allowed precise control over the timing of the pulse in relation to the movements and prevented movement onset from

predicting pulse onset. On 11% of trials, a faint flesh-colored dot ($\sim 1^\circ$ visual angle) appeared at one of six locations on the end-posture image. Participants were instructed to press the space bar with their left hand when they saw a dot. This demanding task ensured that participants were paying close attention to the stimuli. The experimental session consisted of 216 trials (54 presentations of each end-posture stimulus, in random order) and was divided into eight blocks.

Procedure and Stimuli: Training Session

Only index- and little-finger-movement videos were presented during training. These were identical to those used in the TMS sessions. Participants in the compatible training group were instructed to make an abduction of their index finger as soon as they saw the index finger move and to abduct their little finger as soon as they saw the little finger move. Participants in the incompatible training group were instructed to make an abduction of their index finger as soon as they saw the little finger move and to abduct their little finger as soon as they saw the index finger move. Stimuli were presented in random order in 12 blocks of 72 trials each.

Data Analysis: TMS Sessions

For each muscle for every trial, the 500 ms period before the TMS pulse was checked for any background EMG activity; if this was found, the data from both muscles for this trial were rejected. The data from both muscles were rectified, and the area under the curve of the MEP in each muscle was calculated. MEP area was averaged for each muscle for the four different movement conditions. For each muscle, we normalized mean MEP area for observation of each finger movement by dividing it by the mean MEP area for observation of the receding hand to control for interindividual variability in MEP size. This produced the normalized MEP ratio displayed in Figure 2. The average values used for this normalization, i.e., the average MEP areas during observation of the receding hand, expressed in mV \times ms, were as follows: pretraining session: FDI: 2.75; ADM: 1.48; post-training session: FDI: 2.65; ADM: 1.21. Normality of each measure was verified with the Kolmogorov-Smirnov test. To confirm the presence of a muscle-specific action observation effect in the pretraining session, we entered data into a repeated-measures analysis of variance (ANOVA) with two within-subjects factors: recorded muscle (FDI, ADM) and observed movement (index-finger abduction, little-finger abduction). To investigate the effects of training, we entered data from both sessions into a mixed model ANOVA with one between-subjects factor of group (compatibly trained, incompatibly trained) and three within-subjects factors: session (pretraining, post-training), muscle, and movement. Simple interaction analysis was used for investigating the three-way interactions within each group.

Data Analysis: Training Session

For each muscle for every trial, the response time (RT) was calculated in the following manner: A window of 20 ms width was passed over the EMG data in 1 ms steps, starting from the onset of the end-posture stimulus, and the standard deviation of the data within this window was measured. When this value reached 2.8 \times the standard deviation of the period 100 ms before the onset of the end-posture stimulus, this was taken to be the start of the response, and the elapsed time since the onset of the end-posture stimulus was measured for producing the RT. The RTs were verified by eye on a plot of the data for every trial, and errors were recorded. RTs were averaged across muscles for all correct responses for each of the 12 blocks of training.

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