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Research report

Experience modulates automatic imitation

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Abstract

Action observation gives rise to activation in corresponding areas of the premotor and primary motor cortices. We tested the hypothesis that this activation depends on visual–motor connections established through correlated experience of observing and executing the same action. Previous work has shown that hand opening and hand closing gestures are facilitated when subjects observe the movement they are performing, relative to a condition in which they observe a different movement from the one they are performing. Experiment 1 replicated this finding in a simple reaction time (RT) procedure using stimulus–response (SR) movements in orthogonal planes. This implies that the effect is an example of automatic imitation, an instruction-independent tendency to execute movements that are topologically similar to those observed, and not merely an example of spatially compatible responding. In Experiment 2, the automatic imitation effect found in Experiment 1 was abolished by a brief period of training in which subjects responded to hand opening by closing their hands, and to hand closing by opening their hands. This outcome is consistent with the hypothesis that, rather than being innate, the cortical connections mediating motor activation by action observation are formed through experience.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: Action observation; Imitation; Learning; Mirror-neuron system; Motor activation; Stimulus–response compatibility

1. Introduction

There is now a substantial body of evidence that action observation gives rise to matching motor activation, i.e., to activity in the premotor and primary motor cortices normally associated with execution of the observed action [2,3,5,9,10,15,16,17,21,25]. Functional magnetic resonance imaging (fMRI) has indicated somatotopically organized activation of the premotor cortex during observation of hand, foot, and mouth movements [5]. For example, activation of the area of the premotor cortex responsible for execution of mouth movements is greater during observation of mouth movements than during observation of hand and foot movements. Evidence of primary motor cortex activation by action observation is provided by the finding that suppression of the ~20 Hz motor cortex rebound occurs during both action execution and action observation [10,16,17]

Further evidence that action observation activates corresponding motor representations has come from behavioral studies demonstrating movement compatibility or 'automatic imitation' effects [4,6,27]. For example, in a simple reaction time (RT) task, Brass et al. [4] instructed subjects to make one of two finger movements, lifting or tapping, in response to video stimuli showing either a lifting or a tapping finger. They found that subjects' responses were much faster when the stimulus and response movements were the same (compatible trials) than when they were different (incompatible trials). Similarly, in a choice RT task, Stürmer et al. [27] required subjects to open or close their hand when an image of an opening or closing hand changed color. Although the type of stimulus movement (opening or closing) was irrelevant to the assigned task, subjects responded faster on compat-

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ible trials, when the stimulus and response movement were the same, than on incompatible trials. The effects reported in both of these studies suggest that action observation promotes or facilitates imitation, execution of the observed action, and that this facilitation is automatic in the sense that it does not depend on task instructions. Given their automatic character, it is likely that these imitation effects are behavioral products of premotor and primary motor cortical activation by action observation.

Although the evidence that action observation causes matching motor activation is now strong, there has been very little research examining the source of this tendency [13]. Motor activation by action observation implies that areas of the cortex, mediating visual processing of an observed action, are linked, directly or indirectly, to motor areas involved in execution of the same action. However, we do not yet know how these connections are formed. What is the process which has ensured that action observation causes activation of motor areas mediating execution of the same actions, rather than of different actions? Broadly speaking, the candidate processes are natural selection and learning; the visual–motor cortical connections may be innate or formed through experience.

Reports of imitation in newborn infants [22] may indicate that at least some of the cortical connections mediating motor activation by action observation are innate. However, these data are controversial [1,18]. Furthermore, it has been argued that neonatal imitation is intentional, rather than automatic, and, therefore, it is unlikely to be mediated by the 'mirror-neuron system' [23]. In contrast, the Associative Sequence Learning (ASL) hypothesis emphasizes the role of learning in imitation. It suggests that the cortical connections mediating motor activation by action observation arise primarily through correlated experience of observing and executing the same actions [12]. This view has not been tested directly, but it is consistent with two findings. First, mirror neurons in monkey F5 do not initially respond during observation of a mechanical pincer grasping an object, but they begin to do so when the monkey has repeatedly observed the pincer action and, between observation trials, grasped the object with its own hand [24]. Second, muscle-specific facilitation of TMS-induced MEPs by finger movement observation is greater when the model's hand is presented in the orientation at which one normally views one's own hand (heading away) than when it is presented in the orientation at which one normally views another person's hand (heading toward) [20]. This finding is consistent with the Hebbian hypothesis that visual–motor cortical connections are formed through correlated experience of observation and execution because, in most environments, execution of finger movements is more likely to be accompanied by observation of one's own finger movements than by observation of another person's finger movements.

The purpose of the present study was to investigate the role of experience in producing motor activation by action observation. Specifically, we asked whether an automatic imitation effect can be reduced or abolished by prior training in which subjects have correlated experience of observing and executing different actions. This question was addressed directly in Experiment 2, using a test procedure in which subjects were required to perform a pre-specified hand movement (opening or closing) in response to hand opening and hand closing video stimuli. Experiment 1 cleared the way for Experiment 2 by checking whether the tendency to perform the same hand opening/closing movement as a model is a genuine example of automatic imitation.

2. Experiment 1: automatic imitation or spatial compatibility?

The primary purpose of Experiment 1 was to establish whether an effect reported by Stürmer et al. [27] is an example of automatic imitation, or whether it is a spatial compatibility effect. In the experiments reported by Stürmer et al. [27], subjects observed a right hand opening or closing and were instructed to respond either by opening or closing their own right hand, depending on which of two colors appeared on the stimulus hand in the course of its movement. Responses were faster when the stimulus movement and the correct response movement were compatible (both opening and both closing) than when they were incompatible (opening–closing or closing–opening). This effect would be an example of automatic imitation if it reflected a tendency to respond to action observation by performing a movement that is topologically similar to the one observed. In contrast, it would be a spatial compatibility effect if it reflected a tendency to make left responses to stimuli presented on the left, and right responses to stimuli presented on the right. The data reported by Stürmer et al. do not distinguish automatic imitation from spatial compatibility because, in their study, the stimulus hand and the responding hand were both vertically aligned. Thus, at the start of each movement, the fingers and thumb pointed straight upwards, and, for both stimulus and response movements, opening involved movement of the fingers to the right, whereas closing involved movement of the fingers to the left.

To isolate automatic imitation from spatial compatibility, in Experiment 1, the directions of stimulus and response movement were orthogonal. The stimulus hand was vertically aligned, as in the previous study, but the subject's hand, the responding hand, was horizontally aligned. Therefore, when the subject opened their hand, the fingers moved upwards, rather than to the right, and when s/he closed their hand, the fingers moved downwards, rather than to the left. If there is a tendency for automatic imitation of hand opening/closing movements, responding should be faster on compatible than on incompatible trials even when the stimulus and response hands are orthogonally aligned.

The secondary purpose of Experiment 1 was to establish whether an effect like that of Stürmer et al. would occur in a simple, rather than a choice, RT procedure. Thus, like Brass et al. [4], who reported automatic imitation of finger lifting and tapping movements, we instructed subjects to make a prespecified response, opening or closing, as soon as they saw the stimulus hand begin to move. On half of the trials, the stimulus hand opened, and, on half of the trials, it closed, but the type of stimulus movement was formally task-irrelevant. If, in spite of this, responding on compatible trials is faster than on incompatible trials, it would indicate that automatic imitation of hand opening/closing can be detected using a simple RT procedure.

2.1. Materials and method

2.1.1. Subjects

Ten subjects with an average age of 33.6 years, with two males, were recruited from within the Department of Psychology, University College London, and paid a small honorarium for their participation. All were right handed, had normal or corrected-to-normal vision and were naïve with respect to the purpose of the experiment.

2.1.2. Stimuli

Video stimuli were presented on a computer. They showed two movements made by a model's right hand in color on a black background. Both movements were filmed from the angle at which one normally views one's own hands, and began with the fingers closed and pointing upwards in parallel with the thumb (Fig. 1a). In the opening movement, the fingers and thumb splayed (Fig. 1b), and, in the closing movement, they rolled into a fist (Fig. 1c). The final open posture occupied approximately 16° of visual angle horizontally and 23° vertically, whereas the final close posture occupied approximately 10° horizontally and 13° vertically. Viewing distance was 60 cm, and the hands appeared slightly larger than life-size. Each movement consisted of 12 frames and had a duration of 480 ms. The first frame of each stimulus movement video showed the hand in the same neutral starting position. This frame was also used as the warning stimulus (see below).

2.1.3. Data recording and analysis

For both open and close responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus (FDI) muscle using disposable Ag/AgCl surface electrodes. Signals were amplified, high-pass filtered at 20 Hz, mains-hum filtered at 50 Hz and digitized at 2.5 kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with a cutoff frequency of 50 Hz. EMG activity was registered for 95 ms before the onset of the imperative stimulus to define the baseline. A window of 20 ms was then shifted progressively over the raw data in 1-ms steps. Response onset was defined by the beginning of the first 20-ms window after the imperative stimulus in which the standard deviation for that window, and for the following 20-ms epoch, was greater than 2.75 times the standard deviation of the baseline. Whether this criterion correctly defined gesture onset was verified by sight for every trial performed by each subject. Stimulus onset marked the beginning, and EMG onset marked the end, of the response time (RT) interval. Errors were recorded manually.

2.1.4. Procedure

Subjects were tested individually in a dimly lit room. The subject's right forearm lay in a horizontal position across their body, parallel with the stimulus monitor. It was supported from elbow to wrist by an armrest, and, therefore, the subject's hand was free to move. The wrist was rotated so that the fingers moved upwards during opening responses, and downwards when closing. Therefore, given that stimulus movement occurred in the lateral plane (left–right), response movements were orthogonal to stimulus movements. After making each response, subjects were required to return their hand to the neutral starting position shown in Fig. 1a.

In each block of the simple RT task, subjects were required either to open or to close their right hand as soon as the stimulus hand began to move. There were two blocks in which closing was the required response and two in which opening was the required response. The two blocks requiring

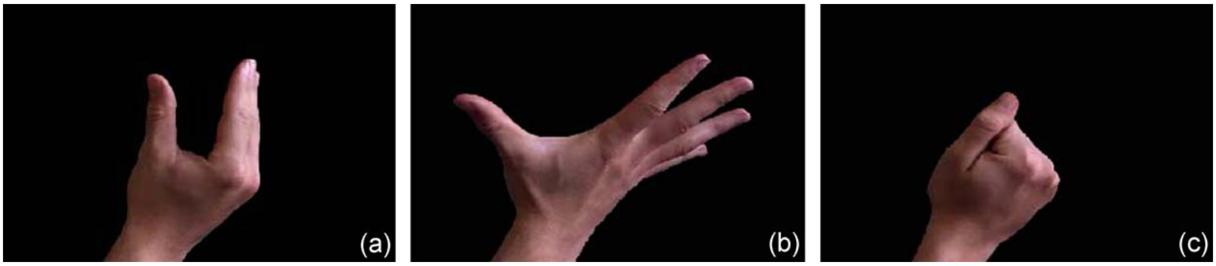

Fig. 1. (a) The first frame of the hand opening and hand closing stimulus videos, which also served as the warning stimulus. (b) The last frame of the hand opening stimulus video. (c) The last frame of the hand closing stimulus video.

the same response were always consecutive, but the order of closing and opening blocks was counterbalanced.

Each block consisted of 60 stimulus trials, in which subjects were required to make the prespecified response (opening or closing), and 12 catch trials, in which they had been instructed not to respond. All trials began with presentation of the warning stimulus. In stimulus trials, this was followed 800, 1600, or 2400 ms later by onset of the opening or closing movement stimulus, which was of 480-ms duration. After the movement stimulus, the screen went blank for 1000 ms before the warning stimulus for the next trial appeared. Each block presented, in random order, 10 stimulus trials of each type defined by combination of the stimulus (opening and closing) and delay (800, 1600, and 2400 ms) variables. In catch trials, which were randomly distributed throughout the block, the warning stimulus remained on the screen for 2880 ms before the 1000-ms intertrial interval.

Before testing commenced with each response type (opening and closing), subjects completed 12 practice trials in which they made the response that was about to be measured. In these practice blocks, two stimulus trials of each type were programmed for presentation in random order, and then one of them was selected at random for replacement by a catch trial.

2.2. Results

The subjects did not make any movement errors on stimulus trials; that is, they did not open their hand when they should have closed their hand (or vice versa), make false starts, or fail to respond. Movement was initiated in less than 1% of catch trials. RTs greater than 1000 ms (0.75%) were excluded from the analysis. On each trial, the stimulus movement was either the same as (compatible) or different from (incompatible) the prespecified response. RT data were subjected to analysis of variance (ANOVA) in which stimulus (compatible and incompatible), response (open and close), delay (800, 1600, and 2400 ms), and block (1 and 2) were within-Ss variables. This revealed only two main effects and no significant interactions. On average, responding was 19 ms faster on compatible trials (M=396 ms, S.E.M.=24) than on incompatible trials (M=415 ms, S.E.M.=27) ($F_{(1,9)}$=23.7, p=0.001). In addition, speed of responding increased with delay (800–M=435, S.E.M.=23; 1600–M=388, S.E.M.=28; 2400–M=394, S.E.M.=27; $F_{2,18}$=29.2, p<0.001). This finding, "the foreperiod effect" (e.g., Ref. [32]), is common in RT studies, and is thought to reflect the influence of both intentional and automatic processes on response preparation (see Ref. [30] for discussion).

2.3. Discussion

Responding was faster when the stimulus movement was the same as the response movement than when the stimulus movement was different from the response movement. This compatibility effect indicates that there is a tendency for automatic imitation of hand opening/closing, and that, in subjects who have not received any explicit training, this tendency can be detected using a simple RT procedure.

3. Experiment 2: the effect of experience on automatic imitation

The ASL hypothesis suggests that the cortical connections mediating motor activation by action observation arise primarily through correlated experience of observing and executing the same actions [11]. In the present case, this implies that it is easier for subjects to, for example, open their hands when observing hand opening than when observing hand closing, because, prior to the experiment, they had seen hand opening while opening their hand more often than they had seen hand closing while opening their hand. It is plausible that hand opening and closing are more commonly correlated with execution of the same response than with execution of a different response because experience of the former kind is provided by looking at one's own hands during movement execution.

To test the ASL hypothesis, the subjects in Experiment 2 were given a relatively brief period of training 24 h before being tested in the same way as the subjects in Experiment 1. The Incompatible Training (IT) group observed hand opening while closing their hands, and observed hand closing while opening their hands. If the ASL hypothesis is correct, this experience should reduce or abolish the automatic imitation effect found in Experiment 1. According to well-established principles of associative learning [8], even a brief period of incompatible training would be expected to establish inhibitory links between visual and motor representations of the same actions (opening–opening, closing–closing), which would slow responding on compatible trials by counteracting the effects of preexisting excitatory links, and to establish new excitatory links between visual and motor representations of opposite actions (opening–closing, closing–opening), which would speed responding on incompatible trials. In contrast, if the cortical connections mediating motor activation by action observation are innate, a brief period of incompatible training should not have any significant impact on the effect observed in Experiment 2.

The performance of the IT group was compared with that of a Compatible Training (CT) control group. During the training period, the CT group had experience of observing hand opening while opening their hands, and observing hand closing while closing their hands. According to the ASL hypothesis, these subjects merely received more of the same kind of experience they had been having all their lives. Therefore, whether the visual–motor connections mediating motor activation by action observation are learned or innate, the CT group would be expected to show an automatic

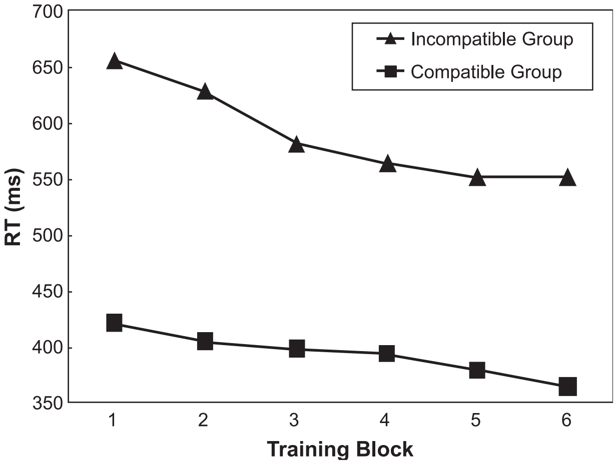

Fig. 2. Mean RT for each training block in Experiment 2, for the Compatible Training (CT) group (■) and the Incompatible Training (IT) group (▲).

imitation effect; that is, on test, they should respond faster on compatible than on incompatible trials.

3.1. Materials and method

3.1.1. Subjects

Twenty additional subjects were recruited from the Department of Psychology, University College London. Their mean age was 23.25 years, eight were male, all were right-handed and had corrected or corrected-to-normal vision, and each was paid a small honorarium for their participation. Subjects were randomly assigned in equal numbers to the Compatible Training (CT) and Incompatible Training (IT) groups.

3.1.2. Procedure

The stimuli, and methods of data recording and analysis, were identical to those of Experiment 1. The test procedure was also the same as in Experiment 1, but 24 h before completing this test procedure, the subjects in Experiment 2 received one of two types of training. In a choice RT task, they were required to respond to an opening hand by opening their own hand, and to a closing hand by closing their hand (CT), or to respond to an opening hand by closing their own hand and to a closing hand by opening their hand (IT).

Training consisted of six blocks of 72 trials each. The opening hand stimulus was presented in half of the trials within each block, and the closing hand stimulus was presented in the other half. The order of stimulus presentation was randomly determined, and the interval between presentation of the warning stimulus and onset of the imperative stimulus was constant at 1 s. Thus, each training trial began with presentation of the static hand warning stimulus (Fig. 1a), which was followed 1 s later by the stimulus movement of 480-ms duration. After the stimulus movement, the screen was blank for 1 s until the warning stimulus for the next trial appeared. A practice block consisting of six opening and six closing trials in random order was completed prior to training.

To encourage accurate performance, the number of movement errors made by the subject was displayed after each training block.

3.2. Results

RTs greater than 1000 ms (0.2%) were excluded from the analysis. Movement errors occurred in less than 0.1% of trials and therefore will not be reported further.

3.2.1. Training

Fig. 2 shows, for each of the two groups, mean RT in each training block. These data were subjected to ANOVA in which block (1–6) was the within-subjects factor and group (CT and IT) was the between-subjects factor. Mauchly's Test indicated that sphericity could not be assumed ($W_{(14)}$=0.051, p<0.001), and, therefore, F values were corrected using the Greenhouse–Geisser method. The analysis revealed significant main effects of block ($F_{(5,90)}$=16.45, p<0.001) and group ($F_{(1,18)}$=22.49, p<0.001), and a significant block× group interaction ($F_{(5,90)}$=3.15, p=0.045). Thus, as expected, responding was slower in the IT group than in the CT group, and whereas the performance of both groups improved in the course of training, the decrease in RT between blocks 1 and 6 was greater for the IT group (M=105 ms, S.E.M.=25.7) than for the CT group (M=58 ms, S.E.M.=10.9).

3.2.2. Test

Fig. 3 shows, for each training group, mean RT for compatible and incompatible test trials. These data were subjected to ANOVA in which stimulus (compatible and incompatible), response (open and close), delay (800, 1600, and 2400 ms), and block (1 and 2) were within-subjects factors, and group (CT and IT) was the between-subjects factor. The analysis revealed a significant main effect of stimulus ($F_{(1,18)}$=23.1, p<0.001), and a significant main

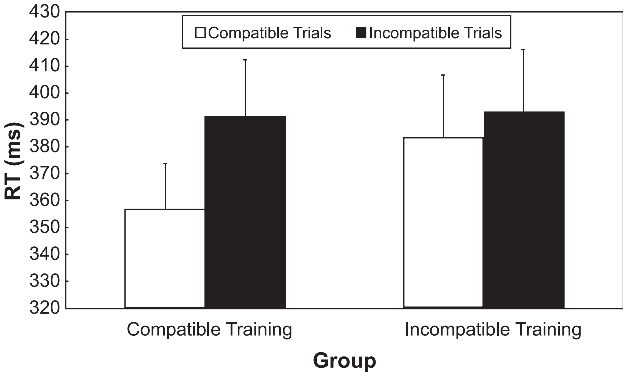

Fig. 3. Mean RT on compatible and incompatible trials in Experiment 2, for the Compatible Training (CT) and Incompatible Training (IT) groups. Vertical bars indicate S.E.M.

effect of delay ($F_{(2,36)}$=26.4, p<0.001). On average, compatible movements were executed 21 ms faster than incompatible movements, and responses following the two longer delays were executed faster than those made after the shortest delay (800–M=401, S.E.M.=16; 1600–M=368, S.E.M.=14; 2400–M=375, S.E.M.=13). The interaction of primary interest, between group and trial type, was also significant, ($F_{(1,18)}$=8.4, p=0.01). Simple effects analysis revealed that the difference in RT between compatible and incompatible trials was significant for group CT (M=34 ms; $F_{(1,18)}$=29.7, p<0.001), but not for group IT (M=9 ms: $F_{(1,18)}$=1.8, p=0.194).

3.3. Discussion

In Experiment 2, an automatic imitation effect, which is observed when subjects are not given explicit training (Experiment 1) and when they are given compatible training, was abolished by training in which subjects responded to hand opening by closing their hands, and to hand closing by opening their hands. This result is consistent with the hypothesis that motor activation by action observation is mediated by connections that are formed through correlated experience of observing and executing the same movements.

4. General discussion

Experiment 1 showed that, even in a simple RT task, and when stimulus movement (left–right) and response movement (up–down) occur in orthogonal planes, performance of hand opening and hand closing gestures is faster when the same movement is being observed than when the opposite movement is being observed. This implies that, like finger lifting and tapping [4], observation of hand opening and closing provokes automatic imitation, rather than merely spatially compatible responding [27].

Higher-order spatial compatibility; that is, a tendency to make left responses to down stimuli, and right responses to up stimuli, has been reported under a narrow range of conditions [14,19]. For example, this tendency is apparent when the up and down stimuli are eyes presented in the context of a rotated human face, and when the responding hand is aligned such that vertical responses can be coded according to their horizontal position with respect to the hand's principal axis. None of the conditions supporting higher-order spatial compatibility were present in Experiments 1 and 2, and, therefore, this research does not cast doubt on the conclusion that hand opening and closing provoke automatic imitation.

The results of Experiment 2 showed that automatic imitation of hand opening/closing can be modulated by experience. The automatic imitation effect observed in subjects who had not been given explicit training (Experiment 1), and in subjects who received compatible training, was abolished by a brief period of training in which observation of hand opening was accompanied by execution of hand closing, and vice versa. In conjunction with previous studies [20,24], this finding supports the ASL hypothesis that motor activation by action observation, a phenomenon that has been detected repeatedly using both neurophysiological and behavioral measures, is mediated by cortical connections which have been established through correlated experience of observing and executing the same action [11].

The effects of incompatible training in the present study were asymmetrical: incompatible training caused RT on compatible trials to increase, but did not cause RT on incompatible trials to decrease. This pattern of results is the opposite of that predicted by a nativist account of automatic imitation. If responding on compatible trials is based on innate visual–motor cortical connections, it should be less, not more, vulnerable than responding on incompatible trials to the influence of a brief period of incompatible training. The ASL model is better able to account for the data because it postulates that incompatible training will establish inhibitory links between visual and motor representations of the same actions (opening–opening, closing–closing), and thereby slow responding on compatible trials. However, the associative account also suggests that incompatible training will establish excitatory links between visual and motor representations of opposite actions (opening–closing, closing–opening), and thereby speed responding on incompatible trials. The latter effect was not detected in the present study.

One potential explanation for the asymmetrical effect of training challenges the ASL model. Instead of establishing new long-term excitatory and inhibitory connections between visual and motor action representations—connections of the same, durable type that mediate stimulus–response compatibility effects (SRC) in naïve participants—a brief period of incompatible training may result in temporary, strategic suppression of long-term excitatory links between visual and motor representations of the same actions. This hypothesis is suggested by studies showing that, in choice RT tasks, spatial compatibility effects are eliminated when compatible and incompatible mappings are mixed within the same block, and the trial-specific mapping rule is given less than 600 ms before stimulus presentation [7,26]. These findings are consistent with temporary suppression of excitatory links between visual and motor representations of the same action (of the 'direct route' in dual-route models, [7]), but not under conditions comparable with those of the present study. In the training phase of Experiment 2, compatible and incompatible mappings were not mixed within blocks, and in the test phase, when our Incompatible Training group failed to show a compatibility effect, they were performing a simple, rather than a choice, RT task.

Using a procedure more like that of Experiment 2, Tagliabue et al. [28,29] showed that brief training with incompatible stimulus–response mappings eliminates a spatial SRC effect in a subsequent Simon task, for which stimulus location is irrelevant. They attributed this elimination effect, which showed the asymmetrical pattern observed in Experiment 2, to the formation during incompatible training of “short-term-memory links” between spatially incompatible stimuli and responses. However, subsequent research has shown that the effect of incompatible training on Simon task performance is modality-specific, and that it endures when there is an interval of one week between training and testing [31]. These findings suggest that the links established through incompatible training have the properties ascribed by the ASL model to long-term associations, and therefore raise the possibility that the difference between the “short-term” and ASL hypotheses is purely terminological. Even if the two hypotheses are distinct, neither readily explains why incompatible training would slow responding on compatible trials without also accelerating responding on incompatible trials. One possibility, which could be investigated by giving more extensive incompatible training, is that fewer trials are necessary to establish inhibitory associations between compatible stimuli and responses than to establish excitatory associations between incompatible stimuli and response.

The results of the present study indicate (1) that hand opening and hand closing gestures are facilitated when subjects observe the movement they are performing, relative to a condition in which they observe a different movement from the one they are performing, (2) that this effect can be demonstrated in a simple RT procedure using orthogonal stimulus and response movements, implying that the effect is an example of automatic imitation and not merely an example of spatially compatible responding; and (3) that the automatic imitation effect found in Experiment 1 was abolished by a brief period of training in which subjects responded to hand opening by closing their hands, and to hand closing by opening their hands. This last finding is consistent with the general hypothesis that motor activation by action observation depends on visual–motor cortical connections established through correlated experience of action observation and execution.

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