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Biol. Lett. published online 21 September 2011

doi: 10.1098/rsbl.2011.0759

Supplementary data "Data Supplement"

http://rsbl.royalsocietypublishing.org/content/suppl/2011/09/19/rsbl.2011.0759.DC1.ht

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Biol. Lett. doi:10.1098/rsbl.2011.0759 Published online

Animal behaviour

# The transfer of motor functional strategies via action observation

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When someone is choosing one piece from a bowl full of fruit, many pieces are within reach and visible. Although the desired piece seems to govern the particular pattern and direction of that person's reaching movement, the selection process is not impervious to the presence of task-irrelevant information (i.e. the other fruits). Evidence suggests that the kinematics of reach-to-grasp actions for a desired object integrates the motor features of all the objects which might become potential targets. Transcranial magnetic stimulation (TMS) and motor-evoked potentials (MEPs) were used by us to establish if that motor integration process can be transferred to an onlooker. Our results indicate that observation of hybrid reach-tograsp movement kinematics is reflected in the observer's pattern of MEP amplitudes. This effect can be defined as a form of motor resonance which operates by 'reading' the kinematics of an observed action. The brain's ability to mirror motor integration processes while observing someone else's action helps an onlooker to understand what the other person is doing and to predict his/her motor alternatives.

**Keywords:** action simulation; motor system; selection for action; transcranial magnetic stimulation; motor-evoked potentials

# 1. INTRODUCTION

Observing another person's actions selectively and implicitly facilitates the brain's motor circuits to carry out the same action. Covert motor activation during action observation has been demonstrated using transcranial magnetic stimulation (TMS) [1]. TMS has been applied to the primary motor cortex representing the hand, and motor-evoked potentials (MEPs) have been recorded from hand muscles contralateral to the stimulated cortex during passive observation of hand movements. It was found that there was a selective increase of MEPs in the same muscular groups used to execute those actions, supporting the hypothesis that perceived actions are mapped onto an onlooker's motor system. In the absence of any detectable muscle activity, mere observation of another person's actions modulates the excitability of the observer's corticospinal system (CS) involved in executing those same movements [2].

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2011.0759 or via http://rsbl.royalsocietypublishing.org.

Although CS facilitation during action observation is a widely accepted concept, experimental environments in nearly all studies are typically sparse, usually containing only one object to be acted upon, while the ambiances in which humans live in and act are far more complex, containing many objects towards which actions could be directed. In the face of the complex dynamic environments in which we move and interact, highly efficient systems are needed to link perception and action [3]. These systems must, by necessity, process not only information about the target object itself, but also about the motor features of all the objects which might become potential targets.

Consider the apparently trivial task of deciding which to choose from a tray full of pastries. Watching the choreography of the hand as it approaches the tray reflects somehow that the decision is a 'difficult' one. In motor terms, the kind of hand shaping involved is one enabling a sudden change of mind. Previous studies on selection-for-action have demonstrated that non-target objects can be processed in parallel with target ones, and this parallel processing activates a motor integration mechanism. The outcome is a hybrid kinematic pattern permitting a range of actions dictated by the environment [4,5]. Noticeably, witnessing another's hybrid kinematic pattern leads an onlooker to simulate the observed motor integration [6].

Although it is clear that observing another person's action activates corresponding motor areas in the observer's brain and primes similar actions, other key issues remain to be clarified, namely: to what extent one person's actions are encoded on someone else and how an observed motor integration process influences an observer's CS activity? Using a selection-for-action paradigm during action observation seemed to us to provide a unique opportunity to investigate these questions. TMS-induced MEPs were analysed while subjects were instructed to observe a model grasping a small target eliciting a precision grip (PG; i.e. the opposition of the thumb with the index finger) or a large target eliciting a whole hand grasp (WHG; i.e. opposition of the thumb with all fingers). In other experimental conditions, the target object was flanked by another article (i.e. distractor) implicitly requiring a PG or a WHG movement in order to be grasped.

We predicted that observing a model grasping an isolated object would elicit CS activity specifically related to the appropriate type of grasp. If, instead, a flanker was present, we predicted a hybrid activity pattern would take place irrespective of the appropriate type of grasp. If these predictions are correct, we will be able to conclude that regardless of pure action goals, our motor system can simulate the outcome of a motor integration process characterizing observed actions.

# 2. MATERIAL AND METHODS

# (a) Participants

Thirty participants (22 females and eight males: age  $= 24 \pm 9$  years) took part in the experiments. All were right-handed according to a Standard Handedness Inventory [7] and had normal or corrected-to-normal vision. None had any contraindication to TMS or experienced discomfort during the experiment.

# (b) Experimental stimuli

A model performing reach-to-grasp actions was filmed in four experimental conditions (figure 1). Differential MEP responses to observation of actions performed in the presence or absence of a



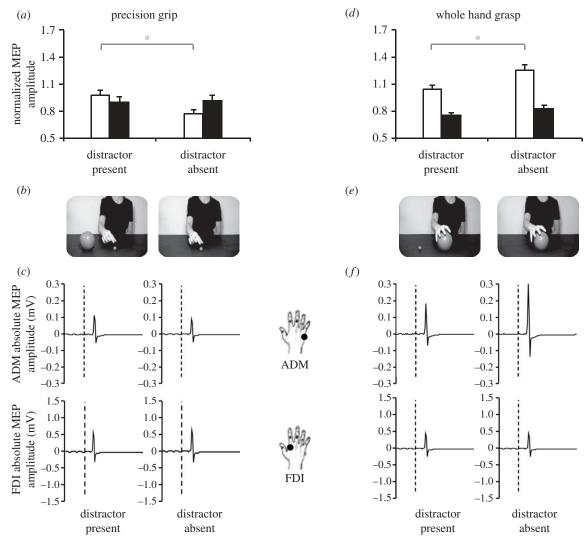


Figure 1. (a) Normalized MEP amplitude for ADM (white bars) and FDI (black bars) for precision grip (PG) in the two distractor conditions. (b) Snapshots representing the model performing a PG in the presence/absence of the large distractor eliciting a whole hand grasp (WHG). (c) Absolute MEP amplitude of a representative participant (c,f) for both ADM and FDI muscles for the two distractor conditions. (d) Normalized MEP amplitude for ADM (white bars) and FDI (black bars) for WHG for the two distractor conditions. (e) Snapshots representing the model performing a WHG in the presence/absence of the small distractor. (f) Absolute MEP amplitude of a representative participant (c,f) for both ADM and FDI muscles for the two distractor conditions. Asterisks indicate significant comparisons (p < 0.05). Bars represent the s.e.m.

distractor were recorded. Analysis of the kinematic model for human motion confirmed that there were distractor effects (electronic supplementary material).

# (c) Transcranial magnetic stimulation and motor-evoked potential recording

TMS was delivered using a 70 mm figure of eight coil connected to a Magstim BiStim [2] stimulator (Magstim, Whitlan, Dyfed, Wales, UK). Pulses were delivered over the left primary motor cortex corresponding to the hand region (electronic supplementary material). The coil was positioned in correspondence with the optimal scalp position (OSP), defined as the position from which stimulation of a slightly suprathreshold intensity consistently produced the largest MEPs from both the abductor digiti minimi (ADM; the muscle serving little finger abduction) and the first dorsal interosseus (FDI; the muscle serving index finger flexion/extension) muscles.

# (d) Procedure

Participants were instructed to lay their hands in prone position as still and relaxed as possible and to watch the video clips avoiding any movement. To encourage the participants to maintain a good level of attention, they were told that they would be questioned at the end of the experiment about what they had seen. Ten trials were presented for each of the four types of video clip, for a total of 40 trials. The order in which the trials were presented was randomized across participants. TMS-induced MEPs from the right

ADM and the right FDI muscles were acquired once for each video presentation, at the point in which the model reached the maximum grip aperture before contacting the object. Each video presentation was followed by a 10 s rest interval. Ten MEPs per muscle were acquired for each video, for a total of 80 MEPs per participant (electronic supplementary material). Baseline CS excitability was assessed prior to and following the video presentations.

# (e) Data analysis

Peak-to-peak amplitudes of the MEPs from both the ADM and FDI muscles were measured and averaged for each condition. MEP amplitudes deviating more than two standard deviations from the mean for each type of action and trials contaminated by muscular pre-activation were excluded as outliers (less than 2%). A paired sample t-test (two-tailed) was used to compare the amplitude of MEPs from the ADM and FDI muscles in the two series of baseline trials at the beginning and at the end of the experimental session. Ratios were then computed using the individual mean amplitude of MEPs recorded in the two fixation cross periods as baseline (MEP  $ratio = MEP_{obtained}/MEP_{baseline}$ ). A repeated measures analysis of variance (ANOVA) was conducted on the MEP ratios with 'distractor' (present and absent) and 'type of grasp' (PG and WHG) as within-subjects factors. On the basis of the model's kinematic analysis, only conditions in which the size of the distractor did not match the size of the target were considered. Sphericity of the data was verified prior to performing statistical analysis (Mauchly's test,

Table 1. Normalized mean (±s.e.m.) peak-to-peak amplitude of MEPs recorded from the ADM and the FDI muscles for each 'type of grasp' (PG and WHG) and 'distractor' (present and absent).

	precision grip		whole hand grasp	
	distractor present	distractor absent	distractor present	distractor absent
FDI ADM	0.90 (±0.01) 0.97 (±0.07)	0.93 (±0.01) 0.79 (±0.08)	$0.73 (\pm 0.01)$ $1.08 (\pm 0.01)$	$0.80 \ (\pm 0.01)$ $1.25 \ (\pm 0.01)$

p > 0.05). Post hoc pairwise comparisons were carried out using t-tests and the Bonferroni adjustment for multiple comparisons was applied.

### 3. RESULTS

TMS per se did not induce any changes in CS excitability during our experiments (electronic supplementary material). Mean MEP ratios from the ADM and the FDI muscles during all the experimental conditions are outlined in table 1. MEP amplitude for the FDI muscle was higher for the PG than for the WHG  $(F_{1,29} = 16.60, p < 0.001)$ , but no 'distractor' effect was noted ( $F_{1,29} = 1.62, p > 0.05$ ). Repeated measures ANOVA on normalized MEP amplitudes for the ADM muscle yielded a statistically significant main effect of type of grasp ( $F_{1,29} = 6.89, p < 0.05$ ). MEP amplitude for the ADM muscle was higher for the WHG than for PG which does not entail little finger abduction (p < 0.05). The 'distractor' interaction by 'type of grasp' was also significant ( $F_{1,29} = 10.38, p < 0.05$ ). Post hoc contrasts revealed that when a small target eliciting a PG was presented along with a large distractor evoking a WHG, MEP amplitude was higher with respect to conditions in which the same small target was presented in isolation (p < 0.05; figure 1). Conversely, when a large target evoking a WHG was presented along with a small distractor potentially evoking a PG, MEP amplitude was lower with respect to what was observed when the same large target was presented in isolation (p < 0.05; figure 1).

# 4. DISCUSSION

These results confirm previous findings that observing another person's actions modulates the excitability of the onlooker's CS [2]. In those conditions in which a target is isolated, CS activity reflects the appropriateness of the type of grasp observed. When the action observed is a WHG, both the FDI and the ADM muscles are activated. Conversely, the FDI but not the ADM muscle is activated when the action observed is a PG. In those conditions in which the target is not isolated, parallel planning for both the target and the flanker stimuli evident in the model's hybrid kinematics is reflected in the onlooker's cortical activity. When the target is small and the flanker large, ADM activation is noted, although in theory that muscle is not recruited during a PG movement. On the other hand, since both types of grasp signify the evolvement of FDI muscle recruitment (although to a different extent), it is activated in both cases.

How can these findings be explained? We hypothesize that there is a simulation mechanism reflecting

the model's action strategies. The MEP activity pattern analysed by us revealed that during observation the motor cortex recruits a hybrid muscular activity in the onlooker just as in the person actually performing the action. Our findings showing that the motor system resonates with the extrinsic visual aspects of what the brain sees [8-10] takes research on this subject a step further. Our results demonstrate that kinematic signatures are capable of automatically influencing an onlooker's action system by allowing motor functional strategies to be transferred. Acknowledging a model's hybrid kinematics dictated by clutter might be useful in order to predict the final outcome of his/her action. An alternative explanation that cannot be excluded is that observation of objects activates motor plans even in the absence of a model. Whether it is the person or the object that is important will be the object of further studies on this subject.

While our understanding of the activity of the human motor system during action observation has until now been limited to actions directed towards single objects, we have shown here that this system can take into account an array of potential actions. Just as subjects prepare for possible changes by integrating parallel motor plans, onlookers are able to mirror the motor integration conveyed in the kinematics of the observed action in order to predict its possible outcomes.

The experimental procedures outlined here were granted ethical approval (electronic supplementary material) and all of the participants gave their written informed consent.

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# 4 L. Sartori et al. The transfer of motor strategies

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