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Direct eye contact enhances mirroring of others' movements: A transcranial magnetic stimulation study

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A B S T R A C T

Direct eye contact is a powerful social cue to regulate interpersonal interactions. Previous behavioral studies showed a link between eye contact and motor mimicry, indicating that the automatic mimicry of observed hand movements is significantly enhanced when direct eye contact exists between the observer and the observed model. In the present study, we aim to investigate the neurophysiological basis of the previously reported behavioral enhancements. Here, transcranial magnetic stimulation (TMS) was applied to assess changes in cortico-motor excitability at the level of the primary motor cortex (M1) to explore whether and how the motor system is facilitated from observing others' hand movements and, in particular, how this process is modulated by eye contact. To do so, motor evoked potentials (MEPs) were collected from two hand muscles while participants received single-pulse TMS and naturally observed video clips of an actor showing hand opening movements or static hands. During the observation, either direct or averted eye gaze was established between the subject and the observed actor. Our findings show a clear effect of eye gaze on observation-induced motor facilitation. This indicates that the mapping or 'mirroring' of others' movements is significantly enhanced when movement observation is accompanied by direct eye gaze compared to averted eye gaze. Our results support the notion that eye contact is a powerful social signal with the ability to direct human non-verbal social behavior. Furthermore, our findings are important for understanding the role of the mirror motor system in the mapping of socially relevant actions.

1. Introduction

Human social interaction is a complex behavior between two or more individuals to communicate thoughts, intentions, emotional states and actions to one another. Ever since their discovery, 'mirror neurons' have been suggested to form an integral part of the neural circuitry that mediates our capacity to understand the meaning of the actions and behaviors of others (Gallese, 2009).

Neurons with mirror properties were first discovered using single-cell recordings in the ventral premotor cortex of macaque monkeys (Rizzolatti et al., 1988), and were shown to have the ability to fire not only when the monkey executes a certain motor action, but also when the monkey observes another individual performing the motor action (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). Using movement observation paradigms in combination with functional neuroimaging techniques such as fMRI (Buccino et al., 2001; Iacoboni et al., 1999) and PET (Grafton et al., 1996; Rizzolatti et al., 1996b) a homologous action observation–execution matching system or 'mirror system' has been localized in the human brain. Particularly, both frontal (inferior frontal gyrus; IFG) and parietal (inferior parietal lobule; IPL) areas have been shown to become increasingly activated during the mere observation of others' actions (Chong et al., 2008; Kilner et al., 2009).

Overall, and according to the notion of 'embodied cognition', this

Abbreviations: APB, abductor pollicis brevis; FC, fixation count; FDI, first dorsal interosseous; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; M1, primary motor cortex; MEP, motor-evoked potential; mPFC, medial prefrontal cortex; RMSE, root mean square error; rMT, resting motor threshold; STS, superior temporal sulcus; TFD, total fixation duration; TMS, transcranial magnetic stimulation

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process of 'mapping' observed actions onto the corresponding sensorimotor representations has been hypothesized to form the core neural mechanism by which others' actions and emotional states can be simulated, recognized and understood (Iacoboni, 2009; Iacoboni et al., 2005; Rizzolatti and Craighero, 2004; Rizzolatti and Fabbri-Destro, 2008). However, note that also weaker accounts of 'embodied cognition' have been put forward, arguing that conceptual 'understanding of actions' may not be represented exclusively in terms of sensorimotor processes, but may additionally involve an abstract or modality-independent representation (Caramazza et al., 2014; Mahon, 2015).

In the past decade, the non-invasive brain stimulation technique transcranial magnetic stimulation (TMS) has been used extensively to measure resonant 'mirror motor' activity in the observer's motor system. By applying TMS over the primary motor cortex (M1), a motor evoked potential (MEP) can be elicited from the contralateral muscles to obtain a measure of cortico-motor excitability (Fadiga et al., 1995). Interestingly, a number of studies (for a review, see Fadiga, Craighero and Olivier, 2005) have shown that during the mere observation of others' actions, cortico-motor excitability within parts of M1 becomes increasingly facilitated, as indicated by significant enhancements in MEP amplitudes. Furthermore, this process has been shown to be highly muscle-specific, such that modulations in M1 cortico-motor excitability are predominantly observed in the muscles that are used in the observed action (Alaerts et al., 2009a, 2009b; Strafella and Paus, 2000). Besides muscular involvement, a number of studies used the TMS technique to explore how different kinematic features of the observed actions are encoded by the observer's motor system, such as temporal dynamics (Gangitano et al., 2001), grip force (Alaerts et al., 2010a; Alaerts et al., 2010b; Alaerts, et al., 2012), orientation (Maeda et al., 2002) and predictability (Maeda et al., 2001).

The mapping mechanism for conveying information from others' behaviors is not only affected by kinematic features, but may also be influenced by the processing of socially relevant cues from the observed environment (Wang and Hamilton, 2012). One such powerful social cue is perceived eye contact. The role of eye gaze in social behavior has been investigated extensively, with several neuroimaging studies showing that observed eye contact is a strong modulator of activity in regions of the 'social brain', a network of structures that is specialized to process social information such as faces, theory of mind and empathy, but also biological motion, action and goal direction (for a review, see Senju and Johnson, 2009). Particularly within the superior temporal sulcus (STS), brain activity has been shown to be specifically enhanced when direct eye contact is perceived (Pageler et al., 2003; Pelphrey et al., 2004). Furthermore, the STS region has also been hypothesized to form an integral part of the 'extended' mirror system network by providing the main visual input to upstream fronto-parietal mirror-motor regions (Grèzes et al., 2001; Grossman and Blake, 2002; Grossman et al., 2000).

To date however, only a handful of studies have explored the effect of perceived eye contact on the processing of the actions and movements of others. In terms of movement mimicry, a recent behavioral study by Wang et al. (2011a) provided first indications that the tendency of an observer to mimic others' actions is enhanced when eye contact exists between the observer and the model. As a form of unconscious imitation, mimicry is strongly associated with the mirror neuron system (Iacoboni, 2009). In particular, reaction times for mimicking a hand closing or opening movement were shown to be faster when direct eye contact was established, rather than when eye gaze was averted (Wang et al., 2011a). Also a magnetoencephalographic (MEG) study by Kilner et al. (2006) provided evidence that the social relevance of a stimulus (modulated in terms of the observer's viewpoint) can enhance putative mirror neuron activity. Together, these observations provide first indications that activity within the human mirror system can be influenced by distinct socially relevant cues from the observed environment.

To the best of our knowledge, no studies to date have directly investigated the neurophysiological basis of the effect of eye contact on motor resonance, as research has mainly focused on mimicry (Wang et al., 2011a, 2011b) or the influence of higher-order cognitive processes such as social relevance observation (Kilner et al., 2006). However, since eye contact is a powerful social cue, it would be interesting to directly explore whether direct eye gaze can modulate the mapping of others' actions in the observer's motor system. In the present study, the TMS technique was used to assess the effect of eye gaze on motor facilitation of M1 during movement observation. In particular, single-pulse TMS was applied over left M1 to measure the level of cortico-motor excitability of two hand muscles (right abductor pollicis brevis (APB) and first dorsal interossei (FDI)) during the observation of an actor performing simple hand movements involving those muscles. During the movement observation trials, the actor looked either directly towards or away from the observing participant to assess the effect of direct versus averted eye gaze on observation-induced motor facilitation at the level of M1. If eye gaze forms a salient social cue for modulating the process of mirror-motor mapping at the level of M1, we expected TMS-evoked MEPs to be higher when accompanied by direct gaze compared to averted gaze.

2. Material and methods

2.1. Main experiment: Measurements of cortico-motor excitability during movement observation

2.1.1. Participants

Thirty-three right-handed individuals (16 males and 17 females) aged between 19 and 26 years old (mean ± SD: 22;7 ± 1;8 years;-months) participated in this study. Handedness was assessed with the Edinburgh Handedness Questionnaire (EHQ; Oldfield, 1971). All participants provided signed written informed consents prior to the experiment, reported no history of neurological/psychiatric illness or motor dysfunctions of the hands/arms and met safety criteria for TMS. Ethical approval for the experiment was granted by the local Ethics Committee for Biomedical Research at the Katholieke Universiteit Leuven and conformed to the Code of Ethics of the World Medical Association (Helsinki, 1964). One female subject was excluded due to technical problems during the experiment.

To explore whether modulating effects of eye gaze were related to inter-individual differences in social responsiveness, subjects completed the Dutch self-report version of the Social Responsiveness Scale for adults (SRS-A; Constantino and Todd, 2005). The SRS-A (64 items) is a widely used screening tool to identify the presence and extent of any social impairments in the typical population using a four-point Likert-scale. It encompasses four subscales, including social awareness (19 items; α=.80), social communication (22 items; α=.88), social motivation (11 items; α=.83) and rigidity/repetitiveness (12 items; α=.79). Lower scores indicate higher social responsiveness. For raw SRS scores, a cut-off point of 54 is suggested for signaling impairments in social responsiveness (Noens et al., 2012).

2.1.2. General procedure

Participants were seated in a comfortable chair approximately 80 cm in front of a widescreen DELL monitor (resolution: 1920×1080 pixels, refresh frequency: 60 Hz) on which video stimuli of hand movements were displayed with a frame rate of 29 Hz. The right hand was placed palm-down on a soft cushion on their lap and participants were asked to relax their hand muscles while spontaneously viewing the presented video clips. During the experiment subjects' vision of their own hands was obstructed by another cushion placed on top of their hands.

2.1.3. Electromyography recordings and TMS

Dependent measures of cortico-motor excitability, i.e. motor-