



Research report

Seeing fearful body language rapidly freezes the observer's motor cortex



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ARTICLE INFO

Article history:

Received 14 June 2014

Reviewed 6 August 2014

Revised 21 November 2014

Accepted 20 January 2015

Action editor Ahmad Hariri

Published online 7 February 2015

Keywords:

Emotional body

Fear processing

Freezing

Motor cortex

Intracortical facilitation

Transcranial magnetic stimulation

ABSTRACT

Fearful body language is a salient signal alerting the observer to the presence of a potential threat in the surrounding environment. Although detecting potential threats may trigger an immediate reduction of motor output in animals (i.e., freezing behavior), it is unclear at what point in time similar reductions occur in the human motor cortex and whether they originate from excitatory or inhibitory processes. Using single-pulse and paired-pulse transcranial magnetic stimulation (TMS), here we tested the hypothesis that the observer's motor cortex implements extremely fast suppression of motor readiness when seeing emotional bodies – and fearful body expressions in particular. Participants observed pictures of body postures and categorized them as happy, fearful or neutral while receiving TMS over the right or left motor cortex at 100–125 msec after picture onset. In three different sessions, we assessed corticospinal excitability, short intracortical inhibition (SICI) and intracortical facilitation (ICF). Independently of the stimulated hemisphere and the time of the stimulation, watching fearful bodies suppressed ICF relative to happy and neutral body expressions. Moreover, happy expressions reduced ICF relative to neutral actions. No changes in corticospinal excitability or SICI were found during the task. These findings show extremely rapid bilateral modulation of the motor cortices when seeing emotional bodies, with stronger suppression of motor readiness when seeing fearful bodies. Our results provide neurophysiological support for the evolutionary notions that emotion perception is inherently linked to action systems and that fear-related cues induce an urgent mobilization of motor reactions.

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<http://dx.doi.org/10.1016/j.cortex.2015.01.014>

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1. Introduction

Different lines of evidence suggest that threat-related signals are rapidly and efficiently processed in the central nervous system (Adolphs & Tranel, 2003; LeDoux, 1996; Öhman & Mineka, 2001) and that attention tends to be prioritized towards threatening stimuli (Fox et al., 2000; Vuilleumier, 2002).

Fearful body language is a salient emotional signal, easily observable from a distance that alerts the observer to the presence of a potential threat (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Tamietto, Geminiani, Genero, & de Gelder, 2007). Perceiving fearful expressions in others requires specific processing in an attempt to garner more information about the source of the threat in the surrounding environment (Whalen et al., 1998). Indeed, behavioral studies have shown enhanced sensory acquisition (Lee, Susskind, & Anderson, 2013), perceptual processing (Phelps, Ling, & Carrasco, 2006) and attention (Davis & Whalen, 2001; Kret, Stekelenburg, Roelofs, & de Gelder, 2013) when exposed to fearful expressions. Notably, electrophysiological studies have also reported a rapid bias in visual attention allocation with greater resources devoted to fearful expressions; they reported increased amplitudes or shorter latencies of early (100–200 msec) occipito-temporal event-related potential (ERP) components when viewing fearful body expressions (Jessen & Kotz, 2011; Van Heijnsbergen, Meeren, Grèzes, & de Gelder, 2007) and facial expressions (Pourtois, Thut, Grave de Peralta, Michel, & Vuilleumier, 2005; Righart & de Gelder, 2006; Williams, Palmer, Liddell, Song, & Gordon, 2006) relative to emotionally positive and neutral expressions.

Besides increasing sensory vigilance for monitoring potential threats, the sight of fearful expressions may affect the motor system. Animal research has shown that initial reactions to sudden stimuli - and potential threats, in particular - involve reducing motor output, i.e., implementing freezing behavior or orienting immobility while monitoring the source of danger (Fanselow, 1994; Hagenaars, Oitzl, & Roelofs, 2014). Similar phenomena have been suggested in humans (Frijda, 2010; Hagenaars et al., 2014; Lang & Bradley, 2010). In keeping with this notion, transcranial magnetic stimulation (TMS) studies have documented fast reductions in motor excitability following salient and potentially noxious stimuli like strong, unexpected or rapidly approaching auditory or visual stimuli (Avenanti, Annala, & Serino, 2012; Cantello, Civardi, Cavalli, Varrasi, & Vicentini, 2000; Furubayashi et al., 2000; Makin, Holmes, Brozzoli, Rossetti, & Farnè, 2009; Serino, Annella, & Avenanti, 2009), and painful stimuli self-experienced (Farina, Tinazzi, Le Pera, & Valeriani, 2003; Farina et al., 2001; Urban et al., 2004) or observed in others (Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2006; Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009a; Avenanti, Minio-Paluello, Sforza, & Aglioti, 2009b). Moreover, a reduction of activity in primary motor cortex (M1) has been reported during periods in which participants expect to receive painful stimuli relative to conditions without pain expectation (Butler et al., 2007).

Remarkably, imaging studies have shown that observing fearful expressions in others activates subcortical (e.g., amygdala, superior colliculus) and cortical regions (e.g., cingulate cortex and supplementary motor area, SMA) known to be

involved in emotional processing and motor control (de Gelder et al., 2004; de Gelder et al., 2010; Grèzes, Pichon, & de Gelder, 2007; Hadjikhani & de Gelder, 2003; Kret, Pichon, Grèzes, & de Gelder, 2011; Thielscher & Pessoa, 2007; Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier & Pourtois, 2007). However, the nature of such activations is ambiguous because imaging can hardly distinguish between motor inhibition (which would support freezing-like body immobilizations) and excitation (which would reflect increased action readiness) and cannot precisely determine when these modulations occur. On the other hand, the high temporal resolution of TMS and its ability to distinguish between excitatory and inhibitory activity in motor areas allow effective exploration of motor dynamics during emotion perception.

The goal of this study was to test whether exposure to fearful body postures rapidly reduces excitability in the observer's M1. To this aim, we used TMS over M1 to non-invasively assess motor excitability during perception of emotional body expressions. In previous studies, we started to investigate the dynamics of the human motor system by assessing corticospinal excitability in the observers' left and right M1 during an emotion recognition task (Borgomaneri, Gazzola, & Avenanti, 2012; Borgomaneri, Gazzola, & Avenanti, 2014b). We recorded motor-evoked potentials (MEPs) at 150 and 300 msec after the presentation of fearful, happy and neutral expressions in which the body posture was presented in isolation, with no contextual or facial cues. In the earlier time window (150 msec) we found a weak increase in corticospinal excitability in the left hemisphere in response to fearful body postures, suggesting action preparation activity in the motor representation of the dominant hand (see also Borgomaneri, Gazzola, & Avenanti, 2014a; Schutter, Hofman, & Van Honk, 2008 for similar findings using fearful facial expressions and negative natural complex scenes). Remarkably, in the same time window, we found a consistent reduction of corticospinal excitability in the right hemisphere for both fearful and happy body postures (Borgomaneri et al., 2014b). This reduction in motor excitability also appeared to be causally related to visual recognition of body postures. TMS over right M1 (but not left M1) at 150 msec after visual stimulus onset also decreased the ability to recognize the observed body postures. The decrease in performance additionally correlated with the reduction in corticospinal excitability, suggesting a close link between motor suppression in the right M1 and perceptual processing of body postures.

At the later stage (300 msec), greater MEP amplitudes were measured when viewing fearful, happy and emotionally neutral dynamic body postures relative to emotionally neutral static body postures. This later increase in motor excitability was similar in the two hemispheres. Moreover, it was comparable for the three dynamic postures (see also Borgomaneri et al., 2012) and likely reflected motor resonance, i.e., the embodiment of the actor's movements into one's own motor system (Bastiaansen, Thioux, & Keysers, 2009; Gallese, Keysers, & Rizzolatti, 2004; Gallese & Sinigaglia, 2011; Keysers & Gazzola, 2009; Niedenthal, Mermillod, Maringer, & Hess, 2010; Oberman, Winkielman, & Ramachandran, 2007; Rizzolatti & Sinigaglia, 2010) that is typically detected in similar time windows (200–400 msec) according to TMS and MEG evidence (Barchiesi & Cattaneo, 2013; Cavallo, Catmur,

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