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ORIGINAL ARTICLE

# Behavioral inhibition system sensitivity enhances motor cortex suppression when watching fearful body expressions

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**Abstract** Influential theories suggest that a defensive behavioral inhibition system (BIS) supports the inhibition of action tendencies when facing potential threats. However, little is known about threat-related inhibitory mechanisms in humans and their relations to inter-individual differences in BIS sensitivity. To address this issue, we used paired-pulse TMS to investigate early human motor cortex (M1) responses to social signals of potential threats, like another's fearful body posture. In two experiments, participants observed pictures of fearful and happy postures, and neutral postures that were either dynamic (in Exp1) or static (in Exp2). To test suppression of M1 excitatory activity, we assessed intracortical facilitation (ICF) in an early phase of threat monitoring by administering TMS pulses at 100–125 ms from picture onset. We investigated the motor representation of hand and arm muscles that are differentially involved in flexion, extension, and abduction. As a control, we also assessed corticospinal excitability and short intracortical inhibition. In both experiments, and independently of the muscle, watching fearful bodies suppressed ICF relative to watching happy and non-emotional (dynamic or static) body expressions. Remarkably, greater fear-related ICF suppression was found in participants who scored higher on a self-report questionnaire assessing BIS sensitivity. These findings suggest that observing fearful body language activates a defensive suppression of M1 excitatory activity that is influenced by the personality disposition to experience fear and anxiety when facing potential threats. This BIS-related motor suppression may have the functional role of transiently suppressing action tendencies to promote threat monitoring and, ultimately, survival.

**Keywords** Fear perception · Emotional body · Behavioral inhibition system (BIS) · Motor-evoked potentials (MEPs) · Intracortical facilitation (ICF) · Transcranial magnetic stimulation (TMS)

## Introduction

One of the fundamental affective systems in human and non-human animals supports the motivation to inhibit action tendencies when facing potential threats (Gray and McNaughton 1996; McNaughton and Corr 2004; Frijda 2010; Lang and Bradley 2010; Hagenaars et al. 2014). Such motivational responses are inherent in affective responses to threats, and trait motivational responses are embedded into personality (Gray and McNaughton 1996; Corr 2004; McNaughton and Corr 2004). Fearful body expressions are powerful social signals that alert the perceiver to the presence of a potential threat (de Gelder et al. 2004; Tamietto et al. 2007). Compared to other threat-related emotional expressions (e.g., angry expressions), those signaling fear are ambiguous as they indicate the presence of danger, but not its source (Whalen et al. 1998; Hortensius et al. 2016). Indeed, detecting signs of fear in others might recruit specific sensory and attentional process in an attempt to garner

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more information about the source of the threat in the surrounding environment (Whalen et al. 1998; Phelps et al. 2006; de Gelder et al. 2012; Lee et al. 2013; Celeghin et al. 2015; Tamietto et al. 2015; Hortensius et al. 2016). For example, watching fearful expressions increases the amplitude of early visual components of event-related potentials (e.g., the P1 component in the 100–125 time range; see Pourtois et al. 2005; van Heijnsbergen et al. 2007), suggesting a rapid allocation of cognitive resources for monitoring potential threats.

Besides rapidly increasing sensory vigilance for threat monitoring, fear perception can transiently modulate motor areas (Schutter et al. 2008; Costa et al. 2013; Borgomaneri et al. 2015a, b) and affect motor behavior (Adams et al. 2006; Lowe and Ziemke 2011; Sagaspe et al. 2011; Blakemore et al. 2016). Animal research has shown that the initial reactions to potential threats involve reducing motor output, i.e., implementing freezing behavior or orienting immobility while monitoring the source of danger, and such motor inhibition is thought to favor threat monitoring (Fanselow 1994; Walker and Carrive 2003; Hagenaars et al. 2014). Similar phenomena have been suggested in humans (Frijda 2010; Lang and Bradley 2010; Hagenaars et al. 2014; Low et al. 2015), and studies have documented fast suppression of motor excitability when processing noxious and potentially threatening stimuli in the somatosensory (Farina et al. 2001; Urban et al. 2004), acoustic (Serino et al. 2009; Avenanti et al. 2012) and visual modalities (Cantello et al. 2000; Makin et al. 2009; Avenanti et al. 2009b). However, the neural mechanisms underlying fear-related motor suppression in humans, and their links with stable personality traits, are poorly known, and are thus the focus of the present research.

Preliminary insights come from a recent transcranial magnetic stimulation (TMS) study in which we documented a fast reduction in motor cortex (M1) excitability when watching fearful body expressions (Borgomaneri et al. 2015c). Participants observed pictures of happy, fearful, or emotionally neutral dynamic body postures, while TMS was administered over M1 to record motor-evoked potentials (MEPs) in the early temporal window of threat monitoring, corresponding to fear-related P1 enhancement (100–125 ms). MEPs were used to tap established measures of motor excitability: MEPs in response to single-pulse TMS were used to assess global changes in corticospinal excitability (CSE), whereas MEPs in response to paired-pulse TMS were used to explore changes in excitatory (i.e., intracortical facilitation, ICF) and inhibitory (i.e., short intracortical inhibition, SICI) cortical mechanisms in M1 (Kujirai et al. 1993; Ziemann et al. 1996, 1998; Liepert et al. 1998; Tandonnet et al. 2010). The SICI effect consists of a reduction in MEP size that is obtained when the suprathreshold test TMS pulse eliciting the MEP is preceded by a subthreshold conditioning TMS pulse administered at short (i.e., 1–5 ms) interstimulus intervals (ISIs). The ICF effect consists of an increase in MEP size that is obtained when the subthreshold conditioning pulse and the suprathreshold test pulse are administered at longer ISIs (i.e., 7–20 ms). Studies indicate that these inhibitory (SICI) and facilitatory (ICF) modulations of MEP amplitude take place at the cortical level without affecting spinal circuits (Kujirai et al. 1993; Ziemann et al. 1996, 1998; Liepert et al. 1998; Tandonnet et al. 2010). The SICI and ICF indices are thought to reflect the activation of separate populations of inhibitory GABA-ergic and excitatory glutamatergic cortical interneurons in M1, respectively, and thus provide reliable measures of motor cortical activations (Kujirai et al. 1993; Ziemann et al. 1996, 1998; Liepert et al. 1998; Di Lazzaro et al. 2000).

The results of our previous study showed that ICF was selectively suppressed when seeing fearful expressions (Borgomaneri et al. 2015c). No changes in CSE or SICI were found, suggesting fearful expressions suppressed motor reactivity through a selective reduction of intracortical excitatory mechanisms within M1, without affecting corticospinal pathways or inhibitory cortical activity. This suggested that seeing fearful expressions reduces the propensity to move the body while monitoring for the possible source of the threat.

In the present study, we sought to expand our understanding of human affective systems by investigating early responses of M1 excitatory circuits to social signs of fear, and the influence of affective personality traits on such motor responses. We hypothesized that the ICF reduction reflects the cortical counterpart of an early and fear-specific suppression of action tendencies, suggesting that this inhibitory response may arise from a defensive motivational system for controlling adaptive behavior—akin to the so-called "behavioral inhibition system" (BIS), as originally hypothesized in Gray's reinforcement sensitivity theory (Gray 1987, 1994; Gray and McNaughton 1996; McNaughton and Corr 2004). According to this theory, the BIS represents a "stop system" that is activated by threat detection and promotes behavioral inhibition as a manifestation of anxiety for and attentional engagement to cues of potential threats (McNaughton and Corr 2004; Amodio et al. 2008). Interestingly, studies indicate the neural bases of the BIS overlap with the neural network recruited when watching fearful body expressions, and involve subcortical (e.g., amygdala) and cortical regions (e.g., cingulate cortex) that are known to be involved in processing salient emotional signals and in motor control (Gray 1987, 1994; Gray and McNaughton 1996; McNaughton and Corr 2004; Vuilleumier and Pourtois 2007; Thielscher and Pessoa 2007; Grèzes et al. 2007; de Gelder et al. 2010).

The operations of the BIS are thought to be embedded into specific personality dimensions. Relevant to this point, Carver and White (1994) developed a self-report measure of BIS sensitivity. The BIS scale offers a measure of the affective dispositions to experience fear and anxiety when facing threats (McNaughton and Corr 2004). Scholars have interpreted the psychological construct underlying the BIS scale as reflecting either behavioral inhibition or active avoidance in response to potential threats. However, recent neuroscientific investigations have suggested that the BIS scale is associated with motor inhibition rather than avoidance (Amodio et al. 2008). Based on this, we hypothesized that stable affective dispositions tapped by the BIS scale would predict the magnitude of the early suppressive response of M1 excitatory circuits at the sight of fearful body postures. We thus designed an experiment aimed at exploring the relationship between BIS and ICF responses to fearful body postures. We also sought to address two outstanding issues, to highlight the phenomenology of such ICF responses, and provide evidence of their underlying mechanism.

Indeed, if fear-related inhibition of action tendencies is the mechanism underlying early ICF suppression for fearful body postures, one would expect this modulation to affect the entire arm, as immobility responses related to threat monitoring are massive (Lang et al. 2000; Walker and Carrive 2003; Hagenaars et al. 2014). However, a limitation of previous research is that MEPs were monitored from one muscle only, the first dorsal interosseous (FDI). While the FDI is widely used to tap motor excitability with TMS, it should be noted that this muscle is critically involved in fine motor control of hand grip during grasping (Chao et al. 1976; Maier and Hepp-Reymond 1995; Perez and Rothwell 2015; Borgomaneri et al. 2015b), i.e., the most functional approaching movement in the human motor repertoire. Hence, it remains unclear whether early ICF suppression for fearful body postures truly reflects a massive inhibition of action tendencies affecting the entire arm (Lang et al. 2000; Hagenaars et al. 2014) or, rather, the tendency to suppress approaching movements (i.e., grasping) that may be inappropriate in the context of a potential threat (Chen and Bargh 1999; Rotteveel and Phaf 2004; Marsh et al. 2005; Frijda 2010; Lang and Bradley 2010).

Another possible issue concerns the stimuli used in the previous research. Indeed, Borgomaneri and colleagues (2015c) presented participants with images depicting fearful and happy postures together with emotionally neutral dynamic body postures with comparable amounts of implied motion. Thus, both emotional and neutral stimuli represented human bodies in motion. No neutral static postures were used. However, such postures are important experimental controls for interpreting the meaning of the motor modulations detected during observation of dynamic body movements. This is because seeing human movements (even when these movements are represented in still pictures) can trigger motor resonance in M1 (i.e., motor activations reflecting mirroring of the observed movements) which is indexed by an increase in MEP size for dynamic relative to static postures (Candidi et al. 2010; Urgesi et al. 2010; Borgomaneri et al. 2012; Avenanti et al. 2013; Naish et al. 2014). It should be noted that the previous studies have reported reduced motor resonance when observing negatively valenced motor behaviors (Liuzza et al. 2014). Thus, without testing static body postures, it remains unclear whether the reduction in ICF for fearful body postures truly reflects a reduction in the propensity to move one's own body (as we previously suggested) or, rather, reduced motor resonance for emotionally negative (fearful) movements (as suggested by the study of Liuzza et al. 2014).

All these issues are dealt within the present study, in which we sought to clarify the meaning of the early cortical motor response to observed fearful body expressions. We used single-pulse and paired-pulse TMS over M1, while participants were presented with emotional (fearful and happy) and neutral body postures, which included either dynamic neutral movements (in Experiment 1, as in Borgomaneri et al. 2015c) or static neutral postures (in Experiment 2). We monitored activity in corticospinal (CSE) and intracortical (ICF, SICI) motor circuits controlling the FDI (as in Borgomaneri et al. 2015c) but also other flexor, extensor, and abductor muscles.

To test the influence of BIS/threat sensitivity (i.e., the dispositional tendency to experience fear and anxiety and to inhibit behavior when facing threats) on neurophysiological responses to fearful body postures, participants filled out the BIS scale (Carver and White 1994) after the TMS experiment. As a control, we also measured scores on the behavioral activation system (BAS) scale that assesses approach motivation. Empirical and theoretical work has established that behavioral inhibition in the BIS/BAS framework refers to a behavioral manifestation of attentional engagement to cues signaling potential threats (Fowles 2000; Yu and Dayan 2005; Amodio et al. 2008). However, high BIS scores are sometimes also associated with avoidance motivation and anxiety disorders (Quay 1988; Fowles 2000). Therefore, to check whether ICF suppression was specifically related to threat sensitivity or influenced by the general disposition to experience anxiety, we additionally assessed trait-anxiety scores using form Y2 of the State and Trait-Anxiety Inventory (STAI-Y2) (Spielberger 1983).

Supporting our hypotheses, we found that seeing fearful body expressions induced a generalized suppression of M1 excitatory circuits controlling upper limb abductor/adductors and flexor/extensors. Moreover, this generalized suppression was predicted by inter-individual differences in BIS, but not in BAS or STAI-Y2. Therefore, our study supports the hypothesis of an inhibitory affective system that is triggered by social cues of threat, operates quickly by suppressing intracortical excitatory transmission in M1, and is influenced by BIS-related personality traits.

## Methods

### Participants

Twenty-six healthy participants took part in the study. Thirteen participants (7 men, mean age ± SD: 22.7 years ± 1.8) were assigned to Experiment 1, and another 13 (7 men, 23.7 years ± 2) were assigned to Experiment 2. All participants were naïve to the purpose of the experiment and gave written informed consent before participation. The experimental protocol was approved by the ethics committee of the University of Bologna and was carried out in agreement with legal requirements and international norms (Declaration of Helsinki 1964). Participants were right-handed and free of any contraindications to TMS. No discomfort or adverse effects during TMS were reported or noticed.

### Visual stimuli

Pictures were presented on a 19-inch screen located about 80 cm away from the participant. Sixty pictures depicting four actors in emotional and neutral body postures (Fig. 1) were selected from a validated database (Borgomaneri et al. 2012, 2015a, c). To focus specifically on body-related information, the face was blanked out in all pictures. In Experiment 1, stimuli included 15 pictures of fearful postures, 15 pictures of happy postures, and 15 pictures of neutral dynamic postures with perceived (implied) motion comparable to that of the emotional body expressions (Fig. 1a). The same 15 fearful and 15 happy stimuli were used in Experiment 2, in addition to 15 pictures of neutral static body postures with no implied motion (Fig. 1b). The only difference between Experiments 1 and 2 was the dynamic or static feature of the emotionally neutral body posture stimuli. The set of stimuli was validated in the previous studies (Borgomaneri et al. 2012, 2015a). These studies ensured that stimuli were well recognized as prototypical representations of the different postures. Moreover, stimuli within each fearful, happy, neutral dynamic, and neutral static category were controlled for emotional variables like arousal and valence (see below) through selection procedures (Borgomaneri et al. 2012, 2015a).

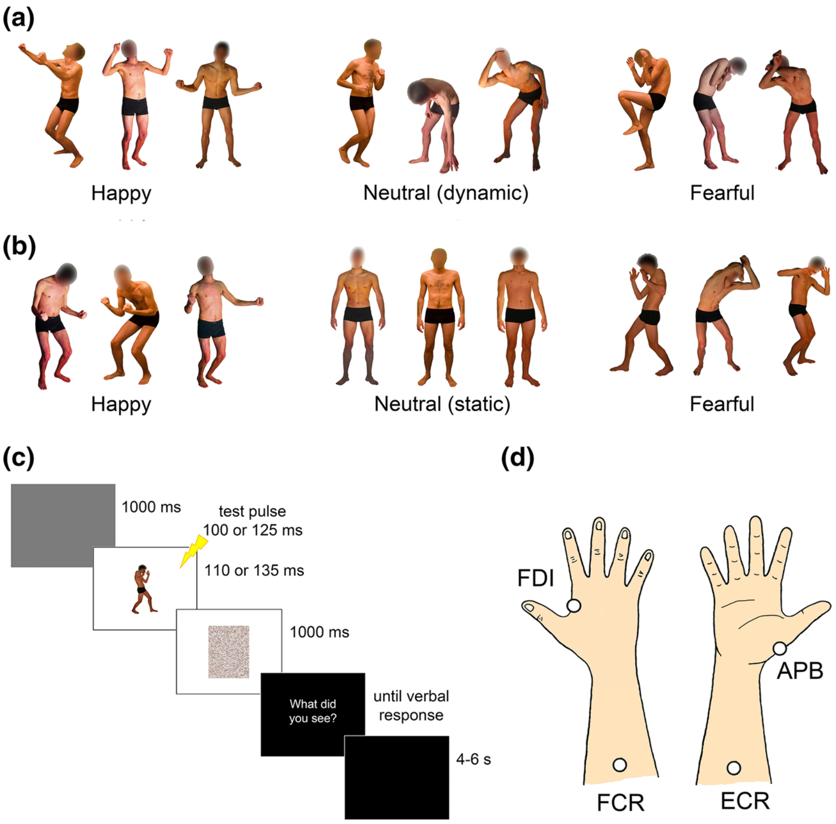

**Fig. 1** Examples of body postures used in Experiment 1 (**a**) and Experiment 2 (**b**). The two experiments included the same set of happy and fearful body expressions but different for neutral body posture that were dynamic and static in Experiment 1 and 2, respectively. Trial sequence during MEP recording (**c**). Site of the target muscles (**d**)

To rule out the possibility that changes in M1 excitability might be due to differing amounts of implied motion in the models' left or right body parts, mirror-reflected copies of the stimuli were also created. Seven participants in each experiment were tested with the original versions of the stimuli, while the remaining participants were tested with mirror-reflected copies. Preliminary analyses showed no effect of stimulus set on MEPs or subjective ratings, so data from the two subgroups of participants were merged.

### TMS and electromyography (EMG) recording

MEPs induced by TMS of the left M1 were simultaneously recorded from two hand muscles, the right FDI and the right abductor pollicis brevis (APB), and from two forearm muscles, the flexor carpi radialis (FCR) and the extensor carpi radialis (ECR). Figures 1d and 2 illustrate muscle sites and examples of raw MEPs. EMG signals from the four muscles were recorded with a Biopac MP-35 (Biopac, USA), band-pass filtered (30–500 Hz), sampled at 5 kHz, digitized, and stored on a computer for off-line analysis. Pairs of silver-chloride surface electrodes were placed in a belly tendon montage over the four muscles with ground electrodes on the right wrist (for hand muscles) and on the right elbow (for arm muscles). A figure-of-eight focal coil was connected to a Magstim Bistim$^2$ stimulator (Magstim, UK). The coil was placed tangentially to the scalp at a 45° angle to the mid-line to induce a posterior–anterior current flow across the central sulcus. The hand motor area of the left M1 was defined as the point where stimulation consistently evoked the largest MEP in the FDI. We chose this scalp position to keep the procedure consistent with what we used in our previous studies (Borgomaneri et al. 2015c; see also Borgomaneri et al. 2014, 2015a, b). Importantly, from that position, a stable signal could also be recorded from the other target muscles which possess largely overlapping representations in M1 (Krings et al. 1998; Devanne et al. 2006). This minimizes the possibility of a bias in the results, in keeping with previous studies reporting comparable hand/forearm MEP modulations during visual or imagery tasks regardless of the chosen optimal scalp position (e.g., Avenanti et al. 2005, 2006; Fourkas et al. 2006; Marconi et al. 2007; Loporto et al. 2013). We defined the resting motor threshold (rMT) as the lowest intensity that evoked 5 small responses (~50 µV) in the relaxed FDI muscle in a series of 10 stimuli (Rossini et al. 2015). The absence of voluntary contractions was visually verified continuously throughout the experiment. When muscle tension was detected, the experiment was briefly interrupted and the participant was invited to relax.

In both experiments, MEPs were recorded in three sessions: a single-pulse TMS session for assessing CSE, and two paired-pulse sessions for assessing ICF and SICI. During the single-pulse session, TMS intensity was set to evoke MEPs with a peak-to-peak amplitude of ~1 mV in the relaxed FDI. During the paired-pulse TMS sessions, ICF and SICI were induced using an established protocol: a conditioning pulse was followed by a test magnetic pulse eliciting a MEP, and both pulses were administered through the same coil (Kujirai et al. 1993; Ziemann et al. 1996). The intensity of the conditioning pulse was 80% of the rMT, a level at which we confirmed that MEPs could

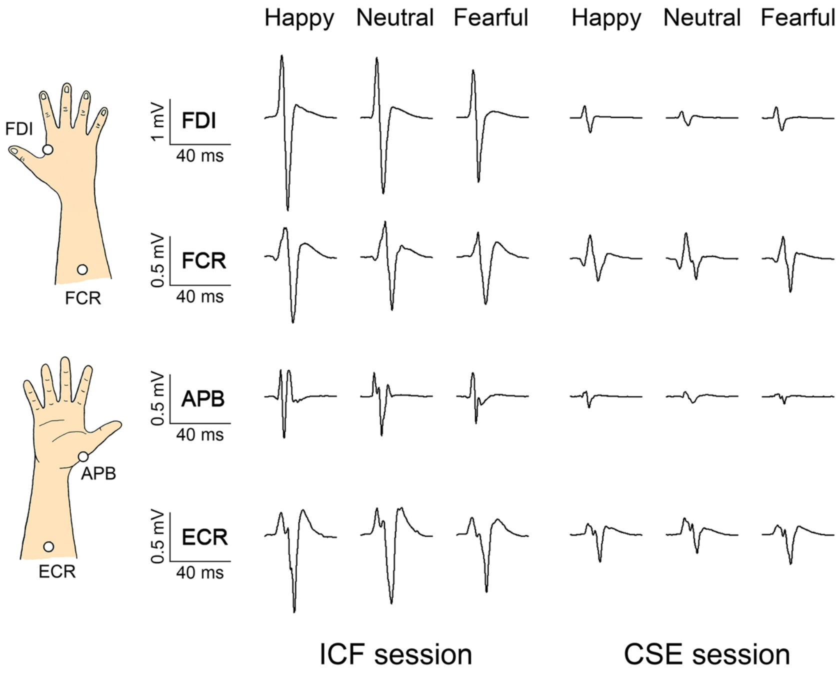

**Fig. 2** Examples of raw MEPs from the FDI, FCR, APB, and ECR muscles of a representative subjects in Experiment 1. MEPs approximately matching the mean amplitude of each visual condition are illustrated. Only MEPs collected in the 100-ms condition of the ICF and CSE sessions are illustrated for simplicity. The figure exemplifies the larger MEP amplitudes detected in the ICF relative to the CSE session (main effect of Session) and the reduction of MEP amplitudes for fearful relative to neutral and happy expressions that were found in the ICF but not in the CSE session. As shown in the statistical analysis, these two effects were similar across the four muscles

never be induced in any muscle. The intensity of the test pulse was the same as the intensity used in the single-pulse session for evoking MEPs. We selected two inter-pulse intervals: 3 and 12 ms, which are typically used to investigate SICI and ICF circuits, respectively (Kujirai et al. 1993; Ziemann et al. 1996). Indeed, a conditioning pulse administered 3 ms before a test pulse is expected to result in MEP inhibition (i.e., SICI), whereas 12-ms inter-pulse intervals should produce MEP facilitation (i.e., ICF) relative to MEPs elicited by an unconditioned test pulse. These MEP modulations take place at the cortical level and are thought to reflect the activation of separate populations of inhibitory and excitatory cortical interneurons without affecting spinal circuits (Kujirai et al. 1993).

## Procedure

The experiments were programmed using the MATLAB software to control picture presentation and to trigger TMS pulses. In each experiment, MEPs were collected in three experimental sessions (CSE, ICF, and SICI). Before and after the experimental sessions, two blocks of 12 MEPs were collected using single-pulse TMS. In these blocks—which served as baselines—participants kept their eyes closed with the instruction to imagine watching a sunset at the beach (Fourkas et al. 2008; Borgomaneri et al. 2012), while single-pulse TMS was administered with an inter-pulse interval of ~10 s.

In the CSE, ICF, and SICI experimental sessions, participants performed an emotion recognition task, in which they were presented with a picture and were asked to categorize it as a happy, fearful, or neutral body posture. Each emotion evaluation block included 90 trials (270 trials in total). In the emotion evaluation blocks, the trial sequence was as follows: a gray screen (1-s duration) indicated the beginning of the trial, and it was followed by the test picture projected at the center of the screen (Fig. 1c). In half the trials, the stimulus was presented for 110 ms, and the single-pulse of TMS (or the test pulse in the paired-pulse sessions) was delivered at 100 ms from stimulus onset. In the remaining trails, the stimulus was presented for 135 ms, and the single-pulse/test pulse was delivered at 125 ms from stimulus onset. In this way, we assessed motor excitability in the early temporal window of threat monitoring (100–125 ms), corresponding to the time window of fear-related P1 enhancement reported in the previous ERP studies (Pourtois et al. 2005; van Heijnsbergen et al. 2007). Stimulus duration was randomly distributed in the two blocks, and the session order was counterbalanced across participants. The picture was followed by a random-dot mask (obtained by scrambling the corresponding sample stimulus using custom-made image segmentation software) lasting 1 s. Then, the question "What did you see?" appeared on the screen, and the participant provided a verbal response (forced choice). Possible choices were: happy, fear, or neutral. An experimenter collected the answer by pressing a computer key. To avoid changes in excitability due to a verbal response (Tokimura et al. 1996; Meister et al. 2003), participants were invited to answer only during the question screen, a few seconds after the TMS pulse (Tidoni et al. 2013). After the response, a black screen appeared for 4–6 s. To reduce the initial transient-state increase in motor excitability, before each session, two single pulses (or two paired pulses) of magnetic stimuli were delivered over M1. In all the experimental sessions, the inter-pulse interval was greater than 10 s, thereby avoiding changes in motor excitability due to TMS per se (Chen et al. 1997). This was confirmed by directly comparing mean MEP amplitudes collected in the first and last baseline blocks using a series of planned paired $t$ tests. As expected, no changes in MEP amplitude were found in any of the muscles in either experiment (all $p > 0.43$). Each of the three experimental sessions lasted about 10 min.

## Behavioral measurements

After TMS, participants were presented with all the stimuli (shown in a randomized order) and asked to judge valence and perceived movement using a 5-point Likert scale. To avoid building up artificial correlations between the different judgments, each rating was collected separately during successive presentation of the whole set of stimuli (Avenanti et al. 2009a). To keep the duration of the experiment short, we did not collect ratings of arousal, which is another important dimension along which emotions vary. However, arousal was collected in the previous validation studies using the same set of stimuli (Borgomaneri et al. 2012, 2015a, b, c). These studies ensured that happy and fearful postures were matched for arousal and were given higher arousal ratings than dynamic and static neural postures.

Subsequently, participants were asked to fill in the Italian versions of the BIS/BAS (Carver and White 1994; Leone et al. 2001) and STAI-Y2 scales (Spielberger 1983; Spielberger et al. 2012).

The BIS/BAS scales are based on the well-established notion that two general motivational systems underlie adaptive behavior (Gray 1987, 1994; Gray and McNaughton 1996; Fowles 2000; McNaughton and Corr 2004). A behavioral inhibition system (BIS) is believed to regulate aversive motives, in which the goal is to alert the organism and stop behavior when facing threatening cues. Indeed, BIS activation is associated with fear and enhanced attention, arousal, vigilance, and anxiety. A Behavioral Activation System (BAS) is believed to regulate appetitive motives, in which the goal is to move toward something desired and escape from punishment (Gray and McNaughton 1996).

The BIS/BAS is a 20-item self-report questionnaire assessing inter-individual differences in the sensitivity of these systems (Carver and White 1994). The BIS scale consists of 7 items designed to assess sensitivity to threats, whereas the BAS scale consists of 13 items assessing the approach components of BAS sensitivity.

The STAI-Y2 is Form Y2 of the Spielberger's State-Trait-Anxiety Inventory (Spielberger 1983) that assesses general anxiety dispositions. It consists of a 20-item self-report questionnaire in which respondents rate how they "generally feel". While both the BIS and the STAI-Y2 provide an assessment of anxiety, the latter assesses how often respondents experience anxiety, whereas the former assesses fear of negative events or how sensitive the respondent is to such events when they do occur, providing a better assessment of fear and anxiety predispositions.

All behavioral measures (valence, perceived movement, BIS, BAS, and STAI-Y2) were collected after the TMS session, to keep the procedure similar to that of our previous studies (Borgomaneri et al. 2012, 2015a, b, c) and avoid any bias due to responding to anxiety related questionnaires on the neurophysiological assessment of fear-related brain responses.

## Data analysis

Accuracy (% of correct responses) in the recognition task was analyzed using a three-way mixed factors ANOVA with Experiment (2 levels: Experiment 1 and Experiment 2) as a between-subjects factor and Session (3 levels: CSE, ICF, and SICI) and Time (2 levels: 100 and 125 ms) as within-subjects factors. Post-hoc comparisons were carried out with the Newman–Keuls tests.

Mean VAS ratings for valence and perceived (implied) movement were not normally distributed (as shown by the Shapiro–Wilk test). Thus, they were analyzed with non-parametric Friedman ANOVAs, and Bonferroni-corrected Wilcoxon matched pairs tests and Mann–Whitney *U* tests for post-hoc within- and between-group comparisons, respectively.

Mean MEP amplitudes in each condition were measured peak-to-peak (in mV). MEPs associated with incorrect answers (~6%) were discarded from the analysis. Thus, CSE, ICF, and SICI reflected indices of motor excitability associated with accurate perception of body postures. MEPs with preceding background EMG deviating from the mean by more than 2 S.D. were removed from further analysis (~7%). This left a mean of 13.2 MEPs (±1.5 S.D.) per condition across participants. In a preliminary analysis (see Supplemental material online), MEPs recorded in the CSE, ICF, and SICI sessions were expressed relative to the baseline (% of the average of the two baseline blocks) and analyzed with a mixed factors five-way ANOVA with Experiment (2 levels: Experiment 1 and Experiment 2) as a between-subjects factor and Session (3 levels: CSE, ICF, and SICI), Muscle (4 levels: FDI, FCR, APB, and ECR), Time (2 levels: 100 and 125 ms), and Body Stimulus (3 levels: happy, fearful, and neutral) as within-subjects factors (Supplementary Fig. 1). Then, to quantify ICF and SICI effects, in the main analysis, we expressed MEPs in the paired-pulse sessions relative to the single-pulse session (to estimate the effects of the subthreshold conditioning pulse on the MEP elicited by the suprathreshold test pulse); for each experimental condition, we calculated the ratio of the mean conditioned MEP over the mean unconditioned test MEP (Kujirai et al. 1993; Ziemann et al. 1996). These data were analyzed with an Experiment × Session × Muscle × Time × Body Stimulus mixed factors ANOVA, as in the previous analysis, with 2 levels of the factor Session (ICF and SICI). All post-hoc comparisons were carried out with the Newman–Keuls test. Effect size indices for main effects and interactions were computed using *partial eta*$^2$, whereas *Cohen's d* was computed for post-hoc comparisons. By convention, *partial eta*$^2$ effect sizes of ~0.01, ~0.06, and ~0.14 are considered small, medium, and large, respectively; *Cohen's d* effect sizes of ~0.2, ~0.5, and ~0.8 are considered small, medium, and large, respectively (Cohen 1992).

The ANOVAs showed a reduction in the ICF effect for fearful relative to happy and neutral body postures. This effect was similar across the factors Experiment, Muscle and Time. To explore the relations between this motor suppression and key personality traits, correlation and regression analyses were performed. An index representing the early motor modulation (the mean ICF effect for fearful postures minus the mean ICF effect for happy and neutral postures; averaged across the four muscles and the two time intervals), was entered as the dependent variable in a stepwise regression model, whereas questionnaire scores were entered as predictors (criteria probability of *F*-to-enter: $\leq 0.05$; *F*-to-remove: $\geq 0.1$). To eliminate the weak multicollinearity of the three predictors, scores were first transformed using a varimax-rotated principal component (PC) analysis that yielded three orthogonal PCs ($\text{BIS}_{\text{PC}}$, $\text{BAS}_{\text{PC}}$, and $\text{STAI-Y2}_{\text{PC}}$), each selectively correlating with the corresponding original variable (Table 1). Simple and partial correlations using raw BIS, BAS, and STAI-Y2 scores were used to confirm the results of the regression analysis. Due to technical failure, data from 2 participants were incomplete; thus, these analyses were conducted on 24 participants. Cohen's effect size ($f^2$) of regression coefficients was calculated using the formula $f^2 = R^2/(1 - R^2)$, with effect sizes of ~0.02, ~0.15, and ~0.35 being interpreted as small, medium, and large, respectively (Cohen 1992).

**Table 1** Results of the principal component (PC) analysis of the three personality scales: eigenvalues, explained variance, and factor loadings of the extracted PCs

| | Eigenvalue | Percentage of cumulative variance (%) | Factor loadings | | |
|---|---|---|---|---|---|
| | | | BAS | BIS | STAI-Y2 |
| PC 1: $BAS_{PC}$ | 1.21 | 40 | **0.996** | −0.048 | 0.074 |
| PC 2: $BIS_{PC}$ | 1.08 | 76 | −0.049 | **0.994** | 0.101 |
| PC 3: $STAI\text{-}Y2_{PC}$ | 0.71 | 100 | 0.075 | 0.102 | **0.992** |

We extracted three PCs to account for the total variance in the original scales. PCs were rotated to simple structure using varimax rotation, yielding three orthogonal variables (a preliminary oblinmin rotation ensured that no significant correlations could be detected between the extracted PCs). For each of the original variables, the highest factor loading is represented in bold. Based on factor loadings, the three PCs were interpreted and labeled $BAS_{PC}$, $BIS_{PC}$, and $STAI\text{-}Y2_{PC}$, respectively

**Table 2** Behavioral measures (mean values ± SD) in the two experiments

| | Experiment 1 | Experiment 2 |
|---|---|---|
| BAS | 41.6 ± 6.6 | 45.5 ± 10.3 |
| BIS | 25.8 ± 4.0 | 24.3 ± 4.1 |
| STAI-Y2 | 43.3 ± 9.1 | 47.8 ± 8.5 |
| Emotion recognition CSE session | 91.7% ± 5.5 | 97.9% ± 2.0 |
| Emotion recognition ICF session | 90.3% ± 4.9 | 97.7% ± 2.4 |
| Emotion recognition SICI session | 91.5% ± 5.3 | 97.8% ± 2.3 |
| Valence rating of Happy posture | 4.34 ± 0.33 | 4.52 ± 0.23 |
| Valence rating of Neutral posture | 3.14 ± 0.18 | 2.98 ± 0.05 |
| Valence rating of Fearful posture | 1.42 ± 0.19 | 1.44 ± 0.22 |
| Implied motion rating of Happy posture | 3.29 ± 0.52 | 3.47 ± 0.59 |
| Implied motion rating of Neutral posture | 3.34 ± 0.55 | 1.02 ± 0.06 |
| Implied motion rating of Fearful posture | 3.03 ± 0.71 | 3.65 ± 0.55 |

## Results

### Behavioral data

Behavioral data are shown in Table 2. Participants assigned to Experiments 1 and 2 scored similarly on the three personality scales. Statistical comparisons showed no differences between groups for the BAS ($t_{22} = -1.25$, $p = 0.22$), BIS ($t_{22} = 0.90$, $p = 0.38$), and STAI-Y2 scale ($t_{22} = -1.20$, $p = 0.24$).

Participants in both experiments performed the recognition task with high accuracy across the three sessions (Table 2). The Experiment x Session x Time ANOVA carried out on accuracy data showed a non-surprising main effect of Experiment ($F_{1,24} = 23.02$; $p < 0.0001$; *partial* $eta^2 = 0.49$), accounted for by better performance in Experiment 2 (97.8% ± 2) compared to Experiment 1 (91.2% ± 5). Indeed, in Experiment 2, participants had to discriminate emotional dynamic fearful and happy postures from neutral static postures, whereas, in Experiment 1, all the body postures were dynamic and thus visual discrimination was more difficult. No other main effects or interactions approached significance in the ANOVA (all $F < 1.01$, all $p > 0.32$), suggesting that recognition was not affected by the type of TMS pulse (single or paired) or stimulus duration.

The Friedman ANOVAs on valence ratings in Experiments 1 and 2 were significant (all $\chi^2 > 26$, $p < 0.0001$). Bonferroni-corrected Wilcoxon tests confirmed that, in both experiments, valence ratings of fearful body postures were more negative than ratings of happy and neutral body postures (all $p < 0.013$). Moreover, valence ratings were more positive for happy than for neutral postures (all $p < 0.013$). There were no differences in valence ratings of fearful, happy, or neutral postures between the two experiments (Mann–Whitney tests all $p > 0.13$).

As expected, the Friedman ANOVA on implied motion ratings in Experiment 1 was not significant ($\chi^2 = 1.63$, $p = 0.44$), suggesting that fearful, happy, and neutral body postures contained similar amounts of implied motion (also confirmed by Bonferroni-corrected Wilcoxon tests, all $p > 0.82$). The Friedman ANOVA carried out on implied motion ratings collected in Experiment 2 was significant ($\chi^2 > 19.54$, $p < 0.0001$). Bonferroni-corrected Wilcoxon tests showed that participants in Experiment 2 perceived more implied motion in the happy and fearful body postures than in the static body postures (all $p < 0.013$), while implied motion ratings were comparable between happy and fearful body postures ($p = 1$; Table 2). Bonferroni-corrected between-group comparisons (Mann–Whitney test) revealed only the expected difference for neutral body postures, which were perceived as conveying more motion in Experiment 1 than in Experiment 2 ($p < 0.0001$). No between-group differences were found for fearful and happy postures (all $p > 0.14$).

### Neurophysiological data

A preliminary analysis of MEP amplitudes (% of baseline) confirmed the robustness of the paired-pulse ICF and SICI protocols (Supplementary Fig. 1): smaller MEPs were induced when the conditioning pulse was administered 3 ms before the test pulse (in the SICI session), and larger MEPs were elicited when the conditioning pulse preceded the test pulse by 12 ms (in the ICF session; see Kujirai et al. 1993; Ziemann et al. 1996).

The analysis also indicated that body expressions modulated MEPs only in the ICF session (lower amplitude for fearful relative to neutral bodies), but not in the CSE or SICI sessions (Supplementary Fig. 1; see also Fig. 2). This confirms the lack of CSE modulation for emotional body postures or neutral movements that we (Borgomaneri et al. 2015c) and others (Ubaldi et al. 2013; Cavallo et al. 2014; Naish et al. 2014) have previously documented when testing CSE in this early temporal window (100–125). Moreover, the preliminary analysis suggested that MEPs in the ICF session, but not in the SICI session, were significantly modulated as a function of body stimulus. However, the intracortical origin of these modulations is uncertain, as simple amplitudes of MEPs elicited by paired-pulse TMS (ICF and SICI sessions) can be affected by spinal excitability.

To rule out a possible contribution of spinal excitability, we thus assessed changes in SICI and ICF effects. These effects unambiguously assess inhibitory and facilitatory M1 intracortical circuits, and were calculated using MEP ratios computed for each condition separately (mean conditioned MEP collected with paired-pulse TMS relative to mean unconditioned test MEP collected with single-pulse TMS) (Kujirai et al. 1993; Ziemann et al. 1996). The Experiment × Session × Muscle × Time × Body Stimulus ANOVA on MEP ratios revealed the expected strong main effect of Session ($F_{1,24}$ = 163.79; $p < 0.0001$; *partial eta*$^2 = 0.87$), with larger MEP ratios associated with the ICF effect (mean amplitude ± SD: 172% ± 72) relative to MEP ratios associated with the SICI effect (44% ± 28). Importantly, there was also a significant Session x Body Stimulus interaction with a medium/large effect size ($F_{2,48}$ = 4.02; $p = 0.02$; *partial eta*$^2 = 0.14$; Fig. 3). The interaction was due to the lower ICF effect in the fearful body condition (165% ± 69) relative to the happy (172% ± 73; $p = 0.04$; *Cohen's* $d = 0.33$) and neutral body conditions (177% ± 78; $p < 0.01$; *Cohen's* $d = 0.51$); moreover, the magnitude of the ICF effect was comparable in the happy and neutral body conditions ($p = 0.16$). No significant modulations of the SICI index were found ($p > 0.46$).

The ANOVA showed only a significant Session × Body Stimulus interaction and did not show a significant Experiment × Session × Body Stimulus interaction ($p > 0.71$; Table 3), suggesting that suppression of the ICF effect for fearful body postures was similar when compared to dynamic (Experiment 1) and static (Experiment 2) emotionally neutral control body postures. Moreover, the factor muscle did not influence the Session x Body Stimulus interaction (all $p > 0.37$; Table 4), suggesting that the reduction in ICF for fearful body expressions was similar across muscles. No other main effects or interactions were significant in the ANOVA ($F < 2.36$, $p > 0.08$).

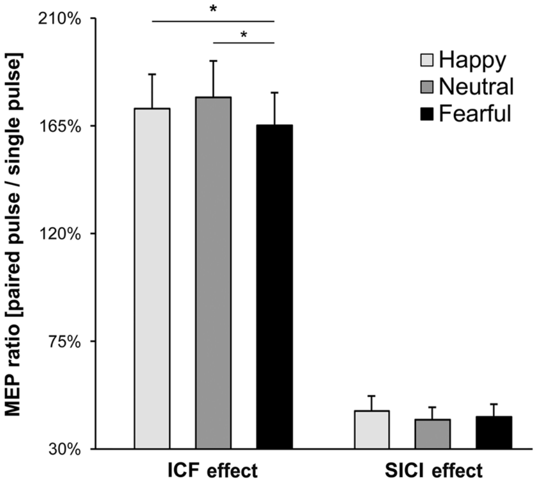

**Fig. 3** Cortical motor modulations during the emotion recognition task. MEP amplitude ratio (paired-pulse/single-pulse) to estimate the magnitude of intracortical facilitation (ICF) and short intracortical inhibition (SICI) effects during perception of happy, neutral, and fearful body postures. Data show the Session × Body Stimulus interaction (average of the two experiments, Experiment 1 and 2, the two time points, 100 ms and 125 ms, and the four muscles, FDI, FCR, APB, and ECR). Error bars indicate SEM. *Asterisks* (*) denote significant comparisons ($p < 0.05$)

The ICF modulation underlying the Session x Body Stimulus interaction was further analyzed using a paired *t* test. This showed that an index of ICF suppression for fearful bodies (ICF effect for fearful postures minus mean ICF effect for neutral and happy postures; computed by merging data from the two experiments, and averaging the difference across the four muscles and the two time intervals; ICF difference ± SD: −9% ± 19) was significantly different from the same index computed for the SICI effect (−1% ± 7; $p = 0.02$, *Cohen's* $d = 0.47$). These findings further indicate that seeing fearful bodies specifically induced an inhibitory modulation that was greater for the ICF effect than for the SICI effect.

## Relation between changes in motor excitability and personality

The reduction of the ICF effect for observed fearful body expressions was found in all the tested muscles, and across both time intervals and experiments. To test whether this neurophysiological effect was related to individual differences in affective personality traits, a series of correlations and a multiple regression analysis were carried out.

**Table 3** Mean ± SD of the ICF effect (paired-pulse MEPs divided by single-pulse MEPs) shown separately for Experiments 1 and 2. Similar ICF reductions for fearful postures were found in both experiments

| | Experiment 1 | Experiment 2 |
|---|---|---|
| ICF effect during happy posture | 192% ± 87 | 153% ± 52 |
| ICF effect during neutral posture | 200% ± 84 | 154% ± 66 |
| ICF effect during fearful posture | 184% ± 79 | 146% ± 55 |

**Table 4** Mean ± SD of the ICF effect (paired-pulse MEPs divided by single-pulse MEPs) shown separately for the FDI, FCR, APB, and ECR. Similar ICF reductions for fearful postures were found in all the tested muscles

| | FDI | FCR | APB | ECR |
|---|---|---|---|---|
| ICF effect during Happy posture | 182% ± 23 | 165% ± 11 | 169% ± 17 | 173% ± 13 |
| ICF effect during Neutral posture | 194% ± 26 | 161% ± 11 | 176% ± 20 | 177% ± 13 |
| ICF effect during Fearful posture | 175% ± 22 | 154% ± 9 | 164% ± 19 | 169% ± 12 |

An MEP contrast, computed based on the results of the ANOVA, was entered into the analysis as a dependent variable, and participants' $\mathrm{BIS_{PC}}$, $\mathrm{BAS_{PC}}$, and $\mathrm{STAI\text{-}Y2_{PC}}$ scores were entered as predictors. We considered the MEP contrast representing ICF suppression when viewing fearful postures (fearful body expression minus mean of happy and neutral postures; computed by merging data from the two experiments, and averaging the difference across the four muscles and the two time intervals). The regression model and simple correlations between the magnitude of ICF suppression and $\mathrm{BIS_{PC}}$, $\mathrm{BAS_{PC}}$, and $\mathrm{STAI\text{-}Y2_{PC}}$ scores were initially not significant ($-0.22 < r < 0.18$, all $p > 0.3$). However, there was a statistical outlier in the data set with standard residuals greater than 2.5 SD. After the removal of the outlier, the magnitude of ICF suppression negatively correlated with the $\mathrm{BIS_{PC}}$ scores ($r = -0.43$, $p = 0.041$), whereas it did not significantly correlate with the $\mathrm{BAS_{PC}}$ scores ($r = 0.11$, $p = 0.62$) or the $\mathrm{STAI\text{-}Y2_{PC}}$ scores ($r = 0.16$, $p = 0.47$). Stepwise regression confirmed that $\mathrm{BIS_{PC}}$ was a negative predictor of the ICF suppression with a medium effect size ($R^2 = 0.18$, $F_{1,22} = 4.73$, $\beta = 0.43$, $p = 0.041$; $f^2 = 0.23$), whereas $\mathrm{BAS_{PC}}$ ($\beta = 0.04$, $p = 0.83$) and $\mathrm{STAI\text{-}Y2_{PC}}$ ($\beta = 0.14$, $p = 0.48$) were not significant predictors. A negative relation with a medium effect size was further confirmed by computing a simple correlation between the magnitude of ICF suppression and raw BIS scores ($r = -0.41$, $p = 0.054$, $f^2 = 0.20$; see Fig. 4). In addition, the effect size remained moderate after partialling out the raw BAS and STAI-Y2 scores ($r = -0.43$, $p = 0.049$, $f^2 = 0.23$). In sum, these findings indicate that participants who scored high on the BIS scale showed greater suppression of the ICF effect (i.e., smaller MEPs) when seeing fearful body postures.

## Discussion

Fearful body postures represent a powerful social signal that is easily observable from a distance and can alert the observer to the presence of a potential threat (de Gelder et al. 2004; Tamietto et al. 2007). Because the source of danger is not signaled, fearful expressions can induce increased threat monitoring of the surrounding environment (Whalen et al. 1998; Pourtois et al. 2005; Phelps et al. 2006; van Heijnsbergen et al. 2007; Lee et al. 2013; Borhani et al. 2015). Threat monitoring is supported by suppression

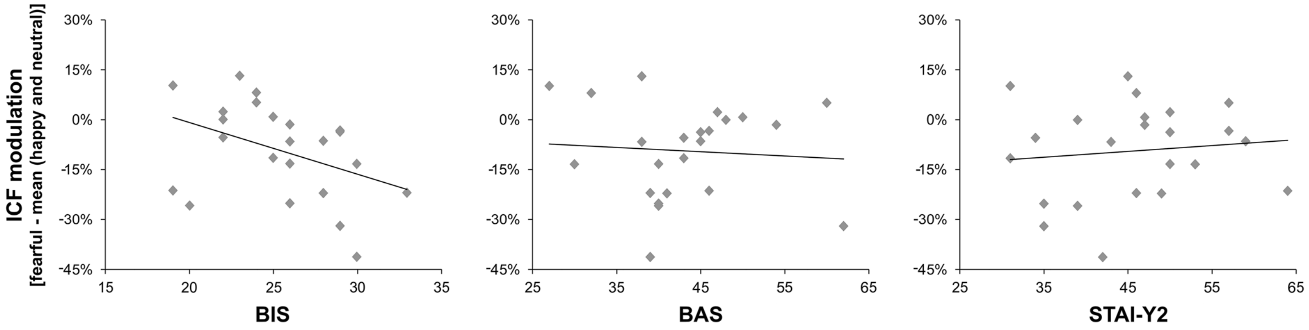

**Fig. 4** Scatter plot of the correlation between the modulation of the ICF effect detected in the main ANOVA (fearful body expression minus mean of happy and neutral postures; averaged across the two time points and the four muscles) and individual scores on the BIS ($r = 0.41$), BAS ($r = -0.08$), and STAI-Y2 scales ($r = 0.11$)

of motor output (e.g., orienting immobility/freezing) which may be crucial for minimizing the negative consequences of potential dangers (Fanselow 1994; Frijda 2010; Lang and Bradley 2010; Hagenaars et al. 2014; Low et al. 2015; Graziano 2016). Influential theories suggest that the tendency to inhibit behavior when detecting a threatening cue reflects the activity of a defense motivation system that is embedded into personality traits and regulates adaptive behavior (Gray 1987, 1994; Gray and McNaughton 1996; McNaughton and Corr 2004). In this study, we hypothesized that stable affective dispositions related to fear and threat sensitivity—tapped by the BIS scale—would affect defense system activation when processing fearful expressions, and this activation would be reflected in a massive suppression of cortical motor circuits for controlling the observer's arm. We thus performed two TMS experiments that monitored indices of motor excitability, while participants observed fearful body postures and control visual stimuli. To test motor inhibition responses during the early phases of threat monitoring, we tested motor excitability in the 100–125 ms time window corresponding to the latency of the P1, i.e., the earliest cortical ERP component that is consistently modulated by fearful expressions (Williams et al. 2006; Vuilleumier and Pourtois 2007; van Heijnsbergen et al. 2007). We assessed functional modulations of CSE, ICF, and SICI from different muscle representations during observation of fearful body postures. As a control, we also tested happy body postures (Exp1 and Exp2) and emotionally neutral postures that included both dynamic (Exp1) and static bodies (Exp2).

We found a Session x Body Stimulus interaction, indicating that viewing fearful body postures reduced ICF relative to viewing happy and neutral postures, whereas the observed body posture did not modulate CSE or SICI. These motor modulations were similar in all the tested muscles and across both experiments, as the factors Muscle and Experiment did not influence the Session x Body Stimulus interaction, either alone or in combination with other factors. This indicates that watching fearful bodies elicited a massive reduction of excitation within the cortical motor representations of the hand (FDI and APB) and the arm (FCR and ECR). This reduction could be detected relative to happy bodies and neutral body postures, whether dynamic (Exp1) or still (Exp2). Importantly, we found that the ICF reduction when watching fearful bodies was predicted by inter-individual differences in BIS sensitivity but not by BAS or STAI-Y2.

These findings support the general notion that emotions prime the body for action (McNaughton and Corr 2004; Frijda 2010; Lang and Bradley 2010; Hagenaars et al. 2014; Borgomaneri et al. 2014; Vicario et al. 2015, 2016) and our hypothesis that detecting fearful expressions can quickly inhibit the cortical motor system. Remarkably, our study highlights the phenomenology of the ICF reduction and its relationship with key personality traits. The reduction in ICF effect hints at a cortical counterpart of a motor inhibition response triggered by the observation of fear cues. Our results suggest that such a response reflects the activity of a defensive motivational system for regulating action tendencies that are embedded into affective dispositions related to threat sensitivity.

## Neurophysiological mechanisms underlying M1 response to fearful bodies

Our findings are in line with our previous results (Borgomaneri et al. 2015c), suggesting that the ICF effect provides a valuable neurophysiological marker for emotion processing. The ICF effect is a complex measure of intracortical excitation, as it is thought to reflect glutamatergic facilitation mainly through N-methyl-D-aspartate (NMDA) receptors (Ziemann et al. 1998) and, to a minor extent, also GABA-ergic inhibition through GABAA receptors (Tandonnet et al. 2010). Fearful postures modulated ICF, but not SICI, which is thought to measure intracortical GABA-ergic inhibition in M1 through GABAA receptors (Liepert et al. 1998; Ziemann et al. 1998). Thus, the results showing modulation of ICF, but not of SICI, support our assumption that motor inhibition contingent upon the observation of fearful body postures is instantiated mainly via reduced excitatory (glutamatergic) transmission in M1. Importantly, the present study expands our previous investigation by addressing a number of outstanding issues that establish the key features of fear-related ICF modulation, and thus provide clues to the underlying neural mechanism.

The first outstanding issue concerns the extent of the ICF suppression and provides evidence for the types of motor reactions triggered by fearful bodies. This issue was left unanswered by our previous study (Borgomaneri et al. 2015c) in which we monitored motor excitability only in the FDI muscle. Here, we showed that ICF suppression similarly affected all the target muscles (see Table 3) no matter whether they are involved in hand/arm flexion (e.g., both the FDI and the FCR), extension (mostly the ECR, but also the APB), or abduction (the APB and the FDI). Therefore, our data speak against the idea that the ICF reduction reflects an active suppression of specific muscle representations and/or movements, such as, for example, the inhibition of approach towards potentially dangerous cues (Cacioppo et al. 1993; Chen and Bargh 1999; Naugle et al. 2010). Thus, the ICF modulation appears to reflect a more generalized suppression of upper limb motor readiness, which may have a functional role in threat monitoring (Fanselow 1994; Hagenaars et al. 2014). This proposal fits with the previous evidence that ICF suppression can be detected in the FDI representations of both hemispheres

(Borgomaneri et al. 2015c), a result that supports the extension of the neurophysiological suppression to different sectors of the motor system.

Such a threat monitoring-related inhibition of the motor system does not rule out the possibility that flight/fight reactions may be also implemented in the motor system at different time points, and these reactions could involve different motor circuits and muscles not sampled in our study (e.g., leg muscles). Yet, to be involved in threat monitoring without counteracting adaptive flight/fight reactions, the ICF suppression should be (1) transient, and (2) not accompanied by inhibition of descending corticospinal pathways. The previous studies have already confirmed these two features of the ICF modulation. First, the transient nature of our findings is supported by the previous studies showing that ICF modulation is specific to the 100–125 ms time window—as different motor modulations were detected at earlier (i.e., 70–90 ms) and later (i.e., 150–300 ms) time intervals (Borgomaneri et al. 2012, 2014, 2015a, b, c). For example, fearful expressions (Schutter et al. 2008; Borgomaneri et al. 2015a) and other emotionally negative, but also positive, stimuli (Oliveri et al. 2003; Hajcak et al. 2007; Coombes et al. 2009; Vicario et al. 2015; Hortensius et al. 2016) were found to increase CSE at latencies greater than 150–300 ms. Second, the previous (Borgomaneri et al. 2015c) and present findings indicate that the ICF modulation at 100–125 is not accompanied by a modulation of CSE—reflecting the net effect of excitatory and inhibitory inputs to the descending corticospinal pathway. In sum, these features support the idea that the transient suppression of ICF when seeing fearful body postures reflects a transient inhibition of action tendencies, possibly promoting threat monitoring.

The transient nature of the ICF modulations and the lack of CSE or SICI (i.e., inhibitory) modulation do not support the hypothesis of a sustained induction of body immobility (Fanselow 1994; Hagenaars et al. 2014) and rather suggest a transient reduction in the propensity to move the body (Borgomaneri et al. 2015c). However, we do not rule out the possibility that seeing fearful body postures would induce a parasympathetic state analogous to freezing, with sustained reductions in spinal excitability and heart rate (Fanselow 1994; Hagenaars et al. 2014). In principle, spinal excitability could be modulated via descending pathways other than the corticospinal tract (e.g., involving amygdala projections to the periaqueductal gray which projects downstream to the spinal cord; see Walker and Carrive 2003; Hermans et al. 2013) and thus could be affected in the absence of CSE modulation. Thus, future studies combining ICF assessment with the assessment of spinal excitability (e.g., via the H-reflex) and heart rate will clarify whether the reduction in ICF extends to more proximal muscles (e.g., the trunk) that are associated with freezing and a reduction in spinal excitability and heart rate during observation of fearful bodies. This will disambiguate whether the changes in ICF reflect a transient reduction in the propensity to move the body—as we propose—or are associated with a more sustained and generalized freezing reaction.

## Early suppression of action tendencies, not motor resonance

Our study also establishes that the ICF modulation reflects a suppression of the observers' action tendencies rather than a modulation of motor resonance processes. It is widely known that seeing emotional or neutral actions activates the motor system as if the observer was directly performing the observed action (Fadiga et al. 2005; Proverbio et al. 2009; Borgomaneri et al. 2012; Avenanti et al. 2013; Naish et al. 2014). This motor resonance is characterized by an increase in MEP amplitude when viewing dynamic compared to static postures (Fadiga et al. 2005; Avenanti et al. 2007; Aglioti et al. 2008; Candidi et al. 2010; Urgesi et al. 2010; Catmur et al. 2011). Liuzza and colleagues (2014) have recently shown that observing negative (i.e., immoral) actions reduces motor resonance (Liuzza et al. 2014). Although CSE was tested in a late time window in that experiment (1000–1200 ms after stimuli onset), and no measures of intracortical excitability were recorded, one may wonder whether our early ICF modulation for fearful bodies may reflect a reduction in motor resonance similar to that reported by Liuzza and colleagues (2014), rather than an active reduction in the propensity to move the body. Using static control stimuli, we were able to ascertain that no signs of motor resonance were at play in our experiment. Indeed, the observation of fearful postures induced similar ICF suppression in both Exp1 (using neutral dynamic postures) and Exp2 (using neutral static postures). As shown in Table 2, the responses to happy (dynamic) and neutral static postures were very similar in Exp2, as were the responses to happy and neutral dynamic postures in Exp1. This is not surprising, as motor resonance in the observer tends to emerge from about 200 ms after observed action onset (Barchiesi and Cattaneo 2013; Cavallo et al. 2014; Naish et al. 2014). In keeping with the previous studies using the same set of visual stimuli, we detected motor resonance (indexed by greater CSE for fearful, happy, and neutral dynamic postures relative to static neutral postures) when MEPs were tested at 300 ms, but not at 150 ms, from stimulus onset (Borgomaneri et al. 2012, 2015a). The present findings support the notion that, before implementing motor resonance, the motor system is actively involved in implementing adaptive motor responses to emotionally salient stimuli such as fearful body postures that may signal potential dangers in the environment.

### BIS sensitivity and M1 inhibitory response to fearful bodies

A final major point of novelty in our study is the demonstration of a unique relation between the magnitude of ICF suppression and inter-individual differences in threat sensitivity. Specifically, we found greater ICF suppression when observing fearful postures in those participants who received high scores on the BIS scale. No relations were found between ICF suppression and BAS or STAI-Y2, indicating a specific link between fear-related suppression of M1 excitatory mechanisms and BIS sensitivity. Thus, all the main findings of our study strongly suggest that ICF suppression reflects the activation of a defensive system that inhibits action tendencies when facing potential threats and that is influenced by stable affective dispositions.

What are the possible neural bases of BIS-related ICF suppression? Psychopharmacology studies in animals have suggested that cortico-subcortical emotional networks are involved in BIS sensitivity, with a prominent role for the amygdala and the septo-hippocampal system, along with the cingulate cortex and interconnected regions (Gray and McNaughton 1996; Corr 2004). In keeping with these findings, participants with high scores on the BIS scale show increased amygdala and hippocampal gray matter volume (Barrós-Loscertales et al. 2006; Cherbuin et al. 2008), and increased amygdala (Mathews et al. 2004; Cools et al. 2005) and cingulate (Amodio et al. 2008; Balconi and Crivelli 2010) responses to negative stimuli, including fearful expressions. Interestingly, greater BIS sensitivity is also associated with a larger P1 enhancement when watching fearful expressions (Li et al. 2008; Krusemark and Li 2011)—an effect that reflects threat monitoring and is mediated by the interaction between the occipito-temporal cortex and the amygdala (Vuilleumier et al. 2004; Rotshtein et al. 2010). Remarkably, imaging and electrophysiology studies have shown that watching fearful expressions consistently activates the occipito-temporal cortex and other brain structures associated with BIS sensitivity, including the amygdala, the cingulate cortex and interconnected regions like the superior colliculus, and parietal, lateral premotor, and supplementary motor regions (Vuilleumier and Pourtois 2007; Thielscher and Pessoa 2007; Grèzes et al. 2007; de Gelder et al. 2010; Borhani et al. 2016; Meeren et al. 2016). These regions are known to be involved in emotion processing and motor control. Moreover, they project directly or indirectly to M1 (Tamietto et al. 2012; Grèzes et al. 2014; Fiori et al. 2016) and thus may provide a neural pathway for the reported suppression of ICF.

Taken together, the previous evidence and our study suggest that people who are overly sensitive to threat show enhanced modulation of both the cortical visual and motor systems when viewing fearful expressions. These visual and motor modulations occur within the same early temporal window (100–125 ms) and may reflect the fast activation of a defensive cortico-subcortical system that promotes processing of threatening cues through a transient suppression of excitatory mechanisms in M1.

In sum, our study supports the notion that fearful body expressions, by virtue of their capacity to signal potential dangers, can quickly inhibit action tendencies through a suppression of excitatory intracortical mechanisms in M1. This transient inhibitory motor mechanism may have several evolutionary advantages, such as optimizing perceptual and attentional processes while preparing for rapid escape or defensive fighting.

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### Compliance with ethical standards

**Conflict of interest** Authors have no conflicts of interest to declare.

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