Harm avoiders suppress motor resonance to observed immoral actions

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Motor resonance (MR) contingent upon action observation is thought to occur largely automatically. Although recent studies suggest that this process is not completely impervious to top-down modulations, much less is known on the possible role of the moral connotation of observed action goal in modulating MR. Here, we explored whether observing actions with different moral connotations modulates MR and whether any modulation depends on the onlookers' personality. To this aim, we recorded motor potentials evoked by single-pulse transcranial magnetic stimulation from hand muscles of participants who were watching images of a model performing hand actions with the same postures and low-level goals (i.e. grasping an object) but with different moral connotations ('stealing a wallet' vs 'picking up a notepaper'). Participants' personality traits were measured using the temperament and character inventory. Results show a selective suppression of corticospinal excitability during observation of immoral actions in individuals with high scores in harm avoidance, a personality trait characterized by excessive worrying and fearfulness. Thus, a combination of dispositional (personality traits) and situational (morality of an action) variables appears to influence MR with the observed actions.

Keywords: motor resonance; moral judgment; TMS; action observation; personality traits; harm avoidance

INTRODUCTION

Observing an action recruits a neural network that largely overlaps with the one involved in the actual execution of the observed action (Rizzolatti and Craighero, 2004). Single-pulse transcranial magnetic stimulation (sp-TMS) of the motor cortex allowed scholars to explore the excitability of the corticospinal path by measuring the electrophysiological activity of the muscle that would be involved in the action (motor evoked potential, MEP). Changes of the MEPs during action observation provide indices of fine-grained motor resonance (MR), which occurs according to somatotopic rules (Fadiga et al., 2005).

TMS studies report that merely observing an action induces a selective increase of MEPs from the muscles that would be active when performing the same actions (Fadiga et al., 1995; Strafella and Paus, 2000; Gangitano et al., 2001). This MR process occurs even when individuals observe static snapshots of body parts implying an action. Thus, MR seems linked to simulation of the future development of an action rather than to its current state (Urgesi et al., 2006a, 2010b; Candidi et al., 2010; Avenanti et al., 2013). MR as inferred from changes of corticospinal activity may reflect the activity of the mirror system (Fadiga et al., 2005).

It is relevant to this study that there is more to an action than a succession of its motor chunks: what really matters is the goal of an action. In fact, two kinematically identical actions, such as throwing a ball to no one or to someone, can lead to a different degree of MR (i.e. increased MEPs when the observed action happens to occur in a social context; Bucchioni et al., 2013). Thus, kinematically identical actions may be quite different in terms of higher order goals (Grafton and Hamilton, 2007). Moreover, intentions inferred from contexts may modulate the human mirror system (Iacoboni et al., 2005) even

when MR supposedly occurs at an automatic, implicit level (Spunt and Lieberman, 2013).

Seminal research about moral reasoning has suggested a central role of reflective, deliberative, rational, controlled, effortful and slow processes in this domain (Kohlberg, 1969). This view has been challenged by an intuitionist account of moral reasoning (Haidt, 2001), which has emphasized the role of reflexive, automatic, fast and emotionally driven processes in moral reasoning (e.g. see Greene et al., 2001). Thus, moral judgments concerning the observed actions could occur quickly and possibly modulate the MR with the action. Thus far, however, no study has tested whether moral connotations of observed actions influence MR. Also relevant to this study is that the tendency to simulate observed actions (Fadiga et al., 1995, 2005; Urgesi et al., 2006b; Aglioti et al., 2008) or the sensorimotor states of other individuals (Avenanti et al., 2005, Minio-Paluello et al., 2009) can be modulated by individual differences such as gender (Cheng et al., 2007, 2008) or attitudes toward the ethnicity of the observed model (Avenanti et al., 2010). Moreover, MR to observed actions was found to be increased in onlookers in whom self-construal (Markus and Kitayama, 1991) was manipulated in collectivistic vs individualistic directions (Obhi et al., 2011). Most importantly, high-level personality traits, such as trait empathy, do play a role in shaping our predisposition to embody the observed sensorimotor states of others (Avenanti et al., 2009). Thus, personality traits seem to strongly influence the brain responses associated with observation of sensorimotor states of other individuals.

The temperament and character inventory (TCI) is a questionnaire aimed at providing a personality profile in the context of a bio-psychological model of personality (Cloninger, 1994). The TCI consists of (i) three scales of character (Self-Directedness, Cooperativeness and Self-Transcendence), which refer to individual differences in the conceptual representation of the self in relation to other people and to the external world. Character features may be related to the functioning of higher-order, cognitive systems and show some degree of plasticity over time; (2) four scales of temperament (Novelty Seeking, NS; Harm Avoidance, HA; Reward Dependence, RD; and Persistence), which refer to individual differences in the activation, maintenance and inhibition of behavior in response to a specific class of stimuli.

These temperamental characteristics are moderately heritable and stable across time. In particular, NS involves behavioral activation and disposition toward being excitable, impulsive, exploratory and quick-tempered. In contrast, HA is related to behavioral inhibition and implies a heritable bias toward being cautious, apprehensive and overly pessimistic. RD involves maintaining behaviors that have been previously associated with reinforcement and is manifested as sensitivity, sentimentality and dependency on others' approval. Finally, Persistence implies a heritable bias toward continuing and persevering behaviors despite fatigue and lack of reward. Using TCI, our research group has been able to demonstrate changes in Self-Transcendence in patients with brain damage (Urgesi et al., 2010a). Moreover, we demonstrated that individual differences as assessed by TCI play an important role in the domain of morality. Indeed, we showed that people who lied the least in an economic game where their reputation was at risk, exhibited higher RD scores (Panasiti et al., 2011). Thus, people who scored high on RD were in fact more sensitive to social (i.e. being judged as morally integer) than to monetary reward. Here we are mainly interested in the temperament dimension of HA, an index of the anxiety-related trait that makes people more vigilant toward negative stimuli in general (Fox et al., 2002; Mathews et al., 2003; Holmes et al., 2006). We hypothesize that high HA individuals, even if they do not judge the observed action differently compared with the low HA individuals, might have a less marked increase in MR when observing immoral actions.

To this aim, we used an sp-TMS procedure to evoke motor potentials in the hand muscles of onlookers as they observed hand actions performed by a model. In keeping with previous studies, the amplitude of the MEPs was taken as an index of CS excitability associated with MR (Fadiga et al., 2005; Fourkas et al., 2006; Urgesi et al., 2006a,b). The observed actions consisted of similar reach-to-grasp hand movements, which, however, were morally neutral (i.e. removing a notepaper stuck on someone else's pants) or immoral (stealing a wallet) actions. Notably, although the presented actions shared the same low-level goals (i.e. grasping an object), they had two radically different moral connotations (stealing a wallet vs removing a notepaper).

MATERIALS AND METHODS

Participants

Twenty participants (10 female, mean age = 24 ± 6 s.d.) were recruited for the study at 'Sapienza' University of Rome. All participants were Italian native speakers, right-handed according to the standard handedness inventory (Briggs and Nebes, 1975) and had normal or corrected-to-normal visual acuity. All participants gave their written informed consent prior to inclusion in the study and were naive as to its purpose. Participants were compensated for their time and received specific information concerning the study only after they had finished all experimental sessions. No participant had a history of neurological, psychiatric, or other medical problems or any contra-indication to TMS (Rossi et al., 2009). Experimental procedures were approved by the local ethics committee and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. During sp-TMS, no discomfort or adverse effects were noticed or reported.

Electromyographic recordings and TMS

Electromyography (EMG)-MEPs from sp-TMS of the left motor cortex were recorded from the right 'first dorsal interosseous' (FDI) and 'abductor digiti minimi' (ADM). Silver/silver chloride surface electrodes were placed over the muscle belly (active electrode) and over the associated joint or tendon of the muscle (reference electrode). A ground electrode was placed on the right wrist. A CED Power 1401 (Cambridge Electronic Design Ltd, Cambridge, UK) was connected to an Isolated Amplifier System Model D360 (Digitimer Limited, Hertfordshire, UK) and interfaced with CED Spike 2 software. The second-order Butterworth filter was set between 20 and 2.5 kHz (sampling rate, 10 kHz). Signals were displayed at a gain of 1000. Auditory feedback of the EMG signal was used to help subjects maintain voluntary muscle relaxation during electrophysiological preparation.

The optimal scalp position for inducing MEPs in the right FDI and ADM muscle was found by moving the coil in steps of 1 cm over the left primary cortex until the largest MEPs were found. Then, the position was marked with a pen on the bathing cap worn by participants. The coil was held tangential to the scalp with the handle pointing backward and laterally at 45° from the midline. Resting motor threshold (rMT) was defined as the lowest stimulus intensity that evoked at least five MEPs out of 10 consecutive magnetic pulses with an amplitude >50 μV. During the experimental blocks, one pulse of TMS was delivered at an intensity of 120% of the rMT. The single pulse was delivered by means of a 70 mm figure-of-eight stimulation coil (Magstim polyhurethane-coated coil). EMG recording started 100 ms before the test magnetic pulse to control for the absence of muscular preactivation in each trial. MEPs' peak-to-peak amplitudes (in millivolts) were collected and stored in a computer for off-line analysis.

Eye tracking

To rule out that any modulation of CS reactivity could be explained by non-specific factors (e.g. a differential general arousal induced by observation of immoral vs neutral actions), we also measured participants' pupil dilation (PD) to obtain information on the activity of parasympathetic and sympathetic systems (Bradshaw, 1967). Pupil size was measured monocularly in real time by means of an infrared video-based system (ASL 504 Remote Tracker, Applied Science Laboratories, USA), which analyzed online monocular pupil size (sampling rate 60 Hz).

Stimuli and procedure

Prior to the experimental task, participants were presented with four video clips. Each video clip showed: (a) a hand grasping a notepaper on a table, (b) a hand grasping a wallet on a table, (c) a hand grasping a notepaper stuck on someone else's trousers and (d) a hand grasping a wallet in someone else's pocket. In order to minimize ambiguity, we added subtitles to the video clips to guide action comprehension as follows: (i) '[he/she] is grasping (a)', (ii) '[he/she] is grasping his/her own wallet', (iii) '[he/she] is grasping a notepaper stuck on someone else's trousers' and (iv) '[he/she] is stealing a wallet'.

During the experimental task, participants viewed pictures of each of the actions shown in the video clips (Figure 1A). The pictures always showed the grasping action before the object was reached. We chose this phase of the grasping action because MR proved maximal for the snapshots evoking ongoing but incomplete actions (Urgesi et al., 2010b). The pictures differed as to the actors' identity (we used two sets of actors), gender and color of their clothing (green sweater vs purple sweater). These model-factors were matched across conditions and randomized within blocks. We checked that the pictures did not differ in luminosity, contrast, size and distance between finger and thumb across the different action conditions.

Participants sat on a chair at a distance of 60 cm from a screen on which the above-described snapshots were projected. The same action (grasping) could be aimed at two different objects (a wallet or a notepaper) and occurs in either a non-social (grasping the object on a table) or a social (grasping the object from another person;
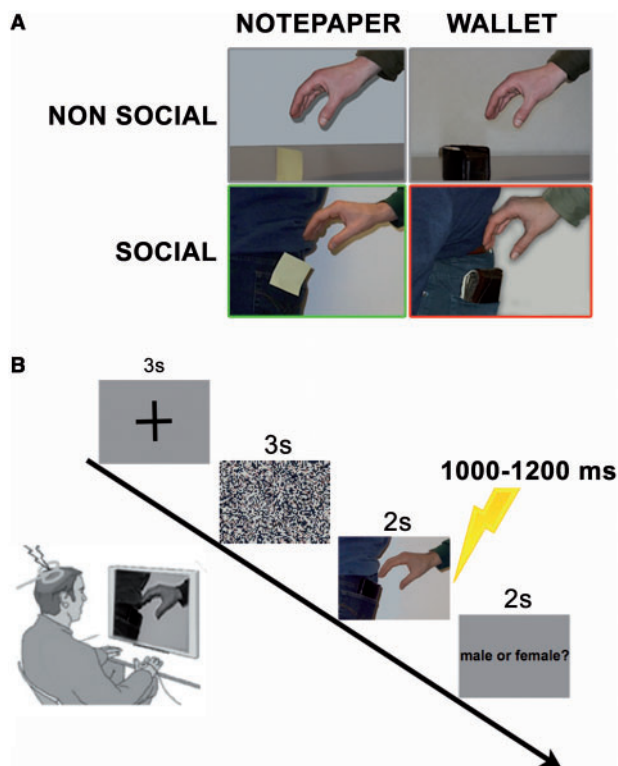
Fig. 1 Stimuli and procedures. (**A**) Examples of stimuli used in the study. Stimuli could depict an action performed in a social context or in isolation and the target of this action could be either a wallet or a notepaper. When it was a wallet in a social condition, the action assumed an immoral connotation (framed in red). When it was performed on a notepaper piece of paper in a social condition, the action was morally neutral (green frame). (**B**) Timeline and subjects' posture during the experimental procedure. sp-TMS was delivered on average 1100 ms (±100 ms) after the action appeared on the screen at intensities of the 120% individual rMT of FDI and ADM. Questions about features of the stimulus that were not related to the experimental manipulation (e.g. gender or color of the clothes of the actor/actress) appeared randomly 33% of the time. In the trials in which no question appeared, participants watched a black fixation cross on a gray background.

Figure 1A) context. Crucially, in the social context grasping had a different moral connotation depending on the object. Each condition was presented 24 times in a blocked design. The order of presentation was controlled across participants by a Latin square. As control condition, MEPs were recorded during observation of a black square in two 18-trial blocks at the beginning and the end of the experiment. Each experimental block began with a fixation cross on a gray background at the center of the screen, which lasted 3 s, followed by the scrambled version of the subsequent stimulus. After three more seconds, the target stimulus appeared on the screen for 2 s. A TMS pulse was delivered to the M1 portion coding for the hand muscles FDI and ADM between 1000 and 1200 ms from the picture onset. MEPs evoked by the sp-TMS stimulation were recorded by computing the peak-to-peak amplitude of the electromyographic signal collected from participants' ADM and FDI. To keep participants' attention focused on the stimuli, we randomly asked them (33% of the trials) questions about the stimuli they had just observed. In particular, we asked them whether the acting hand belonged to a woman or a man and the color of the actor's clothing. Questions remained on the screen for 2 s. When the target stimulus was not followed by a question, participants were shown a blank screen. The interval between trials was kept at 10 s to avoid any effect of TMS stimulation *per se* on general CS excitability (Chen *et al.*, 1997). At the end of each block, participants were asked to verbally describe the action they had just seen. The experimenter coded the verbal response as accurate or not. Participants were also asked to rate how much they believed the action

was morally acceptable on a 7-point Likert scale (where, $1 =$ 'not at all' and $7 =$ 'absolutely').

PD recording started 1 s before stimulus onset (while the scrambled version of the stimulus was on the screen) and ended 2 s after stimulus onset.

Data handling

The absence of background EMG activity was confirmed by visual inspection of the data. In each experiment, individual mean peak-to-peak MEP amplitudes were calculated separately for each muscle and block. There were 24 trials per cell in the experimental condition and 18 in each of the baseline (pre and post) blocks (for a total of 36). Trials with background activity preceding the TMS pulse higher than $50\,\mu$V were discarded (2.7% of the total). To determine whether any global change in CS excitability had occurred during the experiment, we compared the mean MEP amplitudes in the baseline block preceding the experiment with those recorded in the baseline block following the experiment using two paired sample t-tests (one per muscle). No significant difference between pre- and post-baseline conditions was found [$ts(20) < 0.8$; $Ps > 0.4$]. For both of the participants' muscles, MEP amplitudes were converted into a proportion of the baseline value so that values > 1 suggested CS excitation and values < 1 suggested CS suppression.

We divided the pupil size data into three time windows, each consisting of 60 data points (1000 ms). During the first time window, PD during observation of the scrambled target picture was recorded. Mean pupil size in this time window was used as a baseline for computing PD at later time windows. Therefore, PD was defined as the ratio between either the mean pupil size in the early (first 1000 ms) or late (from 1000 to 2000 ms) and in the baseline time window. As emotion-driven pupillary reactions usually peak after 1000 ms (Tamietto *et al.*, 2009; Azevedo *et al.*, 2013) from stimulus onset, we considered only the late window PD.

Personality measures

Participants completed the 125-item version of the TCI (Cloninger, 2008).

RESULTS

After normalization, we tested the experimental conditions for each muscle against the value 1 and found that all showed a significant excitation pattern (all $Ts > 2.18$, $Ps < 0.05$) (Table 1). This finding indicates that MR contingent upon action observation occurred in all conditions. It is worth noting that we used the non-social condition to be sure that no effect could be explained by the object *per se*. Thus, we subtracted the baseline MR in the non-social condition from the MR in the social condition for each muscle and ran analyses of covariance with the muscle (FDI *vs* ADM) and the morality of the action (MR change in the theft condition *vs* MR change in the paper-grasping condition) as within factors and the temperamental traits of TCI as covariates. We found that HA interacted significantly with the morality of the action [$F(1, 15) = 4.49$, $P < 0.05$, partial $\eta^2 = 0.27$]. No other main effect or interaction was found significant (all $Fs < 1.75$, $Ps > 0.2$). To study the interaction between our covariates and MR, we ranked participants on the basis of their HA scores. Then, we split the sample into two groups: participants with HA scores lower ($N = 10$, mean HA score $= 0.28 \pm 0.10$ s.d.) and higher ($N = 10$, mean HA score $= 0.62 \pm 0.11$ s.d.) than the sample median (0.47). We ran a mixed-model analysis of variance (ANOVA) with HA groups as between factor and muscle and morality of the action as within factors. This analysis showed a significant interaction between HA and morality of the action factors [$F(1, 18) = 6.38$, $P < 0.05$, partial $\eta^2 = 0.26$]. Duncan's *post hoc* comparisons showed that high level HA participants

Table 1 MEP facilitation ratios

Group	Object	Non Social	Social
		Context	
Low HA	Notepaper	1.40 (0.1)	1.24 (0.12)
	Wallet	1.32 (0.13)	1.29 (0.10)
High HA	Notepaper	1.14 (0.10)	1.28 (0.12)
	Wallet	1.32 (0.13)	1.22 (0.10)

Values represent the ratios between the mean MEP amplitude in each experimental condition and the baseline condition (s.e.).

Fig. 2 Differences in MR between the social and non-social condition for the two target objects in the two HA groups. Differential MR in the notepaper condition indicates reactivity to neutral actions, whereas differential MR in the wallet condition indicates reactivity to immoral actions. Differences were computed on the mean MEP amplitudes normalized on the baseline activations. Error bars indicate standard errors of the mean. *$P < 0.05$.

displayed less MR for immoral ($M = -0.1 \pm 0.34$ s.d.) than for neutral actions ($M = 0.14 \pm 0.28$ s.d., $P < 0.05$; Figure 2). Low HA showed an opposite, although non-significant, pattern (immoral $M = -0.03 \pm 0.35$ s.d.; neutral $M = -0.14 \pm 0.41$ s.d., $P = 0.28$) instead. No other comparisons reached significance (all $Ps > 0.09$). Also, we tested whether the social vs non-social context manipulation led to different MR in the two groups by testing our Dependent Variable (MR social − MR non-social context) against zero for each condition (moral and neutral) for each group (high HA and low HA). None of the one sample t-tests reached significance (all $Ts < 1.6$, $Ps > 0.13$). Finally, given that the pattern shown in Table 1 might suggest a difference between the two groups in the non-social wallet condition, we tested whether the two groups differ in each of the conditions prior to subtracting the non-social condition from the social one. No two-sample t-tests reached significance included the one that tested the difference in the non-social wallet condition (all $Ts < 1.84$, $Ps > 0.08$).

Pupil dilation

First, we tested whether the mean PD correlated with MEP amplitudes and found that this was not the case regardless of whether or not the muscles were collapsed [$r(18) = 0.1$, $P = 0.6$] or kept separated [$rs(18) < 0.14$, $Ps > 0.54$].

To ensure that the PD analysis would not yield results parallel to those observed for the MEPs, we subtracted the baseline PD in the non-social condition from the PD in the social condition. We entered the resulting data in a mixed model ANOVA with HA groups (high vs low) as between factor and action morality (neutral vs immoral) as within factor. We found no significant main effect or interactions [$Fs(1, 18) < 1.29$, $Ps > 0.19$; Figure 3].

Ratings of the morality of the observed actions

Data were not collected from one participant because of an error in the script. First, to test whether our immoral condition was perceived as such by participants, we entered the ratings on action morality in a 2 (social context vs non-social) ×2 (wallet vs paper) repeated measures ANOVA. Results showed a main effect of both factors [$Fs(1, 18) > 125.73$, $Ps < 0.001$]. Crucially, these effects were qualified by the two-way interaction [$F(1, 18) = 116.82$, $P < 0.001$]. Post hoc pairwise comparisons showed that participants rated the theft action as less morally acceptable ($M = 1.47$) than all of the other actions ($Ms \geq 6.37$, $Ps < 0.001$). Moreover, the action on the paper in the social context ($M = 6.37$) did not differ from the same action in the non-social condition ($M = 7$, $P > 0.05$). To assess whether or not data on the MEPs were paralleled by a similar, significant pattern in the explicit ratings of an action's morality, we subtracted the mean baseline rating in the non-social condition from the mean rating in the social condition. Then, we entered the resulting data in a mixed-model ANOVA with HA groups (high vs low) as between factor and morality of the action (neutral vs immoral) as within factor. As expected, we
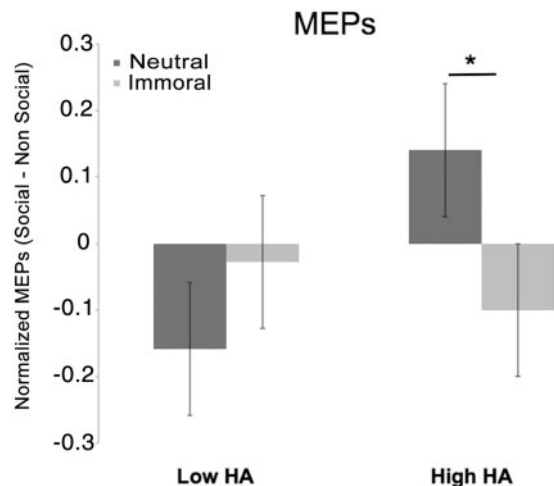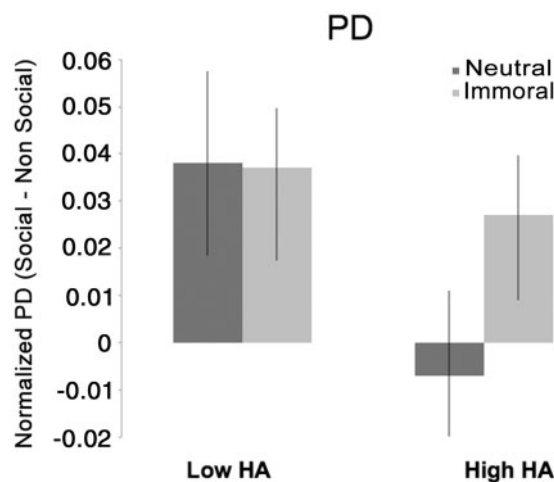

Fig. 3 Differences in PD in the social and non-social conditions for the two target objects in the two HA groups. Differential MR in the notepaper condition indicates reactivity to neutral actions, whereas the differential MR in the wallet condition indicates reactivity to immoral actions. Differences were computed on the mean PD amplitudes normalized on average pupil size during the last second of observation of the scrambled image of the following actions preceding the stimulus. Error bars indicate standard errors of the mean. None of the means differed significantly.

found a main effect for morality of the action [$F(1, 17) = 358.01$, $P < 0.001$]. Indeed, one-sample t-tests against 0 showed that although the difference between social and non-social context did not yield any significant difference in morality ratings for the paper condition (mean difference $= 0.63 \pm 0.33$ s.d., $t(18) = 1.93$, $P > 0.05$), the same difference was significant for the wallet condition (mean difference $= -5.42$, $t(18) = 24.58$, $P < 0.001$). We also found that the social–non-social difference for the wallet was significantly larger than for the paper ($P < 0.001$). In other words, the social context mattered for the moral connotation of the grasping action toward a wallet, but the social context did not matter when the same action was performed on a notepaper. Importantly, we found no significant interaction with personality as between factor [$F(1, 17) = 3.39$, $P > 0.05$]. In order to test whether the explicit judgment might mediate the relationship between the modulation of MR by the morality of the action (MR

interaction term) and HA, we computed the interaction term for the explicit morality judgments [(ratings for the social wallet condition − ratings for the non-social wallet condition) − (ratings for the social notepaper condition − ratings for the non-social notepaper condition)] and correlated it with the same interaction term of the MR and with HA scores. Consistently with our ANOVA findings, the interaction term for the MR correlated with the HA scores ($N = 20$ $r = −0.57$, $P < 0.05$). This indicates that the more people are high in HA, the less they resonate with immoral actions as compared with neutral social ones. Importantly, we found a significant correlation between the MR and explicit judgments interaction terms ($N = 19$, $r = 0.51$, $P < 0.05$). Nevertheless, the interaction term for the explicit judgments did not correlate with HA ($N = 19$, $r = −0.16$, $P = 0.5$). This pattern of results does not support the hypothesis of a possible mediation role of explicit moral judgments in the relationship between HA and the MR modulation of morality-related actions.

DISCUSSION

In this study, we analyzed motor potentials evoked by sp-TMS to investigate how individuals resonate to actions that are identical in terms of movement and immediate goal but have different moral connotations. We tested corticospinal reactivity to TMS, an index of MR, during observation of an immoral action (i.e. a hand stealing a wallet from someone else's pocket) with respect to observation of a morally neutral action (i.e. a hand picking up a notepaper stuck on someone else's trousers). Also, we measured the onlookers' personality traits using the TCI (Cloninger, 1994). Notably, MR modulation to the observation of immoral actions was present only in participants with high scores in HA, a personality trait that characterizes individuals who tend to have inhibited behavior and a heritable bias toward being cautious, apprehensive and overly pessimistic (Youn et al., 2002).

Subjects who score high on HA describe themselves as fearful, pessimistic, shy and fatigued, and they tend to respond intensely to signals of aversive stimuli. In contrast, people who score low on HA are optimistic and outgoing risk-takers (Cloninger, 1994). Functional brain imaging studies found that highly harm avoidant individuals, compared with low harm avoidant, show higher amygdala activation for threatening stimuli even when performing a task that minimizes their attention to this kind of stimuli (Most et al., 2006). It is also worth noting that amygdala activation correlates with HA when a painful stimulus is expected (Ziv et al., 2010). Our results expand behavioral reports by providing neural evidence that HA individuals tend to anticipate the negative outcomes in a quicker and automatic manner, which might explain why high HA promptly suppresses their MR toward an immoral action.

Some studies have suggested that motor cortex excitability can be affected by anxiety (Wassermann et al., 2001). In any case, our data cannot be interpreted in terms of a general effect on motor cortex excitability. Indeed, the MEP modulation in high HA participants is not a main effect but is observed only in interaction with the morality of the observed action. This finding suggests a specific role of HA in the processing of immoral actions.

Some recent reports indicate that anxiety should bring about an increase, not a suppression, of CS excitability (Baumgartner et al., 2007; Coombes et al., 2009; Kelly et al., 2009; Coelho et al., 2010; Borgomaneri et al., 2012). However, our data cannot be interpreted in terms of mere arousal because PD data show a different pattern of results than the MEPs. Rather, our findings suggest that observed MEPs modulation in high HA participants by action morality reflects personality-mediated changes in MR. It is also worth noting that the suppression effect cannot be explained in terms of differences in explicit moral judgments between the two groups because we found no

HA-related modulation of ratings of the morality of the observed actions. Rather, both low and high HA participants rated the action of a hand stealing a wallet as more immoral than the action of removing a notepaper from someone else's trousers. It should be noted, however, that our immoral actions were more dishonest than harmful, because they did not convey any physical threat, but just the non-violent theft, of someone else's money. Research on the neural correlates of moral judgment suggests that the judgment of dishonest, disgusting and physically harmful moral transgression activates brain regions associated with mentalizing, affective processing and action understanding, respectively (Parkinson et al., 2011). Thus, we may speculate that an initial activation of the mentalizing network contingent upon the observation of a dishonest action such as stealing a wallet might then suppress the MR in high HA individuals.

It may also be relevant that HA correlates with amygdala volume (Iidaka et al., 2006), lateralized functional amygdala response to negative social stimuli (Baeken et al., 2009) and resting state functional connectivity (Li et al., 2012). In Li et al.'s (2012) study, participants' HA scores were found to correlate positively with the functional connectivity between the centromedial amygdala region and the premotor cortex at rest. This finding might be coherent with the findings of previous studies on the neurobiological determinants of the temperamental traits measured by TCI (Youn et al., 2002), according to which HA reflects behavioral inhibition tendencies (Cloninger, 1994).

Therefore, we can conclude that high HA individuals are more prone to inhibit MR when they judge the observed action as immoral. Alternatively, HA may affect input processing rather than enhance behavioral inhibition. Indeed, HA, as well as anxiety and neuroticism, may lead people to be more vigilant to social signals. This may allow to decipher moral from immoral actions and quickly avoid interpersonal interactions that may induce negative emotional states in others (Chiao and Blizinsky, 2010). From a phylogenetic point of view, this mechanism may have been quite beneficial in ancestral environments, where a rapid response to potential dangers was needed (Mathews et al., 1997; Rozin and Royzman, 2001; Nettle, 2006). Behavioral evidence suggests that people with high anxiety are more tuned to social cues, especially when they convey information about threats such as angry and fearful facial expressions (Fox et al., 2002; Mathews et al., 2003; Holmes et al., 2006).

A possible limitation of this study is represented by the fact that the immoral action was compared with a neutral, rather than positive, action. Future studies are needed to assess whether a change in MR would occur when the moral valence of the action is reversed. It might turn out that, for example, high HA individuals are tuned to morally meaningful actions in general (independently from their positive/ negative valence) rather than just to negative ones.

CONCLUSIONS

Our results indicate that resonating with the actions of others, as indexed by changes in CS excitability to TMS of the primary motor cortex, can be modulated not only by low level goals but also by prospective social intentions (e.g. grasping to steal). Importantly, the modulation consisted of suppressing MR with immoral actions and occurred only in individuals who exhibited high HA scores, that is, who are more vigilant toward social cues, which convey information about potential danger or harm. Thus, individual differences interact with the way MR is modulated by action morality.

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