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Indignation for moral violations suppresses the tongue motor cortex: preliminary TMS evidence

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Abstract

We commonly label moral violations in terms of ‘disgust’, yet it remains unclear whether metaphorical expressions linking disgust and morality are genuinely shared at the cognitive/neural level. Using transcranial magnetic stimulation (TMS), we provide new insights into this debate by measuring motor-evoked potentials (MEPs) from the tongue generated by TMS over the tongue primary motor area (tM1) in a small group of healthy participants presented with vignettes of moral transgressions and non-moral vignettes. We tested whether moral indignation, felt while evaluating moral vignettes, affected tM1 excitability. Vignettes exerted a variable influence on MEPs with no net effect of the moral category. However, in accordance with our recent study documenting reduced tM1 excitability during exposure to pictures of disgusting foods or facial expressions of distaste, we found that the vignettes of highly disapproved moral violations reduced tM1 excitability. Moreover, tM1 excitability and moral indignation were linearly correlated: the higher the moral indignation, the lower the tM1 excitability. Respective changes in MEPs were not observed in a non-oral control muscle, suggesting a selective decrease of tM1 excitability. These preliminary findings provide neurophysiological evidence supporting the hypothesis that morality might have originated from the more primitive experience of oral distaste.

Key words: moral judgment; disgust; transcranial magnetic stimulation; motor-evoked potentials; tongue cortico-hypoglossal excitability

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Introduction

In its original etymology, the term disgust refers to an unpleasant experience connected with the visceral and interoceptive domain. We also use the word 'disgusting' to describe actions, aims or statements that violate a social norm in line with our culture and system of values, yet it remains unclear whether such a tendency to overlap disgust and morality is genuinely rooted in our cognitive/neural system or merely reflects a metaphorical expression (Royzman and Sabini, 2001; Royzman and Kurzban, 2011).

Research in psychology provides two opposing scenarios. The neosentimentalist perspective (Haidt, 2001), which proposes a causal role of emotions in moral judgment, suggests the existence of a genuine, biologically based link between disgust and morality (Rozin and Fallon, 1987; Rozin et al., 2008; Tybur et al., 2009; Tybur et al., 2013). Several strands of evidence support this theoretical view. For instance, similar activation of the levator labii (a facial muscle typically associated with oro-nasal rejection of aversive chemosensory stimuli; see Susskind et al., 2008) is evoked by the experience of indignation in response to unfair treatment in an economic game, as well as by gustatory distaste or pictures depicting amputations and contaminants (Chapman et al., 2009). Moreover, evoking core disgust experimentally (Moretti and di Pellegrino, 2010), as well as eliciting distaste by consumption of bitter liquids (Eskine et al., 2011), makes moral judgments more severe.

Disgust and morality are also linked at the neural level, as suggested by neuroimaging research in healthy humans (Chapman and Anderson, 2013) and clinical populations (Vicario, 2013; Vicario et al., 2017a). For example, perceiving unpleasant tastes (Small et al., 2003; Jabbi et al., 2008) and smells (Wicker et al., 2003), observing pictures of mutilation and contaminants (Schienle et al., 2006) and even imagining physically disgusting events (Jabbi et al., 2008), increases the activity of an overlapping neural network involving the anterior insula and the orbitofrontal cortex. Interestingly, the activity of these regions also increases in response to unfair treatment in an economic game (Sanfey et al., 2003), when reading statements depicting the scenarios of ethical violations (Moll et al., 2005) and in the presence of actions that are judged to be morally wrong (Schaich et al., 2008). Moreover, individuals with obsessive compulsive disorder, who are notoriously characterized by a pathologically high disgust sensitivity (Brady et al., 2010), are also more judgmental in the condemnation of moral violations (Harrison et al., 2012; Vicario et al., 2017a).

In contrast to the literature discussed so far, other theoretical approaches (i.e. rationalists) place particular emphasis on the role of cognitive inputs to moral judgment. These perspectives conceive of disgust and morality as barely linked, if not completely independent of each other. In this regard, Royzman and Sabini (2001) suggested that the application of the term 'disgust' to moral transgressions only reflects a metaphoric use of the term and that there is little or no common ground between disgust and morality (see also Royzman and Kurzban, 2011). The constructivism perspective (Cameron et al., 2015) does not deny the existence of some general correspondence between moral transgressions and disgust, but it proposes that this should not be construed as an exclusive relationship. In a recent meta-analysis, Landy and Goodwin (2015) suggested that the amplification effect of disgust on moral judgment reported in the literature is modest and possibly due to a publication bias (but see Schnall et al., 2015, for a critical comment on this meta-analysis). In summary, the literature outlined above provides

two contrasting perspectives about the existence of a common cognitive/neural morality-disgust linkage.

Here, we contribute to this controversial topic by studying the activity of the tongue representation in the primary motor cortex (i.e. tM1) in a group of healthy participants evaluating the stories of moral violations. From a merely sensory point of view, the tongue-disgust linkage is intuitive, as this oral muscle works as sensory organ that encodes flavors through its taste receptors (buds). Although the experience of disgust is mediated by these sensory receptors which are connected to the gustatory cortex and, in turn, to the insula and frontal operculum (Ohla et al., 2012), evidence suggests that even tM1 might be suitable for investigating the experience of disgust. In a pioneering investigation, Penfield and Faulk (1955) reported a convergence between motor (e.g. movements of the tongue, swallowing and suppression of chewing) and sensory experiences (e.g. sensation in the throat or indescribable sensations of taste or smell) related to the tongue and the oral region in patients receiving the electrical stimulation of the insula during surgical mapping for focal epilepsy. More recently, Alipour et al. (2002) demonstrated that the tM1 of non-human primates is directly connected with several cortical/subcortical regions (e.g. orbitofrontal cortex, striatum and insula) directly involved in the processing of disgust and morality in healthy humans (e.g. Sanfey et al., 2003; Wicker et al., 2003; Moll et al., 2005) and clinical populations (Vicario et al., 2017a). Converging evidence has been provided by other scholars (e.g. Mesulam and Mufson, 1982; Augustine, 1996). Moreover, neuroimaging findings show that the human tM1 and related sensorimotor networks are activated during the experience of disgust (Calder et al., 2007; Jabbi et al., 2008).

Remarkably, activation of this insular-motor network during disgust might be associated with an inhibition of ingestion-related functions. For example, exposures to visual stimuli representing gustatory disgust and revulsion (i.e. rotten foods and faces expressing distaste) inhibit saliva secretion (Vicario et al., 2017c), which is relevant for digestive functions. Even more importantly, in a recent transcranial magnetic stimulation (TMS) study (Vicario et al., 2017b), we found that visual stimuli representing gustatory disgust and revulsion suppress tM1 cortico-hypoglossal excitability, as measured via motor-evoked potentials (MEPs) from the tongue (TNG). This inhibition was not found for non-oral-related disgusting stimuli (i.e. invertebrates such as worms), suggesting it was specifically related to oral disgust. Moreover, the inhibition was specific to TNG MEPs as it did not extend to MEPs recorded from an arm muscle serving as non-oral control muscle. Remarkably, we found stronger TNG MEP suppression in response to disgust-related stimuli in participants who showed higher disgust sensitivity as measured by a questionnaire (Vicario et al., 2017b). These findings suggested that the suppression of TNG MEPs may provide a neurophysiological marker of oral-related disgust in the human cortico-motor system.

Extending the investigation of tM1 physiological activity to the moral domain might provide important insights into the debate about a disgust-morality linkage (Vicario et al. 2013b). In line with the neosentimentalist (emotional) perspective (Haidt, 2001) and the oral origin hypothesis of morality (Chapman et al., 2009), we expected that neural networks associated with oral disgust would be modulated during moral disapproval experienced while evaluating moral violations. Thus, building on previous evidence for the recruitment of tM1 and oro-facial motor networks in the experience of gustatory disgust (Calder et al., 2007; Jabbi et al., 2008) and a selective reduction of tM1

cortico-hypoglossal excitability during exposure to visual stimuli inducing gustatory disgust and revulsion (Vicario et al., 2017b), we expected that moral disapproval would be associated with a reduction in MEPs from the TNG (but not from a non-oral control muscle) and that stronger moral disapproval would be associated with greater TNG MEP reduction. On the other hand, the absence of such a relationship would be in line with the cognitive perspective, which considers disgust and morality as two independent domains.

Materials and methods

Participants

Fifteen healthy volunteers participated in the study and received a compensation of 25 Australian dollars. Participants were recruited from the School of Psychology, University of Queensland via the SONA system. All participants gave their written informed consent prior to their inclusion in the study and were naïve to its purpose. Specific information concerning the study was provided only after the subjects completed all experimental sessions. The experimental procedures were approved by the ethics committee of the University of Queensland and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. None of the participants had any history of neurological, psychiatric or ongoing medical problems, or any contraindication to TMS (Rossi et al., 2009). Because of technical issues with TNG MEP recording, two participants did not complete the experimental session (one participant could not relax the TNG muscle and another participant showed no reliable TNG MEPs). Thus, the final sample comprised 13 participants (four males, age range 20–26).

Task and stimuli

Moral disgust was induced by using 16 moral and 16 non-moral (control) dilemmas depicted in short vignettes by Harrison et al. (2012), based on the study of Greene et al. (2001). Examples of moral and non-moral stories are as follows: Moral story: 'During the Second World War in Poland Mrs. Jones and her children, a girl and a boy, are imprisoned in a concentration camp. Once they are there, a guard tells Mrs. Jones that she must choose one of her children to live. The other will die in the gas chambers. If she does not choose either of them, both will be killed'. Non-moral story: 'Mr. Jones is going away for the weekend. He is driving his car and comes to a fork in the road. The right turn leads to a seaside town, with a superb beach. The left turn leads to a mountain town, with beautiful views. After thinking for a moment, he decides to take the right way and spend a couple of days by the sea'.

The set of vignettes and stories used in the present study was developed by Harrison et al. (2012) and used in previous investigations (e.g. Vicario and Rafal, 2017; Vicario et al., 2018). They included moral dilemmas that are considered to be particularly emotionally engaging, because they prompt the reader to endorse actions that directly imply bodily harm to a victim (or set of victims), in which utilitarian judgments tend to violate conventional moral social standards (Harrison et al., 2012).

TMS and electromyography recording

We recorded MEPs from the TNG in order to assess the excitability of the tM1 cortico-hypoglossal pathway. As a somatotopic control, we recorded MEPs from a hand muscle, i.e. the first dorsal interosseous (FDI), in order to assess cortico-spinal excitability from the hand area of the primary motor cortex (hM1).

We recorded MEPs with a Grass P511 isolated amplifier, sampled at 10 kHz, band-pass filtered (20 Hz–2.5 kHz) and stored for offline analysis. Two different electrode montages were used for recording MEPs from the target (TNG) and control (FDI) muscles as in previous studies (e.g. Vicario et al., 2014, 2017b). For TNG, we used Ag-AgCl electrodes (1 cm diameter) mounted on a 1 × 1 cm plastic plate and fixed on a metal clip device (Sato et al., 2010). Because the cortical representation of the TNG is mainly bilateral (Muellbacher et al., 1994; Urban et al., 1996), it is debatable whether unilateral TNG motor responses can be safely recorded the devoid of volume-conducted potentials from the contralateral side of the TNG (Muellbacher and Mamoli, 1997; Chen et al., 1999). Thus, we decided to record from the TNG over the midline, instead of a unilateral recording. Accordingly, the active and reference electrodes were placed on the dorsal and ventral aspects of the TNG, respectively, ~1.5 cm caudal to the TNG apex. For the FDI, pairs of Ag-AgCl surface electrodes (1 cm diameter) were placed over the muscle belly (active) and its tendon (Rossini et al., 2015). For both TNG and FDI, ground electrodes were placed over the elbow. TMS was administered using a 70 mm figure-of-eight focal coil connected to a Magstim 200 stimulator. The coil was placed tangentially to the scalp at 45° from the midline so that the current flow direction in the brain was posterior–anterior.

Stimulation of TNG (tM1) and FDI (hM1) motor representations from the same scalp site in one experimental session was not possible. Thus, we performed two separate stimulation sessions whose order was counterbalanced. In these sessions, we first identified the respective muscle hot spots by determining the coil placement, which resulted in the largest MEP amplitudes from the target muscle under a given moderate TMS intensity. To ensure correct coil placement throughout the experiment, these positions were marked on a tightly fitting Lycra swimming cap worn by participants. From each optimal scalp position, we then determined the resting motor threshold (rMT), which was defined as the lowest intensity of stimulation that produced at least five MEPs with an amplitude >50 µV in 5 out of 10 consecutive pulses (Rossini et al., 2015). During the experimental conditions, MEPs were elicited by stimulating the motor hot spot at an intensity of 120% of rMT and stored on a computer for offline analysis.

Procedure

Two days before the experimental session, participants received an e-booklet with the 16 moral and 16 non-moral (control) stories, as they were required to memorize the short description associated with each single vignette. They were asked to read them repeatedly until they could recall the content associated with all the vignettes. Indeed, full memorization of this content was mandatory to take part in this study, to allow the comparison of moral vs non-moral contents prompted by exposure to the vignettes and their effects on tM1/hM1 excitability. In this way, each vignette displayed on the screen during the experimental session was familiar.

To verify the correct memorization of the material, a few minutes before the beginning of the experimental session, participants were asked to verbally provide details about the stories associated with the 32 vignettes. All participants were able to correctly identify all vignettes, providing 100% of correct responses.

During the experimental sessions, participants were comfortably seated in a dimly lit room at a distance of 80 cm in front of a computer screen (computer monitor 20", 60 Hz refresh

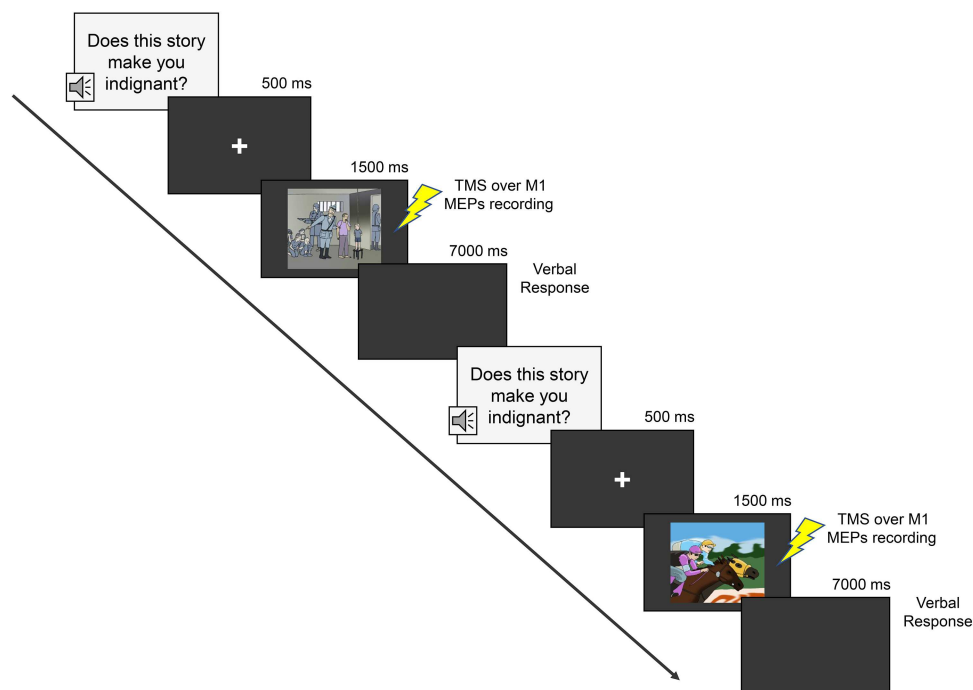


Fig. 1. Typical trial sequence. Participants were asked to provide their answer within a couple of seconds after the single TMS pulse was released by turning up the thumb or shaking the index finger of their left hand to indicate 'yes' or 'no', respectively.

rate). MEPs from the TNG and the FDI were recorded in separate sessions (counterbalanced design). Each session consisted of two blocks of 32 trials (16 moral and 16 non-moral vignettes) and a block of 16 fixation crosses for a total of 48 trials per muscle. Fixation crosses were presented at the beginning and at the end of each session. To be sure that participants recognized the moral vs non-moral outcomes suggested by the displayed vignettes, each trial was preceded by a verbal (pre-recorded) question: 'Does this story make you indignant?' In this question, we choose the term 'indignant', to avoid any explicit reference to disgust that could have biased our participants. Figure 1 provides an example of a typical experimental session.

To avoid changes in motor excitability due to the preparation of verbal responses (Tokimura et al., 1996; Meister et al., 2003), participants were asked to provide their response about 2 s after the release of the magnetic pulse (Tidoni et al., 2013; Vicario et al., 2014, 2017b). All participants successfully answered in all trials. During stimulus presentation, a single TMS pulse was delivered over the participants' muscle hotspot at random times ranging from 1100 to 1400 ms after the onset of the picture to avoid any priming effects that might influence MEP amplitude (Vicario et al., 2013a; Vicario et al., 2015). The inter-stimulus interval was set at 7000 ms. TMS frequency during the experimental blocks was <0.1 Hz to avoid that TMS *per se* would influence motor cortex excitability (Chen et al., 1997). At the end of the experiment, participants were required to rate their disapproval (indignation) of the moral dilemmas using a 10 cm visual analog scale (VAS) with anchor points labeled 'not at all' and 'extremely disapproving'.

Data analysis

Behavioral and neurophysiological data were analyzed offline. We computed mean VAS ratings for moral and non-moral vignettes and analyzed these with a Wilcoxon matched pairs test. Mean MEP amplitude values were measured peak-to-peak

(in mV). Trials with electromyography (EMG) activity prior to TMS or with MEP amplitudes lower than 10 μ V or higher than 3 SD from the mean were identified in each condition and discarded from further analysis (6.9% of all MEPs). MEP amplitudes were log-transformed ($\log[\text{MEP value in mV} + 1]$) to reduce skewness and submitted to a two-way repeated measures ANOVA with muscle (TNG and FDI) and stimulus (moral, non-moral and fixation) as within-subjects factors.

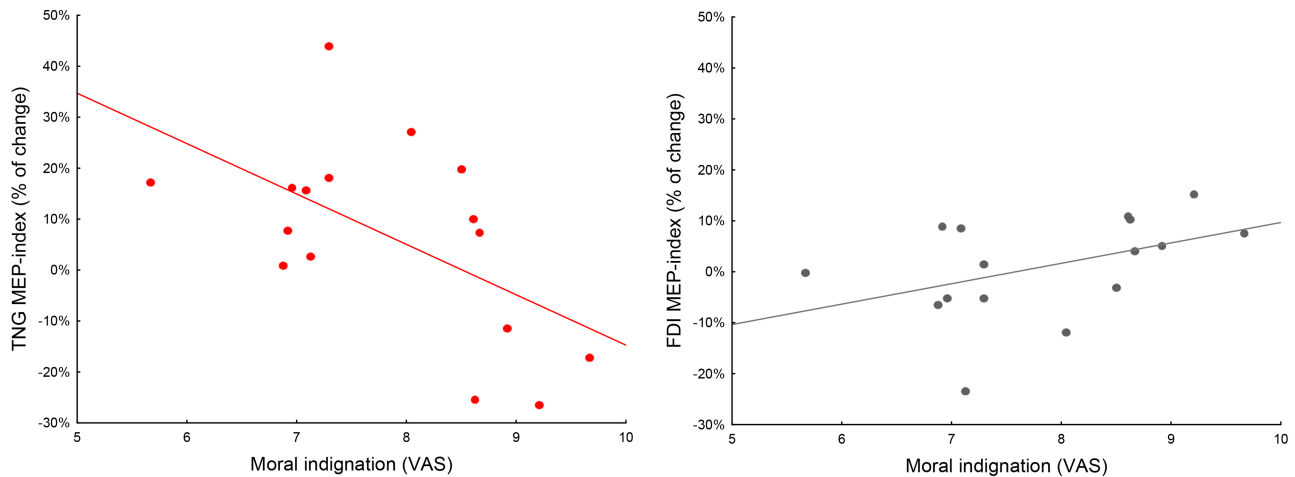
Because the 16 moral scenarios were variable in terms of moral disapproval, we tested whether MEPs during moral vignette presentations were associated with the degree of moral indignation. For each moral vignette, we computed an MEP-index as the difference relative to mean MEPs during the 16 non-moral stories and fixation crosses, following the formula: $\text{MEP-index} = [(\text{moral} - \text{mean non-moral}) / \text{mean fixation} * 100]$. In a first analysis, for each story, we computed a mean MEP-index across participants and tested whether this index was predicted by mean ratings of the 16 moral scenarios via linear regression analysis and a bootstrapping technique using 1000 iterations. In a second analysis, we selected two groups of vignettes, one with the highest ratings of moral indignation ($N = 6$ stories; 37.5% of all vignettes; $M \pm \text{s.d.} = 8.95 \pm 1.24$) and the other with the lowest ratings ($N = 6$, 37.5% of all vignettes; 6.77 ± 1.87) while removing the 25% median ratings (corresponding to $N = 4$ stories). For each participant, we computed the mean MEP-index for high- and low-rated stories and submitted that index to a two-way repeated measures ANOVA with muscle (TNG and FDI) and moral indignation (high and low) as within-subjects factors. Follow-up pair-wise comparisons were performed using the Duncan test to correct for multiple comparisons.

Results

During the MEP recordings, all participants correctly discriminated 100% of the moral and non-moral vignettes. A Wilcoxon

Table 1. MEP amplitudes (mean log-transformed values \pm standard deviation) during exposure to moral and non-moral vignettes and the fixation cross.

	Moral vignettes	Non-moral vignettes	Fixation
TNG	0.06 \pm 0.04 mV	0.06 \pm 0.03 mV	0.06 \pm 0.03 mV
FDI	0.16 \pm 0.11 mV	0.16 \pm 0.10 mV	0.17 \pm 0.10 mV

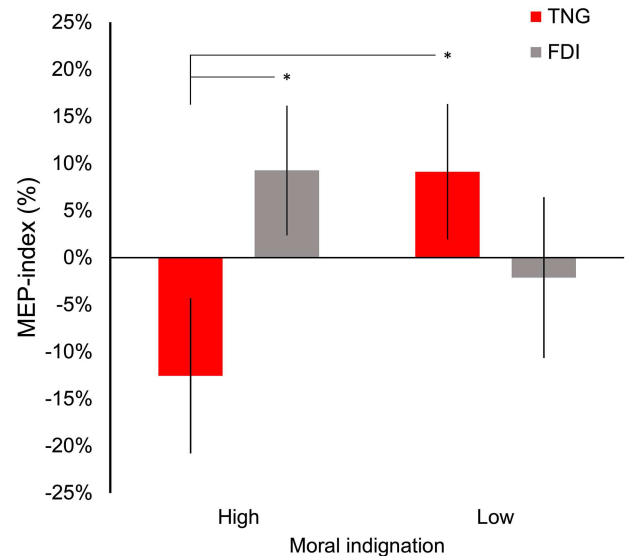
**Fig. 2.** Scatterplot of the average disapproval ratings for the 16 moral stories with the associated average MEP-index [(moral – mean non-moral)/mean fixation*100]. Each dot represents a moral vignette. Left and right panels show the MEP-index recorded from the TNG (showing a negative relation with moral indignation; $r = -0.63$) and FDI muscle (showing a positive relation with moral indignation; $r = 0.44$), respectively.

matched pairs test on mean VAS ratings showed that moral vignettes were judged as eliciting higher moral disapproval than non-moral vignettes (mean \pm s.d.: 7.89 ± 1.37 vs 0.04 ± 0.05 ; $Z = 3.18$, $P = 0.001$).

The repeated measures ANOVA on log-transformed MEP amplitudes over all vignettes showed a significant main effect of Muscle ($F_{1,12} = 15.23$, $P = 0.002$, $\eta_p^2 = 0.59$) with FDI MEPs (mean \pm s.d.: 0.18 ± 0.10 mV) larger than TNG MEPs (0.06 ± 0.03 mV). We found no main effect of stimulus or stimulus \times muscle interaction (all $F \leq 0.45$, $P \geq 0.62$, $\eta_p^2 \leq 0.04$), suggesting no consistent MEP modulation for moral vignettes relative to the other conditions (Table 1; see also Supplementary Table S1 for raw MEP amplitudes).

Remarkably, however, while the 16 moral vignettes elicited relatively high scores of disapproval (mean VAS: 7.9), there were noticeable differences between them, with some vignettes eliciting consistently higher moral disapproval and other vignettes eliciting lower disapproval (VAS range: 5.95–9.68). We leveraged this variability by testing whether motor excitability during moral vignettes was predicted by VAS ratings.

A first regression model showed that VAS ratings negatively predicted the TNG MEP-index ($R^2_{\text{adj}} = 0.36$, $F_{1,14} = 9.46$, $\beta = -0.63$, $P = 0.008$), which was confirmed by bootstrapping [$B = -0.106$, 95% confidence intervals (CIs): $-0.170/-0.042$, $P = 0.006$] and indicated that moral vignettes eliciting higher disapproval were associated with a reduction in tM1 cortico-hypoglossal excitability (Figure 2). A second regression model showed a weak positive relationship between VAS ratings and the FDI MEP-index ($R^2_{\text{adj}} = 0.14$, $F_{1,14} = 3.36$, $\beta = 0.44$, $P = 0.09$; bootstrapping: $B = 0.041$; 95% CI: $0.006/0.084$, $P = 0.038$), suggesting that moral vignettes eliciting higher disapproval were associated with a trend toward a facilitation of hM1 cortico-spinal excitability (Figure 2). Only the first model survived a Bonferroni correction (critical P value = $0.05/2 = 0.025$).

**Fig. 3.** MEP-index [MEPs elicited during presentation of moral vignette subgroup – mean MEPs during non-moral vignettes]/fixation*100] for the subgroups of moral vignettes associated with high and low disapproval. The histograms show lower TNG MEP-index values for highly disapproved moral vignettes. Asterisks indicate significant *post hoc* differences. Error bars denote the standard error of the mean.

A significant negative relationship between changes in tM1 excitability and VAS ratings was also detected using raw (log-transformed) TNG MEP amplitudes (average across participants: $R^2_{\text{adj}} = 0.36$, $F_{1,14} = 9.62$, $\beta = -0.64$, $P = 0.008$; bootstrapping: $B = -0.005$, 95% CI: $-0.008/-0.002$, $P = 0.019$; all single trials pooled together: $R^2_{\text{adj}} = 0.037$, $F_{1,191} = 8.48$, $\beta = -0.21$, $P = 0.004$; bootstrapping: $B = -0.005$, 95% CI: $-0.008/-0.001$,

$P=0.008$; Supplementary Figure S1) and survived Bonferroni correction. No significant relationships were detected for the FDI using either averaged raw MEPs or single trials (all $P \geq 0.10$).

These findings were further corroborated by a muscle \times moral vignettes ANOVA based on the MEP-index computed for high- and low-disapproval vignettes (Figure 3). This analysis showed no main effects of muscle or moral vignettes ($F \leq 1.36$, $P \geq 0.27$, $\eta_p^2 \leq 0.10$), but an interaction between the two factors ($F_{1,12} = 8.28$, $P = 0.01$, $\eta_p^2 = 0.41$). Follow-up analysis showed a lower TNG MEP-index for high-relative to low-disapproval vignettes ($-13 \pm 30\%$ vs $9 \pm 26\%$; $P = 0.03$, Cohen's $d = 0.79$), whereas the same comparison did not reach statistical significance for the FDI MEP-index ($9 \pm 25\%$ vs $-2 \pm 31\%$; $P = 0.21$, Cohen's $d = 0.46$). Moreover, during high-disapproval vignette presentations, the TNG MEP-index was lower than the FDI MEP-index ($P = 0.03$, Cohen's $d = 0.70$), whereas comparable MEP-index values were observed in the TNG and FDI muscles during the presentation of low-disapproval vignettes ($P = 0.19$, Cohen's $d = 0.33$).

Discussion

In this study, we explored whether tM1 cortico-hypoglossal excitability is sensitive to moral violations, to address the hypothesis of a disgust-morality linkage at the neural level. Building on our previous experiment showing that pictures associated with gustatory disgust and revulsion reduce tM1 cortico-hypoglossal excitability (Vicario et al., 2017b), we tested whether a reduction in tM1 cortico-hypoglossal excitability is also found when participants evaluate vignettes representing moral violations committed by other people. Overall, the whole set of moral vignettes did not consistently predict a modulation of TNG MEP amplitudes, compared with non-moral vignettes. However, when participants' individual differences in moral judgments were taken into account, we found that vignettes associated with higher moral disapproval resulted in the expected suppression of TNG MEP amplitudes. Moreover, the higher the moral disapproval, the lower the TNG MEP amplitudes. In contrast, we found a non-significant, opposite relationship between moral indignation and MEP amplitudes in the FDI, which served as a somatotopic (non-oral) control muscle. Thus, the degree of moral indignation was linearly associated with a fine-tuned suppression of tM1 cortico-hypoglossal excitability and a weak, non-significant facilitation of hM1 cortico-spinal excitability.

These findings, although preliminary, are in line with the general hypothesis that emotions prime the body for action (Frijda, 1986, 2009; Lang and Bradley, 2010) and with previous TMS studies showing changes in motor excitability following the administration of a variety of emotionally salient stimuli (Avenanti et al., 2005, 2006; Schutter et al., 2008; Coombes et al., 2009; Borgomaneri et al., 2012, 2015b; Van Loon et al., 2010). Importantly, our findings highlight, for the first time, a relationship between changes in tM1 cortico-hypoglossal excitability and moral indignation.

Neuroimaging studies reported the modulations of fronto-insular sensorimotor networks during moral disgust (Moll et al., 2005; Harenski and Hamann, 2006; Schaich et al., 2008; Chapman and Anderson, 2013; Massau et al., 2017; Vicario et al., 2017a; Oaten et al., 2018; Ying et al., 2018). Chapman et al. (2009) reported that, when people receive an unfair offer in an ultimatum game, they show facial expressions of disgust. Yet, these previous studies did not specifically investigate the modulations

of neural networks controlling the tongue and could not establish whether network activity alterations reflected excitatory or inhibitory processes. Moreover, the use of peripheral facial EMG has been criticized, as facial expressions might reflect strategic social performance, rather than a valid, direct read-out of the internal states of an individual (e.g. Fridlund, 1994; Fernández-Dols et al., 1997; Royzman and Sabini, 2001; Royzman and Kurzban, 2011).

Our study expands knowledge gained from previous neuroimaging and EMG studies in the following aspects. First, we provide the first neurophysiological evidence of a specific involvement of tM1 in moral indignation. Second, our data indicate that tM1 cortico-hypoglossal modulation is inhibitory and reminiscent of a similar motor inhibition observed when participants are exposed to pictures of disgusting foods (see Vicario et al., 2017b), as shown by a reduction in TNG MEPs. Importantly, this reduction of tM1 cortico-hypoglossal output during moral disgust cannot be attributed to strategic social performance—as Royzman and Kurzban (2011) questioned when referring to levator labii activation in response to unfair offers in the study by Chapman et al. (2009). In contrast with the ultimatum game, our task did not involve any social interaction or reward that could bias participants' voluntary behavior. Moreover, MEPs were detected in the absence of any voluntary EMG activity and TNG movements. Thus, they reflect inhibitory cortico-motor modulations that were detected in spontaneous conditions while evaluating moral vignettes. At last, our findings show that motor inhibition is restricted to TNG MEPs (tM1) and does not extend to FDI MEPs (hM1), thus providing somatotopic specificity and support to the hypothesis of an 'oral' origin of moral disgust (Chapman et al., 2009).

Suppression of tM1 cortico-hypoglossal output when facing stimuli eliciting gustatory disgust and revulsion might reflect an implicit avoidance-defense mechanism of motor inhibition to prevent the ingestion of potentially harmful contaminants (Rozin et al., 2000; Oaten et al., 2009). Indeed, TNG MEPs reflect descending cortico-hypoglossal pathways involved in controlling preparatory oral activity that precedes swallowing (Mistry et al., 2007; Matsuo and Palmer, 2008; Steele and Miller, 2010), but also in preventing swallowing, e.g. when sensing potentially toxic foods (Vicario et al., 2017b). In these circumstances, ingestion has to be inhibited in advance to prevent contamination from potentially lethal substances. The present finding that a similar inhibition of tM1 output occurs during high moral indignation (in absence of oro-facial cues) supports the hypothesis that moral disgust activates an avoidance-defensive mechanism that was similar to that recruited for rejecting unpalatable and potentially harmful foods. An argument against this hypothesis could be the potential lack of emotional specificity. Indeed, moral vignettes used in our study might have elicited not only moral disgust but also other negative emotional states such as anger or sadness (e.g. Rozin, 1997; Rozin et al., 1999; Ciaramelli et al., 2013). In principle, these negative emotions might have contributed to the reduction in tM1 excitability reported in our study. However, it is unlikely that changes in tM1 excitability were merely due to a general influence of any negative emotion. In previous studies, we observed that negative emotions following choices that caused monetary loss (mostly regret, anger and sadness) were associated with increased hM1 cortico-spinal excitability (Vicario et al., 2015) and increased tM1 cortico-hypoglossal excitability, as well (Vicario et al., unpublished data). Based on these prior observations, and in line with the evidence of TNG MEP reduction in response to distaste-related stimuli (Vicario et al., 2017b), one might speculate that the reduction in tM1

cortico-hypoglossal excitability reported in the current study reflects a functionally specific avoidance-defense mechanism mainly related to disgust.

The tendency toward an increase in hM1 cortico-spinal excitability during highly disapproved moral scenarios is in line with prior studies reporting motor facilitation in response to different negative stimuli associated with fear, anger and disappointment (e.g. Schutter et al., 2008; Coombes et al., 2009; Borgomaneri et al., 2014, 2015a; Vicario et al., 2015; Hortensius et al., 2016). Studies addressing the time course of hM1 excitability have suggested that the earliest hM1 response to negative and/or highly salient stimuli (~50–150 ms from stimulus onset) is often inhibitory, reflecting a generalized freezing response (e.g. Cantello et al., 2000; Farina et al., 2001; Urban et al., 2004; Makin et al., 2009; Avenanti et al., 2012; Borgomaneri et al., 2015c, 2017). At later time points, i.e. in conditions similar to those tested here, the hM1 response to negative stimuli is excitatory, possibly reflecting increased hand motor readiness (Schutter et al., 2008; Coombes et al., 2009; Van Loon et al., 2010; Borgomaneri et al., 2014). In light of this, the present findings suggest parallel action tendencies while processing moral disgust, with the tM1 implementing oral rejection tendencies and the hM1 showing a weak increase in hand motor readiness.

In general, our findings appear to support the ‘oral origin’ hypothesis of morality stating that a rejection impulse originally evoked by oral disgust might have been co-opted to promote the withdrawal from moral transgressions (Chapman et al., 2009). Indeed, if moral disgust originates from the same emotion involved in the rejection of rotten foods, then moral disapproval should elicit similar neurophysiological markers of oro-facial rejection (e.g. tM1 cortico-hypoglossal suppression) as oral disgust, despite moral disgust being clearly different from its purported origin in food rejection and protection from the ingestion of potentially harmful contaminants. This also fits with the neural reuse hypothesis (e.g. Gallese and Lakoff, 2005; Pessoa, 2008; Anderson, 2010), which states that neural circuits can continue to acquire new uses after an initial or original function is established. It should be noted, however, that while our data appear in line with the neosentimentalists’ view, they do not provide ultimate support to it. Indeed, we cannot rule out the possibility that our findings reflect associative learning (whereby disgust and moral transgressions have been extensively linked) rather than a causal, biological link between disgust and indignation.

Our study has some potential limitations. First, the sample size of our study is small and homogenous, with most of our participants being young females. Thus, our study should be considered preliminary, and a replication with a larger sample including more male participants would be welcome in future studies. Second, we did not measure the individual gustatory disgust sensitivity of our participants. This prevented us from directly exploring any relations between the oral disgust sensitivity of our participants and their experience of moral indignation in relation to their tM1 excitability. Third, to minimize the discomfort of stimulating a ventral scalp position (tM1), we chose to collect a relatively low number of MEPs and stimulate at 120% of each individual’s rMT, instead of thresholding to a predetermined amplitude associated with more stable MEPs (e.g. 1 mV). These aspects may have contributed to the observed variability.

In conclusion, our study shows that indignation for moral violations selectively reduces the excitability of the tM1 and that this suppression is predicted by the degree of disapproval of the moral transgression. This suppression pattern supports an avoidance-defense mechanism in the human tM1 in response

to moral indignation, which is similar to what has been reported for pictures of unpalatable foods and vicarious activation of the tM1 during social perception of others’ distaste (Vicario et al., 2017b). These findings thus support the idea of shared neural representations of disgust and morality in the central nervous system and provide preliminary, novel evidence supporting the hypothesis that morality might have an oral origin.

Supplementary data

Supplementary data are available at SCAN online.

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Conflict of interest

M.A.N. is a member of Advisory Board of Neuroelectrics who has no role in the present research. None of the remaining authors have potential conflicts of interest to be disclosed.

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