Research report

A causal role for inferior parietal lobule in emotion body perception

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ABSTRACT

Recent investigations of emotion body perception have established that perceiving fearful body expressions critically triggers activity in dorsal stream structures related to action preparation. However, the causal contributions of these areas remain unclear. In the current experiment, we addressed this issue using online transcranial magnetic stimulation (TMS) of the inferior parietal lobule (IPL) in the dorsal stream and visual areas (extrastriate body area — EBA in the ventral stream and early visual cortex — EVC). Participants performed a delayed-match-to-sample task requiring detection of a change in posture of body expressions that were either neutral or fearful. Results revealed a significant interaction between the stimulation site and the emotional valence of stimuli, indicating that processing of emotional versus neutral bodies is affected differentially by stimulation of different central areas in body processing. IPL stimulation specifically enhanced fearful body processing. These findings relate emotion processing to separate processing streams, and moreover provide the first evidence that IPL plays a causal role in processing of fearful bodies.

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1. Introduction

Some emotional body expressions that we see in people around us prompt us to flee, while others prompt us to fight. Recognizing bodily emotion expressions is obviously an important social ability and failure to process such expressions may make us miss important cues and have undesirable consequences. Emotional body expressions are complex stimuli because they convey simultaneously visual information about a body and cues about the emotion it expresses, as well as information about the action taking place (de Gelder, 2006). It is still an open question exactly how the information flows between the early visual cortex (EVC), sensitive to affective valence of the signal, visual areas in temporal cortex which encode object shape, and dorsal areas involved in action perception. In this paper, we use multi-site transcranial magnetic stimulation (TMS) to identify the specific causal role of areas at different stages of visual processing, namely the

early visual, temporal and parietal areas, during processing of neutral and fear bodily expressions.

Consider the role of early cortical visual areas in the processing of emotional stimuli. A recent TMS experiment with healthy participants, in which single TMS pulses were given over V1 at phosphene location, showed an impairment of discrimination of neutral bodies. However, stimulation did not affect discrimination of threatening bodies (Filmer & Monsell, 2013). This finding is consistent with evidence from patient studies showing that, despite destruction of primary visual cortex (V1), processing of emotions can still occur via a subcortical route to the amygdala, independent of the geniculo-striate pathway (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Morris, de Gelder, Weiskrantz, & Dolan, 2001; Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012; Van den Stock & de Gelder, 2014; Van den Stock et al., 2011). Based on this, we expect that stimulation of EVC will have a different effect depending on whether the stimuli are neutral or fearful.

A next question concerns the role of stimulus representation in ventral areas. Some investigations of neutral body images have mainly focused on the role of a category specific area in the temporal cortex, dedicated to body perception, the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001). By now the role of EBA in processing of neutral body images has been established by many studies (Kret, Pichon, Grèzes, & de Gelder, 2011; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Pitcher, Goldhaber, Duchaine, Walsh, & Kanwisher, 2012; Urgesi, Berlucchi, & Aglioti, 2004). But it is still unclear whether body category representation in EBA is an essential stage in emotion processing (de Gelder, 2016). Previously found activations in EBA in response to emotion bodies may be driven by attention and arousal effects (Downing & Peelen, 2011). Given the role of EBA in body processing, we predict that TMS stimulation of this area should selectively affect the processing of neutral bodies.

In contrast to ventral processing structures, recent studies have discovered an important role for the parietal cortex in emotional action observation (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Goldberg, Christensen, Flash, Giese, & Malach, 2015; Grèzes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grezes, 2008). Consistent with this, Goldberg, Preminger, and Malach (2014) recently provided fMRI evidence for this emotion-action link by showing that dynamic emotional whole-body stimuli preferentially activate parietal areas, traditionally associated with the mirror neuron network. Furthermore, evidence from TMS experiments shows that confrontation with emotional bodies leads to an increase in cortical excitability in primary motor cortex (Borgomaneri, Gazzola, & Avenanti, 2012, 2014). Thus, seeing emotional bodies may involve dorsal parietal structures and prime motor responses more than seeing neutral bodies (Borgomaneri et al., 2012; de Gelder et al., 2004).

The goal of the current study was to disentangle the causal roles of the inferior parietal lobule (IPL) in the dorsal stream, EBA in the ventral stream and EVC during visual processing of neutral and fearful bodies using online triple pulse TMS (tpTMS). IPL is a hub in the dorsal action stream that is strongly connected with premotor and motor areas as well as with subcortical areas (Clower, West, Lynch, & Strick, 2001), and is thus hypothesized as a key structure in emotion body perception.

Given the evidence for the link between parietal dorsal stream areas and processing of emotion bodies, we predict that stimulation of IPL should selectively alter performance in a fear body condition as compared to a neutral body condition.

2. Methods

2.1. Participants

Twenty healthy volunteers [11 female, mean age (SD) = 26(3,5)] participated in the TMS experiment. Eighteen were right handed and all had normal or corrected to normal vision. Participants were unaware of the goal of the study until after the completion of the experiment. Participants were screened for fMRI and TMS safety. The study was performed in accordance to the Declaration of Helsinki and approved by the local ethical committee. Two participants were excluded from analysis because of missing data.

2.2. Brain imaging

We determined the location of EBA by using fMRI-guided neuro-navigation, because this method has been shown to be superior compared to using group functional Talairach coordinates (Sack et al., 2009). Each participant took part in an fMRI localizer experiment, in which five different visual stimulus categories were presented. Static images of each condition (bodies, faces, houses, tools and words) were shown pseudo-randomized in a blocked design, with 7 blocks per condition. Functional images were acquired using a 3T MAGNETOM Prisma fit scanner with a 64-channel head–neck coil. A gradient-echo EPI sequence [repetition time (TR) = 2 sec, echo time (TE) = 31 msec, voxel size = 2 × 2 × 2 mm, 64 slices] providing whole-brain coverage was used. The localizer scan started with a fixation period of 6 TRs, followed by blocks of stimuli of 6 TRs separated by fixation periods of 6 TRs, and ending with a fixation period of 12 TRs. A total of 432 volumes were acquired. We defined right EBA by contrasting the fMRI responses to bodies and houses and selecting the cluster that showed the greatest relative activation for the bodies' condition.

A high-resolution T1-weighted MPRAGE anatomical scan was performed to determine the two other stimulation sites based on individual brain anatomy (EVC and IPL). Without access to a straightforward localizer as was available for EBA, and considering that individual MRI-guided TMS localization can lead to adequate effect sizes (Sack et al., 2009), stimulation locations for IPL and EVC were determined based on MRI landmarks. For 'IPL', we targeted a location directly underneath IPS; either the end of the upper branch of superior temporal sulcus or the end of the posterior branch of the Sylvian Fissure, depending on individual anatomy (see Cattaneo, Sandrini, & Schwarzbach, 2010). For EVC, we targeted the spot between the calcarine sulci of both hemispheres. Functional and anatomical brain imaging data were pre-processed and analyzed offline using BrainVoyager QX (Brain Innovation BV, Maastricht, The Netherlands). All three target locations are visualized on the template brain shown in Fig. 1(B) and average Talairach coordinates of all stimulation sites are reported in Table 1.
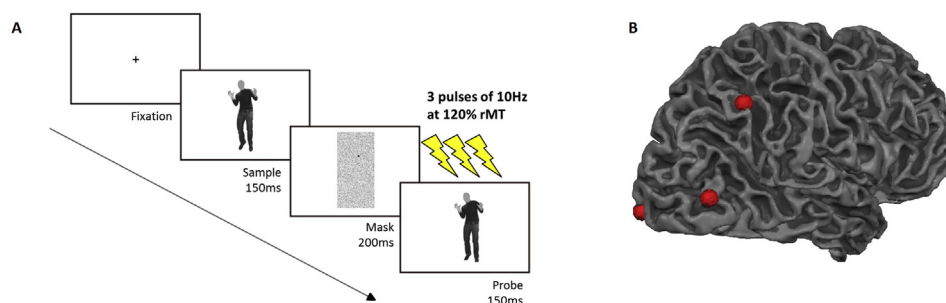
Fig. 1 – **An example of a timeline of the experimental trial procedure (A) and TMS target sites (B).**

2.3. Stimuli

Body stimuli were selected from a set of dynamic video clips showing the frontal view of four male actors jumping backwards with their hands forward (fearful body) or swinging their arms along the side of their trunk (neutral body). Two different frames were selected per actor for each condition. All faces were covered with a gray mask. The bodies were presented centrally on a gray background using a LCD monitor (resolution, 1920 × 1080) at an eye–screen distance of ~57 cm.

2.4. Task

A similar delayed-match-to-sample task was used as described in Candidi, Stienen, Aglioti, and de Gelder (2011), in which participants had to judge whether a sample stimulus matched a probe. Each trial showed either neutral or fearful bodies and the identity of the body was kept constant within a trial. The sample stimulus was presented for 150 msec, followed by the presentation of a 200 msec mask, after which the probe was shown for 150 msec (see Fig. 1(A) for an example trial). After the presentation of the probe, the participants had to give a response. The inter-trial interval was jittered around 7 sec. The Presentation software package (NeuroBehavioural Systems, Albany, CA) was used for stimulus presentation, recording of responses and triggering of the TMS pulses.

2.5. TMS stimulation and site localization

During the performance of the task, online triplets of TMS pulses with a 100 msec interval were delivered at 120% resting motor threshold (mean stimulation intensity 39% MSO) using a MC-B70 figure-of-eight coil and Magpro X100 stimulator (Medtronic Functional Diagnostics A/S, Skovlunde, Denmark). Onset of TMS pulses coincided with the appearance of the probe stimulus, so that the period of stimulation overlapped with previously found critical points of body processing for

each of the stimulation sites: EBA at 100–110 msec (Pitcher et al., 2012), V1 70–140 msec (Filmer & Monsell, 2013) and IPL 80–110 msec post stimulus onset (Meeren, Hadjikani, Ahlfors, Hämäläinen, & de Gelder, 2014). For the stimulation of IPL, the coil was positioned with the handle pointing backward and outward at a 45° angle from the mid-sagittal axis. For the stimulation of EBA, the coil was positioned with the handle pointing backward and inward and medially at a 45° angle from the mid-sagittal axis. During the stimulation of bilateral EVC, the coil was positioned with the handle pointing upward aligned with the mid-sagittal axis. During the sham stimulation the coil was positioned roughly in-between the other three stimulation sites, with the coil tilted so that no real stimulation was applied. For each stimulation condition, the coil was fixed in a coil holder for the entire duration of the run.

2.6. Procedure

Participants came in for a two-hour TMS session in which all four stimulation sites were tested. First, a 32 trial practice of the delayed-match-to-sample task was performed to ensure above chance level performance. After the participant was comfortable with the task, motor threshold was established by moving the coil over primary motor cortex until an optimal position was found for eliciting muscle twitches in the hand muscles. After this, the stimulation intensity was decreased until a threshold was found at which 5 out of 10 pulses still evoked a motor response at rest. Next, the correct coil location on the scalp was determined for each stimulation site by using the BrainVoyager TMS Neuronavigator system (Brain Innovation, Maastricht, The Netherlands). The anatomical and functional data acquired during the fMRI session were imported into the neuro-navigation software and used for stereotaxic co-registration of the participant's brain with the TMS coil, allowing for online coil positioning. For each stimulation site, the participant performed 64 trials of the task (32 fear trials and 32 neutral trials). The order of stimulation sites and sham stimulation were randomized for each participant.

2.7. Analysis

The dependent variable in this experiment is accuracy in detecting a postural change between sample and probe. As a measure of how sensitive the participant was to detection of the signal from the noise, i.e. the detection of postural change,

Table 1 – **Average Talairach coordinates per stimulation site ± standard deviation.**

Talairach coordinates	EBA	IPL	EVC
x	47 ± 3	42 ± 6	0 ± 3
y	−72 ± 6	−54 ± 4	−90 ± 1
z	1 ± 5	48 ± 4	−7 ± 5

we calculated d', an unbiased measure of performance accuracy. D' is normally calculated by subtracting transformed hit (H) and false alarm rates (FA). A d' of 0 reflects the inability of the participant to correctly identify postural change. To correct for ceiling effects, a corrected hit rate (H') and false alarm rate (FA') were calculated, as proposed by Snodgrass and Corwin (1988), using the following formulas:

$$H' = (h + 0.5)/(h + m + 1)$$

$$FA' = (fa + 0.5)/(fa + cr + 1)$$

where h is the number of hits, m is the number of misses, fa is the number of false alarms and cr is the number of correct rejections (Candidi et al., 2011; Snodgrass & Corwin, 1988; Tamietto, Geminiani, Genero, & de Gelder, 2007).

To ensure that possible differences between the neutral and fear condition did not affect direct comparisons within a stimulation site, difference scores were calculated by subtracting individual d' sham scores per condition (fear/neutral) from each individual d' score per stimulation site and condition.

A repeated measures ANOVA was performed on difference scores with condition (fear/neutral) and stimulation site (EBA/IPL/EVC) as within subject factors. Before calculation of d', outliers were removed based on reaction times (RTs) that deviated more than 2.5 times the standard deviation from the mean within a subject per stimulation site and condition. Multivariate results (Pillai's trace) are reported.

It is important to control for possible differences in implied motion between the neutral and fear condition. To this end, a control experiment was run in an independent sample of 10 participants. They performed 64 trials of the task with the same parameters as the delayed-match-to-sample task, only they were asked to express in millimeters the difference in implied movement they perceived between the sample and the probe (see Fig. 2). Results indicated that there was no
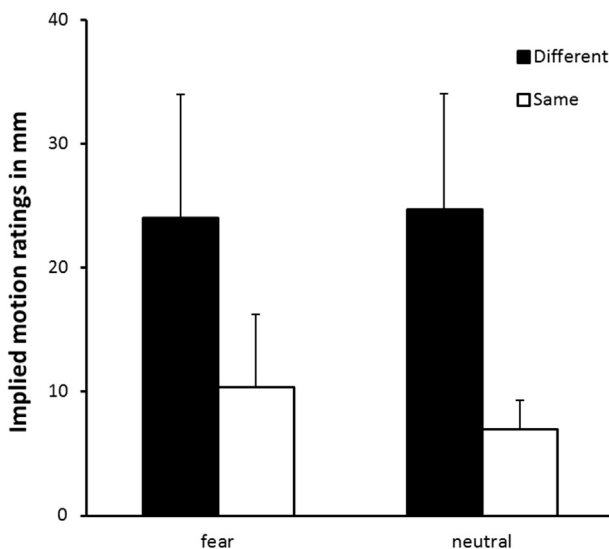
significant difference of implied motion between the neutral and fear condition ($p = .673$), but there was a significant difference between same and different stimuli ($p = .031$). Thus, participants subjectively noticed the change in posture, but importantly did not perceive more motion for fearful stimuli as compared to neutral stimuli.

To ensure that neutral and fear stimuli were identified as such, a validation experiment was performed in the same sample of participants from the control experiment just described. Each stimulus was presented for 150 msec and the participant had to indicate whether they thought the body posture was in a neutral or fearful posture. Average accuracy for the fear bodies was 96% and for the neutral bodies accuracy was 91%.

To rule out any influences of speed-accuracy trade off effects, an analysis on RTs was performed (see Table 2 for average RTs per condition). Results showed that there were no main effects of condition [$V = .023, F(1,17) = .402, p = .534$], stimulation site [$V = .212, F(3, 15) = 1.348, p = .296$], nor a significant interaction [$V = .259, F(3,15) = 1.747, p = .2$].

To see if TMS had any effects on response bias, criterion values were calculated by multiplying the sum of H' and FA' by $-.5$. Results of the analysis of the criterion values showed a main effect for condition [$V = .701, F(1, 17) = 39.767, p < .00$], reflecting a bias to answering 'same' in the fear condition. There was no main effect of stimulation site [$V = .034, F(3, 15) = .174, p = .912$], nor a condition × stimulation site interaction [$V = .235, F(3, 15) = 1.533, p = .247$], showing that TMS stimulation did not alter response bias.

A preliminary analysis was performed on raw $'d$ scores. Results of this analysis showed that there was no main effect for condition [$V = .052, F(1, 17) = .938, p = .346$]. There was, however, a main effect for stimulation site [$V = .464, F(3, 15) = 4.334, p = .022$], as well as a significant condition × stimulation site interaction [$V = .502, F(3,15) = 5.046, p = .013$]. Analysis of the sham conditions showed that there was no significant difference between the two conditions [$V = .053, F(1, 17) = .946, p = .344$], ruling out any possible differences in task difficulty between neutral and fear.

3. Results

In this experiment, participants performed a delayed-match-to-sample tasks on neutral versus fearful body postures, while receiving online TMS over either the IPL, the EBA, the EVC, or sham TMS. Results indicated a significant main effect for stimulation site [$V = .448, F(2, 16) = 6.492, p = .009$], as well as a significant condition (fear/neutral) × stimulation site (IPL/EBA/EVC) interaction [$V = .472, F(2, 16) = 7.152, p = .006$].

Based on the significant interaction effect, data were first split per stimulation site (EBA/IPL/EVC), to see how fear and neutral bodies differentially affect one of the stimulation sites. There was no significant main effect of condition in EBA [$V = .077, F(1, 17) = 1.421, p = .25$], IPL [$V = .083, F(1, 17) = 1.547, p = .231$] or EVC [$V = .068, F(1, 17) = 1.242, p = .281$].

To further disentangle the significant interaction effect, data were then split per condition (fear/neutral), to see how emotion can affect different nodes within the body processing network. The results of the analysis looking only at the fear

Fig. 2 — Implied motion measured in a separate sample of participants showed that the subjective experience of motion did not differ significantly between the fear and neutral conditions.

Table 2 – Raw d' and reaction time means $\pm$ standard error.

		EBA	IPL	EVC	Sham
d'	Fear	.84 ± .13	1.30 ± .15	1.01 ± .15	.98 ± .18
	Neutral	1.20 ± .11	1.26 ± .13	.95 ± .16	1.17 ± .14
RTs (msec)	Fear	950 ± 64	895 ± 54	903 ± 55	920 ± 53
	Neutral	934 ± 61	896 ± 60	916 ± 57	888 ± 51

condition showed that a significant main effect of stimulation site, V = .563, F(2, 16) = 10.298, p = .001. Bonferroni corrected post-hoc pairwise comparisons showed a significant differential effect of stimulation of EBA and IPL in the fear body condition (p = .001), but no such effect was apparent for comparisons between EBA and EVC (p = .67), or IPL and EVC (p = .133). To check for the direction of the effect of EBA and IPL in the fear body condition, one sampled t-tests were performed for EBA and IPL. The mean of EBA in the fear body condition did not significantly differ from 0, [t(17) = −1.018, p = .165], whereas for IPL there was a significant effect [t(17) = 2.6, p = .0095].

A repeated measures ANOVA, looking only at the neutral condition, showed a significant main effect of stimulation site, V = .323, F(2, 16) = 3.818, p = .044. Bonferroni corrected post-hoc pairwise comparisons showed a significant differential effect of stimulation of IPL and EVC (p = .035), but this effect was absent in the comparison between IPL and EBA (p = 1), or EBA and EVC (p = .351). One sample t-tests did not show a significant increase or decrease from 0 for either IPL [t(17) = .663, p = .258] or EVC [t(17) = −1.244, p = .115]. Statistical results of analysis of the difference scores are visualized in Fig. 3.
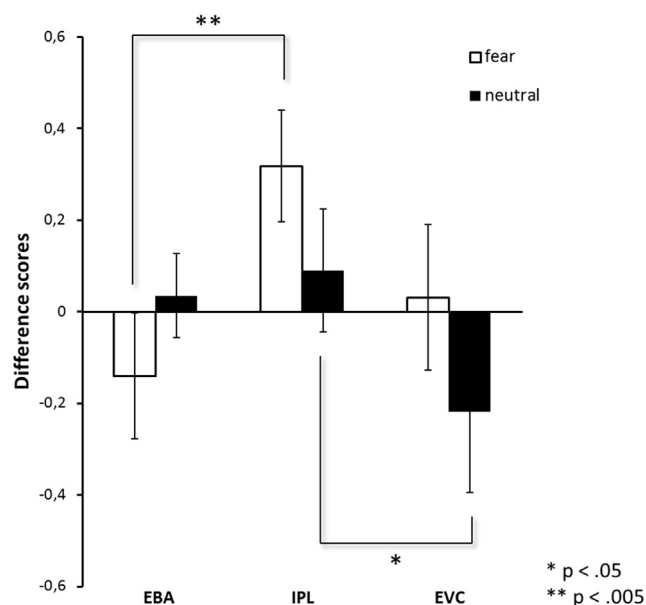

Fig. 3 – In the fear body condition, stimulation of IPL resulted in increased accuracy, as expressed in difference scores to sham, compared to stimulation of EBA. In the neutral body condition, stimulation of EVC resulted in a decrease of accuracy.

These results demonstrate that the IPL is causally engaged in emotion body processing, whereas the selective disruption of neutral body processing after EVC stimulation demonstrates that emotional information from fear bodies can still be processed independent of EVC.

4. Discussion

The goal of the current study was to dissociate the causal roles of dorsal stream (IPL), ventral stream (EBA) and EVC using online TMS, while participants had to detect subtle posture changes of bodies that either expressed fear, or were in a neutral position. Given the importance of efficient recognition and appropriate response to bodies conveying emotions, our hypothesis was that body emotion expressions are processed in the dorsal action stream, as assumed in the separate pathway models (de Gelder & Hadjikhani, 2006; Rudrauf et al., 2008; Tamietto & de Gelder, 2010; Zhan, Hortensius, & Gelder, in press). Therefore, in contrast to emotional bodies, perception of neutral bodies that do not necessitate action related processing, is more likely to engage the ventral processing stream. Perception of emotional content should thus not be affected by disruption of areas involved in perception of neutral bodies.

Consistent with this, we found that stimulation of IPL led to a significant increase in task accuracy compared to the condition in which EBA was stimulated, and importantly this effect was specific to the fear body condition. In direct contrast, stimulation of EVC led to decreased performance compared to IPL, specifically for the neutral body condition, while performance in the fear body condition remained unaffected.

4.1. The role of IPL in the processing of fearful bodies

As hypothesized, the observed TMS effect in IPL was specific to the fear condition. This critical role of IPL in emotion body processing is consistent with the literature on the functions of the parietal cortex. Neuroimaging experiments suggest the involvement of the parietal dorsal stream in the processing of emotions. It has, for example, been shown that both haptic and visual identification of the facial expression of emotions leads to activations in IPL (Kitada, Johnsrude, Kochiyama, & Lederman, 2010). Similarly, IPL activation was found for the rating of dynamic expressive faces versus rating of gender (Sarkheil, Goebel, Schneider, & Mathiak, 2013). Such findings have been extended by looking at activations specific for bodies expressing emotions. Kana and Travers (2012) found that in female participants the right IPL was significantly more activated for emotional bodies versus baseline, whereas male

participants showed greater activation in superior parietal lobule (SPL), while judging emotional bodies. Consistent with this idea, a recent MEG study has found early parietal activations in response to fearful bodies (Meeren et al., 2014). They directly compared perception of fearful and neutral bodies and found a significant cluster in right parietal cortex at 80—110 msec post stimulus onset.

Previously, Borgomaneri et al. (2012) showed that when neutral and emotional bodies were matched for implied motion, there was no difference between these two categories of stimuli in terms of their effects on motor cortex excitability. These findings raise the question whether with regard to the triggering of motor facilitation, it could rather be the implied motion that leads to previously observed effects of valence on motor excitability rather than emotional bodies by themselves (Borgomaneri et al., 2014; Hajcak et al., 2007; Van Loon, van den Wildenberg, van Stegeren, Hajcak, & Ridderinkhof, 2010). In the current experiment, implied motion was equal between neutral and fearful body conditions, and therefore the observed effect of IPL stimulation cannot be attributed to differences in implied motion alone.

Although we had no *a priori* expectation regarding the direction of TMS-induced behavioral changes, TMS is traditionally viewed as a virtual lesion approach, suggesting the expectation of a condition- and site-specific behavioral impairment. In contrast, we report here a condition- and site-specific behavioral improvement. For the empirical testing of the functional relevance of a given area, the direction of the induced behavioral change is irrelevant. While the exact workings of TMS are far from understood, it has been suggested that whether performance on a task is facilitated or inhibited by TMS depends on the baseline activity and thus, state of that specific area (Silvanto, Cattaneo, Battelli, & Pascual-Leone, 2008).

The current experiment has now provided causal evidence about the involvement of parietal cortex, and specifically IPL, in emotion body perception.

4.2.   Involvement of EVC in neutral body processing

Post-hoc tests looking at the neutral condition revealed a main effect for stimulation site, and the biggest modulation across sites was a decrease in performance with TMS over EVC. This suggests that TMS impaired neutral body processing when EVC was stimulated. However, since difference scores of EVC in the neutral condition did not significantly differ from 0, this observation should be regarded with caution.

A specific effect of EVC in the neutral condition would be in line with the experiment by Filmer and Monsell (2013). Their study used a TMS masking paradigm (for recent review see de Graaf, Koivisto, Jacobs, & Sack, 2014) and showed that TMS over V1 led to a selective impairment on categorical discrimination of neutral, but not threatening bodies. These results are in accord with the idea that geniculo-striate pathway is not essential for emotion recognition and that emotional information could still be accessed via a subcortical route via amygdala (LeDoux, 1996; Tamietto et al., 2012). Previous studies have explored the implications of V1 lesions on emotion processing. These studies have found that despite the lack of conscious awareness of a stimulus, information about the emotional state of the presented stimulus is still processed to a certain extent (de Gelder & Hadjikhani, 2006; de Gelder et al., 1999; Morris et al., 2001).

The results of EVC stimulation in the current experiment again hint at how emotion processing is possible independent of the geniculo-striate pathway, and are in direct contrast with the findings of stimulation of IPL, which selectively affected emotion body processing. This dissociation between EVC and IPL shows how emotion bodies can be processed in a specific non-geniculo-striate pathway, that can quickly relay emotion information to motor areas involved in action preparation. One possibility is that the information about an emotional body travels from superior colliculus directly to IPL (Clower et al., 2001). Based on current results, however, the possible involvement of extrastriate areas cannot be ruled out.

4.3.   Processing of neutral bodies in the ventral visual stream

In the current experiment, we did not find a significant change in performance in either the fearful or neutral body condition during stimulation of EBA. From the large subject sample and reliable localization procedure, this null result has some credibility (de Graaf & Sack, 2011) Moreover, it is consistent with other TMS studies using emotional body expressions (Candidi et al., 2011). In contrast, earlier studies using only neutral bodies showed that EBA played a role in body processing, as stimulation of EBA led to disrupted performance in a delayed-match-to-sample task (Pitcher et al., 2009, 2012; Urgesi et al., 2004; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). However, Urgesi et al. (2007) showed that in a delayed-match-to-sample task, rTMS to EBA only interfered with processing of inverted, and not upright bodies, suggesting that rather than whole body units, only processing of individual body parts occurs in EBA. Likewise, Urgesi, Candidi, Ionta, and Aglioti (2007) found that stimulation of EBA only interfered with morphological features of human bodies and not observed whole body actions. This could explain why in the current study no results were found after EBA stimulation, and is also in line with lesion studies showing deficits in processing of body parts, but not body actions (Moro et al., 2008).

The role of EBA in emotion processing is still unclear. Some neuroimaging studies have found activations in EBA in response to emotion body stimuli (e.g., Kret et al., 2011). However, a review by Downing and Peelen (2011) suggests that, rather than playing a role in emotion processing, previously found activations for emotion bodies are probably driven by attention and arousal rather than valence.

5.   Conclusion

Taken together, our results indicate that IPL is a central component in the processing route of emotion body expressions, consistent with the notion that seeing emotion body expression triggers action structures. This emotion processing takes place relatively independent of the visual representation of the body. Furthermore, this information may reach the

parietal cortex via subcortical to extrastriate areas, independent of early visual areas.

Acknowledgments

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