Dance and Emotion in Posterior Parietal Cortex: a low-frequency rTMS study.

Grosbras Marie-Hélène [1], Tan Haodan[2], Pollick Frank[2]

Institute of Neuroscience and Psychology ; School of Psychology University of Glasgow, UK

Corresponding author
MH Grosbras
Psychology
University of Glasgow
58 Hillhead street
G128QB Glasgow, Scotland, UK
Tel +44 141 330 5264
Fax +44 141 330 3666

Marie.grosbras@glasgow.ac.uk

Keywords: rTMS, emotion, dance, neuro-aesthetic, parietal cortex

Running title: Brain stimulation, dance and emotion

ABSTRACT

Background: The neural bases of emotion are most often studied using short non-natural stimuli and assessed using correlational methods. Here we use a brain perturbation approach to make causal inferences between brain activity and emotional reaction to a long segment of dance.

Objective/Hypothesis: We aimed to apply offline rTMS over the brain regions involved in subjective emotional ratings to explore whether this could change the appreciation of a dance performance.

Methods: We first used functional magnetic resonance imaging (fMRI) to identify regions correlated with fluctuating emotional rating during a 4-minutes dance performance, looking at both positive and negative correlation. Identified regions were further characterized using meta-data interrogation. Low frequency repetitive TMS was applied over the most important node in a different group of participants prior to them rating the same dance performance as in the fMRI session.

Results: FMRI revealed a negative correlation between subjective emotional judgment and activity in the right posterior parietal cortex. This region is commonly involved in cognitive tasks and not in emotional task. Parietal rTMS had no effect on the general affective response, but it significantly ($p<0.05$ using exact t-statistics) enhanced the rating of the moment eliciting the highest positive judgments.

Conclusion: These results establish a direct link between posterior parietal cortex activity and emotional reaction to dance. They can be interpreted in the framework of competition between resources allocated to emotion and resources allocated to cognitive functions. They highlight potential use of brain stimulation in neuro-æsthetic investigations.

INTRODUCTION

How we process emotion and how this interferes with other mental activities has long been a topic of intense research. To identify brain circuits important for emotion, brain imaging studies have looked at neural activity related to short stimuli designed to display and/or elicit particular, discrete emotions. In most everyday situations, however, our emotions are continuously fluctuating in relation to a continuously fluctuating environment. One way to study brain processing of emotion in a more naturalistic context is to use dance as stimulus. Indeed, dance by a combination of music and body movements conveys a variety of emotions that spectators can identify accurately and resonate with (e.g. 1;2). And actually, one of the main reasons for an audience to go and watch dance is to be moved as a result of exposure. Also, one important aspect of the dynamic nature of the emotions triggered by dance is that feelings build up and change in terms of their valence and arousal as a show unfolds (3). But not everyone responds identically to the same dance piece (4).

In the present study we aimed to relate brain activity to the subjective emotional response elicited by passively watching a piece of dance. The stimulus we used was a duet choreographed specifically as part of an interdisciplinary research project (www.watchingdance.org) with the endeavour to include different moments evoking different degrees of kinaesthetic empathy, as well as positive and negative emotions. We adopted a two-steps approach. Firstly, we used functional magnetic resonance imaging (fMRI) to identify brain regions whose activity correlates with the spectators' subjective perception of emotion. We asked participants to continuously rate their positive or negative emotional response on a linear analogue scale, using a slider. This procedure has the advantage over other standard methods such as Likert scales to maintain the stimulus uninterrupted. Thus it preserves the ecological value of the dance stimuli, while allowing us to relate ratings to specific moments in the dance. Secondly, we aimed at investigating whether altering brain activity could modify how we react to dance. Common sense observations as well as numerous scientific studies show that an altered mood can change emotional response to external stimuli and associated neural activity for instance in the amygdala (5,6). Likewise change in background brain activity also modulates emotional responses(7). However these correlational studies do not allow us to identify brain regions crucially responsible for emotional judgements. In contrast, non-invasive brain stimulation allows researchers to manipulate transiently neuronal activity in restricted brain circuits. Thereby they offer a tool to establish causal links between brain activity and behaviour. Thus, we might expect that modulating brain activity in regions engaged during the perception of high emotion moments in the dance might change the emotional engagements.

Regions classically involved in emotion processing, however, are difficult to reach with non-invasive brain stimulation. Indeed they comprise subcortical regions as well as the amygdala and orbitofrontal and ventral prefrontal regions (8). An alternative approach to considering those "affective" regions in isolation is to look at how they are linked to other brain networks such as those involved in cognitive control (fronto-parietal cortex and anterior cingulate; 9). Indeed cognitive control is altered under emotional context; while conversely cognitive activity can attenuate emotional processing. At the neural level, a range of studies evidence the intertwining between affective and cognitive brain circuits (review in 10). Using independent component analysis of meta-data coming from over 8000 published experiments, Laird and al (11) observed that several independent component networks emerged. Some of them were related to emotional processing with no link with reasoning functions, while other networks were related to cognitive or perceptual functions with no connectivity with emotion/interoception. This can be related to brain imaging data showing that when fronto-parietal cognitive control regions are active, affective regions are less active and *vice-versa* (12; 13).

Here, we were interested in identifying brain regions classically attributed to the affective or the cognitive brain networks that could be related to emotional effects of dance. With used fMRI to relate brain activity to the fluctuating subjective emotions while watching the dance piece. We then employed a perturbation approach targeting with transcranial magnetic stimulation (TMS) nodes identified in the fMRI study. We hypothesised that TMS should modulate the dynamic evaluation of the dance stimuli. More specifically it could be expected that inhibiting regions correlated to the strength of emotional judgement could reduce the range of ratings, while inhibiting circuits negatively correlated should increase it.

METHODS

Stimuli

The stimulus material was a contemporary dance with strong physical body movements, selected for its variability in emotional valence and intensity. The dance was performed by two professional dancers (one male and one female) on a dimly lit stage. Three different sound tracks played in succession: breathing sounds of the dancers, techno and classical music. Cameras recorded the dance performance from different angles, and the video was edited by a professional. The duration of the video was 3 minutes 38 seconds. It can be seen at http://www.watchingdance.org/research/Research%20activities_RK/index.php (2nd video)

FMRI scanning

The 16 healthy participants (8 Females, mean age 23) were naïve to the purpose of the study and had no experience in dance. The study was approved by the Ethics Committee of the Faculty of Information and Mathematical Sciences, University of Glasgow and subjects gave written informed consent before starting. Scanning was performed on 3Teslas-Tim Trio scanner equipped with a 32-channels head coil using integrated parallel imaging techniques (IPAT factor: 2). We acquired whole-brain echo-planar functional images (echo-time 30 ms TR 2sec, 3x3x3mm3 voxels) while participants passively watched, through a mirror, the dance video back-projected to a screen behind the scanner. Subsequently a high-resolution structural image was acquired with a 3D ultrafast gradient-echo sequence (ADNI_MPRAGE 1 mm^3 resolution) for spatial localisation of brain activity.

Emotion rating

After the scanning session, subjects were taken to another room and the dance video was re-shown to them. This time an analogue scale was displayed on the right side of the video while the dance was played. Participants were instructed to use the mouse to move a cursor on a vertical line in order to indicate their emotional response to the dance performance continuously as it unfolded. The upper part of the scale indicated positive emotional feelings and the lower part negative. The ratings ranged from -250 to +250 but only the zero point was shown in the middle of the slider. Subjects were instructed to make their ratings as close as possible, in accordance with their experience during scanning. Data was sampled at 33Hz. We chose to use retrospective emotion rating rather than online rating to avoid contaminating emotion responding during the first viewing with a concurrent task of analysing and summarizing this response on a scale. Research in social science, arts audience or psychology indicates the advantage of this approach and the validity of the *a posteriori* rating as a proxy of the initial experience (14, 15). For example Goldin and al (16) found that, when participants were asked to rate their emotional response to films twice, the correlation between the two time points was 0.95.

FMRI analysis and results

We performed two separate analyses. First to look at brain regions related to valence judgements we used the original data. Second to look at brain regions related to intensity judgement, i.e. high or low emotional engagement either positive or negative, we used the absolute values of the ratings. In both cases the time-series were normalized into Zscore and resampled to 2-seconds time-bins (using Matlab signal processing toolbox) to match the fMRI time-series, and then used individually as regressors in the analysis of brain imaging data. After standard preprocessing of the brain images (motion correction, spatial smoothing slow drift correction in Fsl software package) individual models were estimated in a voxel-based regression analysis where individual regressors were convolved with a gamma function (17). Those parameter estimates maps were transformed into MNI space using FLIRT (18) and entered into a mixed-model second-level group analysis using FLAME stage 1 with automatic outlier detection (19). Statistic maps were thresholded using clusters determined by Z>2.3 and a (corrected) cluster significance threshold of P=0.05 (20). We looked at both positive and negative correlations.

In the "valence" analysis, we observed no significant positive correlation. We observed significant negative correlation in bilateral occipito-temporal (MNI coordinates at maximum: *x*=49 *y*=-72 z=5, *z*=-5 Z= 4.78; x=-20 y=-100 z=-8 Z=4.68) and fusiform cortex (*x*=42 *y*=-66 *z*=-14 ;Z=4.14). In the "intensity" analysis (absolute value of rating used as predictors), we observed positive correlation in visual cortex only (*x=14 y* =-96 *z*= 8; Z=4.12; *x=-10 y* =-96 *z*= 8; Z=3.76). Negative correlation was observed in occipito-temporal and fusiform cortex (*x=-30 y* =-58 *z*= -16; Z=3.78; *x*=40 *y*=-66 *z*=-14 Z=3.62); as well as in the right parietal cortex (max *x*=26 *y*=-56 *z*=42 Z= 3.05; See Figure 1B). Utilizing a threshold of p<0.001 uncorrected, without cluster threshold, additionally revealed a peak in the left parietal cortex and in the right dorsolateral prefrontal cortex (*x*=28 *y*=10 *z*=58) and a bilateral precentral region probably corresponding to frontal eye fields.

Analysis of the parietal peak

The significant negative correlation between subjective affective ratings and activity in the posterior parietal cortex is reminiscent of reports of decreased activity in "cognitive-control" regions during emotional perception (see introduction, 12; 21). We thus characterized this region further using meta-analytical tools. We searched the Brain Map database (22) for experiments reporting activation in a 1000 mm^3

region around the peak (*x*=26 *y*=-56 *z*=42). This database archives a large number of brain-imaging results in the form of 3D standard coordinates alongside metadata such as subjects, tasks, experimental parameters. It contains over 10000 experiments classified into 83 paradigm-classes regrouped into five domains: Cognition, Emotion, Action, Perception, Interoception (see http://brainmap.org/scribe/index.html) . Our search revealed 259 experiments: the majority of them (64 %) belonged to the Cognition domain, 15% to Action, 28 % to Perception and 2 % to the Emotion domain. The most represented task was the n-back task, a paradigm that assesses working memory and accounted for 24 experiments (see Figure 1C). Thus this confirms that this region, which is more active when the subjects feel neutral emotionally than when they feel engaged positively or negatively, belongs to the "cognitive" brain network and not the "affective" one.

[PLEASE INSERT FIGURE 1 ABOUT HERE]

TMS experiment

Eighteen different healthy participants (8 Female, average age 28.7 +/- 10 SD) took part in this experiment. All reported having no experience in practicing dance and watched dance only in rare occasions. Each participated in two TMS sessions, one for parietal TMS and one for a control TMS (vertex stimulation), with the order counterbalanced across participants. Both sessions took place on the same day separated by at least 40 minutes. First we identified the targets for TMS using frameless stereotaxy (Brainsight, Rogue Research inc). The standard coordinates identified in the fMRI experiment (*x*=26 *y*=-56 *z*=42) were converted into each individual's MRI native space using FLIRT. Then we applied TMS for 15 minutes at 60% of maximum stimulator output, while continuously monitoring coil position and eventually adjusting it. Stimulation was delivered by a Magstim rapid-2 stimulator (Dyfed, Wales) through a 7-cm diameter figure-of-eight coil. Participants wore commercial earplugs to protect their hearing.

After the stimulation, subjects moved to a nearby desk and completed the judgement task in the same way as described for the fMRI experiment. First they practiced for one minute on an unrelated dance video. This practice ensured that they understood the task. Also experiments in motor cortex have shown that sometimes effects of stimulation are stronger a few minutes after the end of the TMS session (e.g 23).

Immediately after, they filled a short questionnaire asking to rate, on 5-points Likert scales, their present emotional states and to which extent it was related to the dance movements or to the music. In addition we asked them to explain briefly what they had judged the most positive and the most negative and why.

Analyis of TMS session data.

We employed methods commonly used to analyse continuous ratings (15).

(i) Analysis of the entire rating.

We computed the mean and standard deviations of the individual time-series and compared those for the control and the parietal TMS conditions. Increase in mean would reveal globally more positive judgement. Increase in variance would indicate that an individual tend to use more extreme points of the scale, while a decrease in variance will indicate more constant emotion. To assess changes absolute intensity we repeated the same analysis on rectified time series.

In addition we computed the “Emotional Bandwith” , an entropy measure derived from information theory which quantifies the informational complexity of ratings. It is equivalent to measuring the number of levels effectively utilized on the rating scale. Increase in entropy would reveal globally higher emotional response. As described in Lottridge and Chignell (24), we divided the entire rating scale (-250 250) into 50 bins of 10 points. For each of this bin we computed the proportion rating points falling into this bin and multiplied it by its neperian logarithm.

Entropy $= - \Sigma\, p(x_i) \log_2 p(x_i)$; Emotional Bandwidth = 2^{entropy}

Increase in emotional bandwidth will indicate increase in the emotional engagement with the stimulus.

We ran a separate analysis of variance for each of these measures (mean, variance and emotional bandwith) to compare their values in the two TMS conditions (repeated factor). To take into account the effect of exposure we also added a between-subject factor to compare the TMS effect in the group of participants who received parietal TMS first with those who had control TMS first.

Time-wise analysis

Finally, to test whether TMS had an effect at any specific moment of the dance, we adapted analyses used in event-related electroencephalography (26). First, to smooth the data and limit computation, we resampled data into 722 time-points (using Matlab resample function with decimation by factor 10). Then, at each time-point, we calculated the difference between judgement in the control condition and judgement in the parietal-TMS condition in each participant and then we computed a paired t-test across the eighteen participants. To assess at which time points the t-value was significantly different from 0, we built a distribution of t-statistics by randomly permuting the sign of the t-values (under the null hypothesis the values obtained for each subject are interchangeable and thus the sign of the difference is also changeable). For each permutation we extracted the maximal t-value (Tmax) across the time-series. We built a distribution of Tmax for 10000 permutations. To conduct two-tail tests while controlling for multiple comparisons we determined the t-values that cut the Tmax distribution at 0.025 on each tail and compared each of the 722 values of the original t-test to these values to determine significance at $p<0.05$. In addition we repeated the procedure to compare the groups of participants who had parietal TMS in the first or second session and assessed whether the effects qualified as significant were higher than those due to multiple exposures.

Results:

Data from two participants had to be excluded due to technical errors during rating-data recording. Rating data in the TMS experiment are thus reported for sixteen participants (8 females).

Ratings.

As can be seen on figures 1 and 2A, the ratings obtained in the group of participants in the fMRI experiment and those obtained in the group of TMS participants were alike. Despite some interindividual variability, a general pattern emerged with globally the first half being linked to negative emotion and the second half to positive emotion, with higher ratings on the positive side of the scale. In the average and in most individual participants, clear transitions could be observed at the moment of the changes in music.

Effect of TMS on global measures:

We observed no effect of TMS condition on the global average or variance of raw data, nor global average of absolute data, nor emotional bandwith (paired t-tests all $p>0.3$). There was also no effect of order of viewing nor interaction between TMS condition and order.

Time-specific analysis:

This is displayed on Figure2. We identified only one segment for which the emotional judgement significantly differed after parietal compared to control TMS, independently of stimulation order: the positive judgement occurring in the last third of the dance-video was rated as eliciting more positive emotion after parietal TMS. It is in this part of the dance-video that the music changes to classical music.

Questionnaires analysis

We observed no difference between the mood ratings between the two sessions (related-samples Wilcoxon signed ranks test, $p>0.256$). Also subjects did not change their judgement of how the music ($p=1$) , the movement ($p>0.29$) or the dance in general ($p>0.40$) influenced how they felt. The analysis of the open questions asking them what in the dance made them feel positive or negative revealed recurring references to the music, to the interaction between the two dancers and to the synchronicity between movement and music or fluidity of the dance. Those were different between the two conditions, however. Music was reported as a determining factor by half of the participants indifferently in both TMS conditions. Interaction was mentioned by 10 participants in the control condition and 13 in the parietal TMS condition (χ^2 =2.025, P>0.15). In contrast synchronicity or fluidity of movement and music was mentioned significantly more often after the parietal stimulation (13/18=73% against 6/18= 33% in the control condition, χ^2=12.25, p<0.001). Thus, after parietal rTMS, participants attributed their subjective ratings more to the perceived harmony between movement and music.

[PLEASE INSERT FIGURE 2 ABOUT HERE]

DISCUSSION

Using fMRI we identified a region in the right posterior parietal cortex whose activity was negatively correlated with the dynamic emotional reactions of participants while they watched a dance video. Our main finding is that modulating this brain region artificially, by means of offline non-invasive brain stimulation, changed the subjective emotion rating for specific moments in the dance. We discuss this result in relation to the role of the parietal cortex in the interaction between perception, cognition and emotion. We also discuss more generally the advantages of using naturalistic stimuli in Cognitive Neuroscience as well as potential applications of non-invasive brain stimulation in the field of neuro-aesthetic.

Parietal TMS and subjective emotion perception in dance.

Most brain-stimulation studies of emotion focus on the prefrontal cortex: A wealth of fundamental and clinical investigations has demonstrated that changing the excitability of the dorsolateral prefrontal cortex improves mood and depression symptoms (rev. in 27; 28). TMS over the medial prefrontal cortex has also been shown to impair processing of negative facial expressions (29; 30) and TMS over the inferior frontal cortex impairs emotional prosody perception (31). Those studies in general consider emotion processing in isolation of other functions. Yet a growing number of theoretical and empirical work points towards the intertwined neural control of emotion and cognition (9). While in specific contexts, like in presence of threatening stimuli, emotion and executive control can enhance each other so as to focus resources on reaction, in other contexts both range of processes can compete. In particular, seminal (12) and more recent (e.g. 21; 13) studies evidence an interaction between regions involved in executive or cognitive control (dorso-lateral prefrontal cortex, dorsal anterior cingulate, parietal cortex) and regions involved in emotion processing and perception (amygdala, rostral anterior cingulate, orbito-frontal cortex), such that the former are less active when the latter are engaged and *vice versa*. This also illustrates the interest of looking at "de-activation" or negative correlation when exploring functional networks with brain imaging (32). We set the present study in this framework and, guided by our fMRI results, focused on one particular node of the executive control brain network located in the posterior parietal cortex. Interrogating the BrainMap database confirmed that the region we identified and targeted with TMS belongs to a network reliably activated during mental processes required in working memory, verb generation, response selection or high-level visuo-spatial tasks. Previous brain stimulation studies have also shown that interfering with this region impairs cognitive tasks such as working memory (33; 34). On the other hand, enhancing the activity of this and adjacent brain areas by cathodal transcranial direct current stimulation can improve cognitive functions such as numerical learning (35). We are not aware of any brain stimulation study having investigated the role of posterior parietal cortex in emotion processing. Our results are in line with the competition model outlined above, which suggests that a disruption of this parietal region involved in cognitive control, will “free” resources for emotional processing. In other words, inhibiting the parieto-frontal executive control system could reduce the more cognitive processing of the dance watched (such as expectancies, judgement of the quality of movement, action observation mechanisms) and thereby exacerbate more automatic emotional evaluation. This in turn could explain the higher ratings we observed after parietal rTMS.

Our data, however, don’t show a general effect on emotion during watching dance: the mean ratings over the entire performance were similar across the two TMS conditions, as was the number of periods rated as eliciting positive or negative emotion or the range of emotional rating used. This was further corroborated by the questionnaire data, which did not reveal any significant different affective judgement between parietal and control TMS. Thus unlike rTMS of dorso-lateral prefrontal cortex, rTMS of the right posterior parietal cortex doesn’t seem to influence general affect or mood.

In contrast we observed an effect specific to the aspects of dance that were rated as triggering the highest (positive) feeling: following parietal rTMS, they were rated as even more positive. This indicates that the reaction to events triggering positive emotion can be enhanced when the right posterior parietal cortex is less active, suggesting more sensitivity to emotional context. Facilitation resulting from disinhibiting interactions between different processes through TMS has been described in a variety of situations: for instance aspects of visuo-spatial attention can be facilitated with TMS (rev in 36); Mullin and al (37) recently showed that rTMS applied over the lateral occipital cortex impaired object categorization but facilitated scene detection. Our result thus adds to this body of experiments that indicate indirect release of resources by using inhibitory brain stimulation; It also shows a context-specific effect of TMS (38). Indeed, the effect was observed for the positive segments of the dance only. This could be related to the approach/avoidance model of emotion representation in the brain, which posits that both kinds of emotion are processed by evolutionary distinct brain circuits (10). Interestingly a recent study showed that rTMS of another regions important for action perception, the posterior superior temporal cortex, had facilitatory effect of emotional body postures perception, but for threatening stimuli (44).

Possible link with parietal sensory representation functions.

In addition to its involvement in executive function, the posterior parietal cortex has been repeatedly related to higher perceptual functions linked to action control, like intersensory integration (39 ;40), and own and others body representation (45,46). Thus, alternatively, the specific change we observe could reflect an effect on these other functions which in turn would alter emotion perception. First rTMS on the parietal cortex could affect the perception of synchronisation of dance and music. This is suggested by the questionnaires where many participants mentioned the perception of fluid movements well synchronised to music as determinant for their affective reaction. The neural noise induced by rTMS may have increased the threshold for dyssynchrony perception and thereby increased the fluidity perception resulting in enhanced positive feelings. Further, more focused, experiments should be designed to explore this possibility.

Along the same line of reasoning one could also argue that the effect on emotion is the consequence of an effect on body perception. This is suggested by the qualitative questionnaires that indicate that moments perceived as more negative looks like exercise or difficult movements to execute. Maybe adding noise to the body schema representation may help a more aesthetic and less physical effect of the dance in those inexperienced spectators. It would be interesting to conduct experiments to test this hypothesis.

In sum, our data highlight the key role of the posterior parietal cortex mediating emotional perception, which is in line with the functions of this region in integrating various sensory and representational and action signals.

Emotion, art and the brain: non-invasive brain stimulation and neuroaesthetic.

Our study further demonstrates that neuroscience methods can be applied to dance study and therefore adds to the corpus of neuro-aesthetic research, which explores the relationships between art and the brain (41). A previous study has shown that aesthetic preference for dance postures could be diminished after rTMS of body-sensitive extrastriate cortex and enhanced after rTMS of the ventral premotor cortex, a region involved in action perception and execution (42). Also the focus is slightly different in their and our study (aesthetic judgement *vs* emotional judgement), as well as the stimuli (discrete *vs* continuous), both converge in showing that modulation in brain activity can alter subjective appreciation of art. Our study also illustrates the benefit in combining different approaches, namely continuous ratings, functional MRI, meta-analysis, and brain stimulation to address complex interdisciplinary questions experimentally.

More generally this exemplifies how non-invasive brain stimulation can be applied in interdisciplinary research (43). Contrary to other brain imaging studies that have been used in neuro-aesthetic investigations, brain stimulation allows us to draw causal inferences between the functional integrity of specific brain regions and the way spectators react to art. These forms of experiments can serve as bases for building new bridges between scientists and choreographers; they can help understanding what emotional messages are conveyed by dance and how they are perceived.

Conclusion

In conclusion, our data show that rTMS applied over the right posterior parietal cortex enhance positive judgement of the dance segments that elicit the most positive emotions, without changing the general mood of participants. Perhaps positive valence stimuli are perceived as more intense when we don't think about them. Further studies are ongoing to explore the roles of cognitive processes and emotional processes in watching dance. Ultimately this has implications for understanding emotion regulation as well as emotional reaction to art.

Acknowledgements.

This work was supported by a research grant from the UK Arts and Humanities research council (AHRC AH/F011229/1).

We thank Corinne Jola, Phil McAleer, Matthew Reason, Dee Reynolds and Larissa Szymaneck for their help in designing or conducting the experiment, as well as the Rosie Kay Dance Company (www.rosiekay.co.uk) and Ilka Schulz for stimuli production.

Figures Legends

Figure 1: ***FMRI results.*** A) Averaged ratings (Zscores; n=16) +/- standard error over the 218 seconds of the dance video. B) Brain regions showing significant correlation between absolute values of emotional ratings and brain activity. Note that individual correlation maps were computed with individual ratings and not the average rating; the maps were then averaged across the 16 participants. Red color map: positive correlations; green: negative correlations. The site of TMS is indicated by a pink arrow. C) BrainMap database interrogation results: Color code indicates BrainMap paradigms domains: Red= action; orange= cognition; yellow= emotion; blank= interoception; blue=perception.

Figure 2: ***TMS results***: averaged (n=16) Zscored ratings after parietal (red) or control (green) rTMS +/- standard errors and paired t-statistic (cyan) computed at each time points between the two time-series Horizontal lines represent the threshold t-value (dotted line) or exact threshold t-value (plain line) for $p<0.05$. Grey area represents regions of the curve showing statistical significance using non-corrected (light grey) or exact t-test (darker grey).

References

1. MacFarlane L, Kulka I, F.E.Pollick p-. The representation of affect revealed by Butoh dance. Psychologia. 2004;47(2):7.

2. Boone RT, Cunningham JG. Children's decoding of emotion in expressive body movement: the development of cue attunement. DevPsychol. 1998;34(5):1007-16.

3. Jola C, Reason M, Grosbras M, F. E. Pollick. Audiences' neurophysiological correlates to watching a narrative dance performance of 2.5 hrs. Dance research electronic. 2012.

4. Reason M, Reynolds D. 'Kinesthesia, Empathy and Related Pleasures: An Inquiry into Audience Experiences of Watching Dance'. Dance Research Journal 2010;42(2):26.

5. Fruhholz S, W.M Prinz, Herrmann M. Affect-related personality traits and contextual interference processing during perception of facial affect. Neurosci Lett.. 2010;469(2):260-4.

6. Etkin A. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. Neuron. 2004;44(6):1043-55.

7. Bishop SJ, Duncan J, Lawrence AD. State anxiety modulation of the amygdala response to unattended threat-related stimuli. J Neurosci. 2004 17;24(46):10364-8.

8. Fusar-Poli P, Placentino A, Carletti F, Landi P, Allen P, Surguladze S, et al. Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. J Psychiatry Neurosci. 2009;34(6):418-32.

9. Pessoa L. On the relationship between emotion and cognition. Nat Rev Neurosci. 2008;9(2):148-58.

10. Pessoa L. Emergent processes in cognitive-emotional interactions. Dialogues Clin Neurosci. 2010;12(4):433-48.

11. Laird AR, Fox PM, Eickhoff SB, Turner JA, Ray KL, McKay DR, et al. Behavioral interpretations of intrinsic connectivity networks. J Cogn Neurosci. 2011;23(12):4022-37.

12. Drevets WC, Raichle ME. Suppression of Regional Cerebral Blood during Emotional versus Higher Cognitive Implications for Interactions between Emotion and Cognition. Cognition & Emotion. 1998;12(3):32.

13. Mitchell DG, Luo Q, Mondillo K, Vythilingam M, Finger EC, Blair RJ. The interference of operant task performance by emotional distracters: an antagonistic relationship between the amygdala and frontoparietal cortices. Neuroimage. 2008 ;40(2):859-68.

14. Gottman J, Levenson R. A valid procedure for obtaining self- report of affect in marital interaction. Journal of Consulting and Clinical Psychology. 1985;53:9.

15. Ruef AM, Levenson RW. Continuous measurement of emotion. In: Coan JA, Allen JJB, editors. The handbook of emotion elicitation and assessment. New York: Oxford University Press. 2007. p. 286-97.

16. Goldin PR, Hutcherson CA, Ochsner KN, Glover GH, Gabrieli JD, Gross JJ. The neural bases of amusement and sadness: a comparison of block contrast and subject-specific emotion intensity regression approaches. Neuroimage. 2005 1;27(1):26-36.

17. Woolrich MW, Ripley BD, Brady M, Smith SM. Temporal autocorrelation in univariate linear modeling of FMRI data. Neuroimage. 2001 Dec;14(6):1370-86.

18. Jenkinson M, Bannister P, Brady M, Smith S. Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage. 2002;17(2):825-41.

19. Woolrich M. Robust group analysis using outlier inference. Neuroimage. 2008;41(2):286-301.

20. Worsley KJ. An improved theoretical P value for SPMs based on discrete local maxima. Neuroimage. 2005;28(4):1056-62.

21. Greene JD, Sommerville RB, Nystrom LE, Darley JM, Cohen JD. An fMRI investigation of emotional engagement in moral judgment. Science. 2001 14;293(5537):2105-8.

22. Fox PT, Laird AR, Fox SP, Fox PM, Uecker AM, Crank M, et al. BrainMap taxonomy of experimental design: description and evaluation. Hum Brain Mapp. 2005;25(1):185-98.

23. Chouinard PA, Van Der Werf YD, Leonard G, Paus T. Modulating neural networks with transcranial magnetic stimulation applied over the dorsal premotor and primary motor cortices. J Neurophysiol. 2003;90(2):1071-83.

24. Lottridge D, Chignell M, editors. Emotional Bandwidth: Information Theory Analysis of Affective Response Ratings Using a Continuous Slider. 12th IFIP TC13 Conference on Human-Computer Interaction INTERACT; 2009.

25. Levenson RW, Gottman JM. Marital interaction: Physiological linkage and affective exchange. Journal of Personality and Social Psychology. 1983;45(3):10.

26. Blair RC, Karniski W. An alternative method for significance testing of waveform difference potentials. Psychophysiology. 1993;30(5):518-24.

27. Barrett J, Della-Maggiore V, Chouinard PA, Paus T. Mechanisms of action underlying the effect of repetitive transcranial magnetic stimulation on mood: behavioral and brain imaging studies. Neuropsychopharmacology. 2004;29(6):1172-89.

28. Georges MS, Lisanby SH, Sackeim HA. Transcranial Magnetic Stimulation . Applications in Neuropsychiatrie. Arch Gen Psychiatry. 1999;56(161):300-11.

29. Harmer CJ, Thilo KV, Rothwell JC, Goodwin GM. Transcranial magnetic stimulation of medial-frontal cortex impairs the processing of angry facial expressions. Nat Neurosci. 2001;4(1):17-8.

30. Mattavelli G, Cattaneo Z, Papagno C. Transcranial magnetic stimulation of medial prefrontal cortex modulates face expressions processing in a priming task. Neuropsychologia. 2011;49(5):992-8.

31. Hoekert M, Vingerhoets G, Aleman A. Results of a pilot study on the involvement of bilateral inferior frontal gyri in emotional prosody perception: an rTMS study. BMC Neurosci. 2010;11:93.

32. Raichle ME. Two views of brain function. Trends Cogn Sci. 2010 ;14(4):180-90.

33. Tseng P, Hsu TY, Muggleton NG, Tzeng OJ, Hung DL, Juan CH. Posterior parietal cortex mediates encoding and maintenance processes in change blindness. Neuropsychologia. 2010;48(4):1063-70.

34. Prime SL, Vesia M, Crawford JD. Transcranial magnetic stimulation over posterior parietal cortex disrupts transsaccadic memory of multiple objects. J Neurosci. 2008;28(27):6938-49.

35. Cohen Kadosh R, Soskic S, Iuculano T, Kanai R, Walsh V. Modulating neuronal activity produces specific and long-lasting changes in numerical competence. Curr Biol. 2010;20(22):2016-20.

36. Fecteau S, Pascual-Leone A, Theoret H. Paradoxical facilitation of attention in healthy humans. Behav Neurol. 2006;17(3-4):159-62.

37. Mullin CR, Steeves JK. TMS to the lateral occipital cortex disrupts object processing but facilitates scene processing. J Cogn Neurosci. 2011;23(12):4174-84.

38. Ruff CC, Blankenburg F, Bjoertomt O, Bestmann S, Freeman E, Haynes JD, et al. Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. Curr Biol. 2006;16(15):1479-88.

39. Molholm S, Sehatpour P, Mehta AD, Shpaner M, Gomez-Ramirez M, Ortigue S, et al. Audio-visual multisensory integration in superior parietal lobule revealed by human intracranial recordings. J Neurophysiol. 2006;96(2):721-9.

40. Pasalar S, Ro T, Beauchamp MS. TMS of posterior parietal cortex disrupts visual tactile multisensory integration. Eur J Neurosci. 2010 May;31(10):1783-90.

41. Zeki S. Inner Vision: an exploration of art and the brain. Oxford University Press; 1999.

42. Calvo-Merino B, Urgesi C, Orgs G, Aglioti SM, Haggard P. Extrastriate body area underlies aesthetic evaluation of body stimuli. Exp Brain Res. 2010;204(3):447-56.

43. Jola C, Abedian-Amiri A , Kuppuswamy A, Pollick FE, Grosbras, MH. Motor simulation without motor expertise: enhanced corticospinal excitability in visually experienced dance spectators. PlosOne 2012; *in press*

44 Candidi M, Stienen BM, Aglioti SM, de Gelder B. Event-related repetitive transcranial magnetic stimulation of posterior superior temporal sulcus improves the detection of threatening postural changes in human bodies. J Neurosci. 2011 Nov 30;31(48):17547-54.

45 Grosbras MH, Beaton S, Eickhoff SB. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis.Hum Brain Mapp. 2012 Feb;33(2):431-54.

46 Andersen RA, Snyder LH, Bradley DC, J. Xing Multimodal representation of space in the posterior parietal cortex and its use in planning movements Annual Review Neuroscience, 20 (1997), pp. 303–330

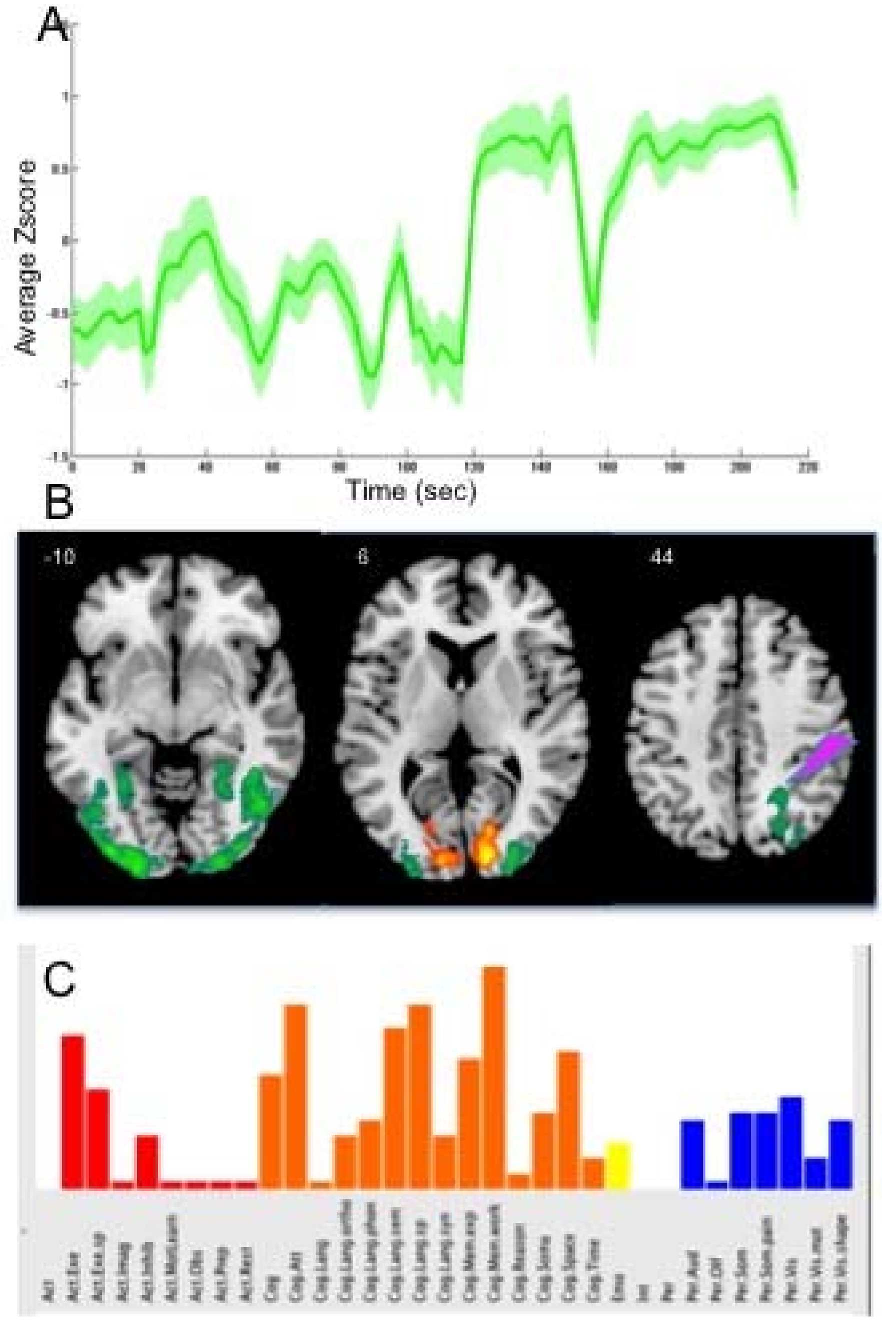

Figure1

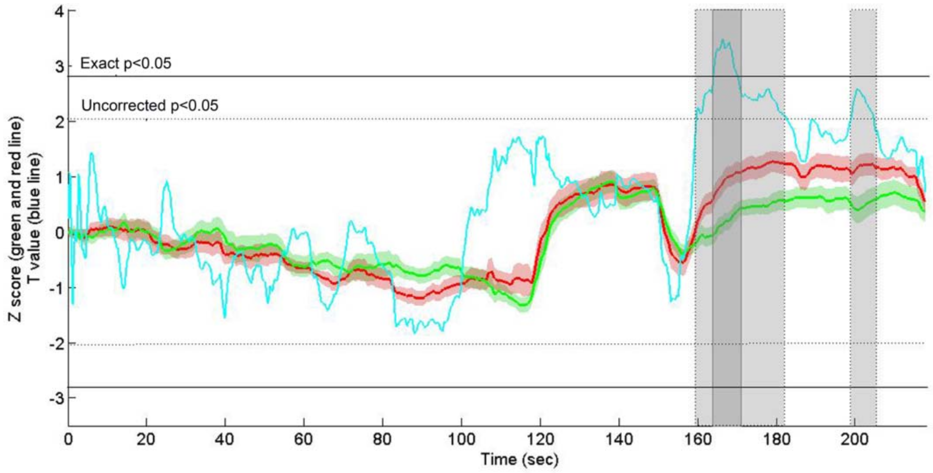
Exact p<0.05
Uncorrected p<0.05
Z score (green and red line)
T value (blue line)
Time (sec)
4
3
2
1
0
-1
-2
-3
0
20
40
60
80
100
120
140
160
180
200

Figure 2