RESEARCH PAPER

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The influence of mood on visual perception of neutral material

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In the study we investigated how current mood affects spontaneous perceptual processes of neutral stimuli of low-arousal, unrelated to any specific task. Two separate but similar procedures were carried out: one using functional magnetic resonance imaging (fMRI), the other using electroencephalography based source localization. In both experiments, sessions of passive viewing of neutral pictures were preceded by either a negative or positive mood induction. In response to neutral stimuli, we observed higher activation of visual areas after positive mood induction and lower activations in medial prefrontal and right frontotemporal regions after negative mood induction. We conclude that in relatively safe laboratory conditions, after being exposed to negative emotional content, automatic processes of affective control are recruited by the prefrontal cortex. This results in attenuation of processing of incoming stimuli, as the stimuli do not carry salient information with respect to bottom-up or top-down processes. The observed effects may therefore represent an implicit mechanism of perceptual modulation.

Key words: mood, visual perception, sensory modulation, fMRI, EEG

INTRODUCTION

The influence of emotional states on various cognitive functions including perception, reasoning, executive functions, and responding is well-known (Brzezicka 2013, Mincic 2010, Mitchell and Phillips 2007). Numerous behavioral studies show the impact of current mood on visual perception, including modulation of sensory processing and changes in attentional characteristics. Several reports suggest that anxiety and tension affect the recognition of negative content, with lower thresholds for detecting and recognizing negative stimuli (Bishop et al. 2004, Pessoa 2005). Other studies focus on changes in spatial characteristics of visual perception, which shift from local to more global modes of processing in positive mood states. Positive affective states simultaneously broaden the attentional scope and affect visual selective attention (Fredrickson and Branigan 2005, Rowe et al. 2007). In contrast, negative mood is thought to narrow the field of attention compared to a neutral baseline (Gasper and Clore 2002, Schmitz et al. 2009). From an evolutionary perspective, such perceptual tuning of the visual system may allow for more efficient utilization of limited processing resources.

Importantly however, little research goes beyond behavioral data and uses neuroimaging techniques to examine the neural mechanisms underlying mood-related modulation of perception. Further, few reports consider the effects of mood on spatial characteristics of attention, which are evident in the early stages of attentional processing. For example, the evoked C1 component, which originates in the primary visual cortex (V1), is higher in response to task-irrelevant, peripheral stimuli during positive mood states (Vanlessen et al. 2013). This increase in response suggests that positive moods attenuate early spatial-encoding selectivity (Vanlessen et al. 2013). Similar effects of emotional state on early stages of processing during spatial attention were also shown by Rossi and Pour-

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tois (2012). In that study, the authors reported that the state of anxiety compromises the processing of peripheral stimuli. In another study using the Flanker task (Moriya and Nittono 2011), the authors found that early visual components (P1 and N1) were affected, but that the effects depended on the location of stimuli. In particular, in positive mood states, attentional focus was less oriented towards task-relevant parts of the visual field.

Importantly, the existing research focuses on task-irrelevant stimuli presented in the peripheral visual field. This is in contrast to the majority of our everyday experience in which perception is centrally located, and involves mostly neutral stimuli. The modulation of centrally located neutral stimuli by mood remains largely disregarded by scientific research. In a previous study by our group, we examined changes in network communication between brain structures involved in emotional processing of presented pictures. We demonstrated that emotional tension is associated with increased top-down influences from the dorsolateral cortex to both ventral and dorsal attentional systems, as well as to visual areas (Wyczesany et al. 2015). However, we lack data showing how current emotional state affects the depth of processing of relatively neutral stimuli — to which we are typically exposed in everyday situations. To our knowledge, there are no reports examining how the structures involved in perception are modulated by the subject's emotional state.

The apparent lack of neuroimaging data concerning mood-related changes in perceptual processes can be only partially supplemented by clinical research, in which involved subjects are characterized by permanent shifts in their baseline emotional state. The issue of processing of neutral stimuli has been investigated by Gmaj et al. (2016). In the study, patients with anxiety disorders exhibited increased activation in perceptual and attentional areas when viewing non-arousing content; this was reflected in higher event-related potential (ERP) components and Low Resolution Electromagnetic Tomography (LORETA) derived activation. Similarly, others studies have reported a general increase of the P1 component in patients with spider and social phobias in response to both aversive and neutral pictures, indicating tonic hypervigilance of the perceptual system (Kolassa et al. 2006, Michalowski et al. 2009). These findings suggest that anxiety adjusts the sensory system to a hypervigilant state, which results in enhanced processing of even non-emotional stimuli. Of note, the aforementioned studies have examined perception changes in clinical groups only. Changes observed in particular disorders may not generalize to mood-dependent processing modulations in healthy subjects.

The present study was designed to fill the existing gap in the literature on neural mechanisms of mood-related changes in processing of neutral stimuli of low and moderate arousal. Two complementary experiments were designed to investigate brain activation associated with watching neutral stimuli after positive and negative mood inductions. Importantly, two neuroimaging methods were used in order to verify the observed effect more thoroughly, and allowed us to benefit from the advantages offered by both. In the first procedure, functional magnetic resonance imaging (fMRI) was applied; in the second, electroencephalography (EEG) measurement and source localizing calculations were carried out.

We hypothesized that negative mood induction would be associated with a general increase in reactivity of the visual cortex, which would be manifested as higher occipital and occipito-temporal activations. Further, we hypothesized that this increase in processing within the visual stream would be observed primarily during early phases of information processing, prior to the full determination of meaning and motivational value of stimuli.

The present study may have important implications for the broader topic of modulation of sensory and attentional systems that adapt our perception according to the current situational needs. A broader framework of emotional regulation describes the mechanisms involved in implicit modulatory processes, which can either attenuate or boost the depth of perceptual processing (Wyczesany et al. 2015). In recent years, interest has grown in extending the concept of affective regulation to include both voluntary and involuntary processes (Gyurak et al. 2011). Within this theoretical framework, tuning perceptual processes according to the current requirements can be considered as a part of implicit modulatory processes, which are initiated by prefrontal centers of cognitive and emotional control. As such, our study allows one to test whether mood induction triggers processes that subsequently change the perceptual processing of incoming stimuli.

METHODS

Experiment 1 (fMRI)

Subjects

Eighteen female volunteers (mean age: 24.2 years, SD=3.3) were recruited by the university student recruitment system for participation in the experiment.

One person was subsequently excluded due to a technical problem in data recording. All subjects were right-handed, medication-free (excluding possible intake of oral contraceptives), and had normal or corrected-to-normal vision. No subjects reported history of any neurological or psychiatric disorders or substance abuse. Subjects received the equivalent of €20 for participation.

Procedure

Both experiments described in this report were compliant with the directives of the Helsinki Declaration (1975, revised 2000) and approved by the Ethical Committee of the Institute of Psychology, Jagiellonian University. Informed consent was obtained from all subjects.

The procedure comprised of four sessions which were intended to induce different emotional states (i.e., negative, NEG; positive, POS) in subjects by presenting emotional pictures, intermixed with neutral target pictures (see Fig. 1). The sequence of sessions was fixed: NEG, POS, NEG, POS. Sessions were separated by a 1 min break. The standardized pictures used as stimuli were chosen from the Nencki Affective Picture System (NAPS) database. Selection of POS, NEG, and neutral (NEU) slides was based on stimuli valence ratings, and selected stimuli were balanced in category (i.e., items, people, animals, landscapes, faces). Selected images for positive and negative images were matched on arousal. For each set, pictures were selected with the following parameters: NEG: n=42, mean valence=3.62 (SD=1.23), mean arousal=5.85 (SD=0.99); NEU: n=84, mean valence=5.06 (SD=0.57), mean arousal=4.72 (SD=0.38); POS: n=42, mean valence=7.81 (SD=0.42), mean arousal=5.76 (SD=0.85). Each session consisted of seven blocks, consisting of two trials each for a total of 56 trials. Each trial began with the presentation of three pictures

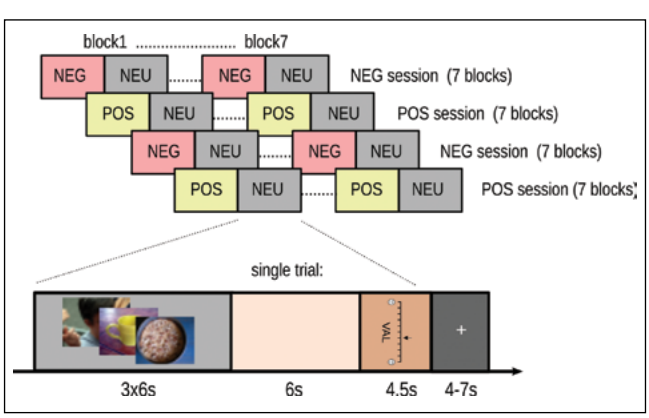

Fig. 1. The procedure timeline of Experiment 1. POS, NEG, and NEU denote positive, negative and neutral emotional state, respectively.

(3×6 sec), randomly chosen from the preselected sets. In the first trial, the pictures were always of high valence (either NEG or POS, depending on the session). For the second trial, the pictures were always NEU. After each trial, a blank screen with a fixation cross was presented for 6 sec followed by a 7-level Likert scale to rate subjects' current affective state The scale ranged from -3 (for negative affect) to 3 (positive affect), with 0 reflecting neutral affect. Subjects were instructed to rate their current affective state rather than the valence of the pictures. The response was limited to 4.5 s and marked with an arrow, which could be moved using a response key with the left or right index finger; the choice was submitted using either the left or right thumb. A fixation cross was again presented for a period of random length between 4 and 7 sec.

Experiment 2 (EEG)

Subjects

Thirty five undergraduate student volunteers (mean age: 21.5 years, SD=1.7) were recruited by the university student recruitment system for participation in the experiment. One subject was subsequently excluded due to technical problem in data recording. All subjects were right-handed, medication-free (excluding possible intake of oral contraceptives), and had normal or corrected-to-normal vision. No subjects reported history of any neurological or psychiatric disorders or substance abuse. Subjects received the equivalent of €10 for participation.

Procedure

The pictorial stimuli used in the experiment were the same as in Experiment 1. Additionally, for mood induction, 18 POS and 18 NEG video clips were selected from the Internet which had previously been ranked by four competent judges as either negative or positive. During the experiment, subjects were seated in an air-conditioned soundproof cabin in front of a 24'' LCD monitor. The experimental conditions were similar to Experiment 1. Again, the procedure consisted of four sessions in the same sequence: NEG, POS, NEG, POS. However here, each session consisted of four blocks, each starting with three either NEG or POS video clips (18 sec each), which served as the mood induction (see Fig. 2). Video clips were followed by 2 sec of blank screen and then 1 sec presentation of 40 neutral images in random sequence, and the estimation of the subject's current state. Here, subjects rated along two continuous dimensions: arousal (ranging from 0

to 6 points) and valence (ranging from -3 to 3 points). There were no response time limits. Each block ended with a break. The subject could advance forward by pressing a key. To ensure that subjects paid attention to the pictures during the whole procedure, once in each block at a random moment an additional response was required in the form of a keypress corresponding to the digit shown on the screen.

DATA ACQUISITION AND ANALYSIS

Experiment 1 (fMRI)

A one-tailed repeated measures *t*-test was applied to test if mood during presentation of neutral pictures in positive sessions was higher (i.e., more positive) compared to negative sessions.

MRI data acquisition took place at the Laboratory of Brain Imaging, Nencki Institute of Experimental Biology, Warsaw, on a 3-Tesla MR scanner (Siemens Magnetom Trio TIM, Erlangem, Germany) equipped with 32-channel phased array head coil. For anatomical reference and spatial normalization, T1-weighted images were acquired in interleaved ascending order (176 slices, field of view (FOV)=256, repetition time (TR)=2530 ms, echo time (TE)=3.32 ms, flip angle (FA)=7 deg, voxel size=1x1x1 mm)

Functional data were acquired using a T2*-weighted gradient echo planar imaging (EPI) sequence (39 slices, FOV=224, TR=2.5, TE=27 ms, FA=90 degrees, voxel size=3.5×3.5×3.5 mm). Additional field map data of EPI images were received. Head movements were minimized with foam cushions placed around the subject's head. None of the subjects were excluded from further analysis due to excessive head movement, which was set to 0.75 mm for linear translation (x, y, z) and 0.5 deg of rotation (pitch, yaw, roll).

The fMRI data were preprocessed and analyzed using Statistical Parametric Mapping (SPM12, Wellcome Trust Centre for Neuroimaging, London, UK) software. First, the functional data were unwarped (using field-map images) to compensate for magnetic field inhomogeneities and realigned (using trilinear-sinc interpolation) to correct for motion. Subsequently, structural images were co-registered to mean functional image and segmented. Finally, all images were normalized to MNI space and smoothed with an 8 mm isotropic Gaussian kernel.

The signal for each subject was modeled within a general linear model (GLM) derived by convolving a canonical hemodynamic response function with 12 regressors for each session (6 reflecting experimental procedure and 6 reflecting parameters of estimated

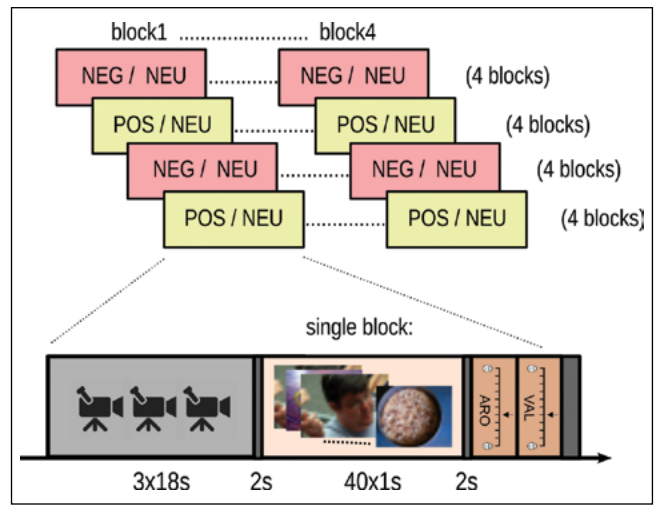

Fig. 2. The procedure timeline of Experiment 2.

movements). The first and third sessions (NEG) included the following regressors, reflecting the stages of the experiment: 1) presentation of negative pictures; 2) presentation of neutral pictures after presentation of negative ones (both 18 sec, beginning with the pictures onset); 3) blank screen after presentation of negative pictures; 4) blank screen after presentation of neutral pictures (both 6 sec, beginning with the blank screen onset); 5) estimation after presentation of negative pictures; 6) estimation after presentation of neutral pictures (both 4.5 sec, beginning with the estimation onset); 7-12) estimated movement parameters. The second and the fourth sessions included the same regressors; however here, regressors reflected positive picture presentation (POS) instead of negative ones. Of note, the 4-7 sec fixation period was not explicitly modeled as the GLM and was thus treated as an implicit baseline period.

Individual subject contrast images were computed for NEU pictures presented after NEG pictures (i.e., NEU pictures in the first and the third session) *vs.* NEU pictures presented after the POS pictures (i.e., NEU pictures in the second and the fourth session) and entered into a random-effects group-level analysis. These individual subject contrasts were submitted to a group-level whole-brain analysis, and group level T-maps were subsequently thresholded using a voxelwise level of $p<0.001$ and cluster size of at least 30 voxels. The main peaks of activation with t-values within each cluster and their corresponding brain structures are reported.

Experiment 2 (EEG)

For EEG data recording, a Biosemi Active Two high impedance amplifier was used with 64-channels placed on a 10-10 headcap. Four additional mo-

nopolar electrodes were placed over the eye muscles. Data analysis was performed with EMEGS software (Peyk et al. 2011). The signal was sampled with 256-Hz frequency, and subsequently filtered using a 0.1 Hz high-pass and 46 Hz low-pass zero-phase filters, and then average referenced. Ocular artefacts were corrected using Biosig toolbox and artefact rejection was subsequently conducted using a method developed for statistical control of artefacts in high density EEG/MEG data (Junghöfer et al. 2000). Analysis focused on the epochs -100 to 1000 ms relative to picture onset. The average number of included neutral trials per subject was 564. After averaging, the L2 minimum-norm inverse modeling method (Hämäläinen and Ilmoniemi 1994) was used to estimate activity of ERP cortical sources with relatively good spatial accuracy. The method does not require any prior assumptions regarding localization or number of sources. As source model, a spherical shell consisting of 350 evenly distributed dipole pairs was used with a radius of 90% of the averaged head (roughly corresponding to gray matter depth), with the Tikhonov regularization parameter k set to 0.1. This resulted in topography maps showing activation of sources underlying recorded neural activity for each condition (i.e., POS and NEG sessions). These maps were subsequently projected onto realistic brain geometry (Bröckelmann et al. 2013). To reveal spatiotemporal differences in brain activation between conditions, a non-parametric cluster-mass statistical procedure with multiple comparisons correction was used (Junghöfer et al. 2017, Maris and Oostenveld 2007). During this procedure, *t*-values exceeding critical alpha-levels (p=0.05; sensor-level criterion) were summed across neighboring dipoles and adjacent time points to the spatiotemporal cluster masses. Only dipoles located within an angle of 120 degrees from the vertex were considered, which reflects cortical dipoles. The masses were compared to a random permutation cluster-based alpha-level (cluster-level criterion; p=0.05), established via Monte Carlo simulations (1000 permutations) for early (<200 ms) and later (>200 ms) effects, separately. Only the clusters in which the spatiotemporal extent (reflected by obtained masses) exceeded critical level (based on cluster-level criterion) are reported.

RESULTS

Experiment 1 (fMRI)

Based on subject self-reports, results of the mood induction were as expected. In particular, participants reported more positive affective states during presentation of neutral pictures in the positive session (M=0.71; SD=0.75) as compared to during the negative session (M=0.54; SD=0.86; $t15$=1.86; P=0.04).

FMRI analyses revealed higher activity to NEU pictures in the POS compared to NEG session in the lingual gyrus, middle occipital gyrus, middle temporal gyrus, middle frontal gyrus, and precuneus (see

Table I. Brain regions showing differential response to neutral stimuli during a) positive > negative sessions, and b) negative > positive sessions.

A) POS > NEG comparison							
	brain region	Brodmann Area	peak T	MNI coordinates			cluster size
				x	y	z	
L	lingual gyrus	17	4.5852	-6	-91	-4	141
L	middle occipital gyrus	19	6.1605	-45	-76	5	466
R	middle temporal gyrus	19	4.5276	45	-73	11	266
R	middle frontal gyrus	44	4.1279	42	23	32	133
L	precuneus	7	4.1089	-15	-61	47	33
B) NEG > POS comparison							
	brain region	Brodmann Area	peak T	MNI coordinates			cluster size
				x	y	z	
R	superior temporal gyrus	21	5.0824	51	-1	-10	76
L	medial frontal gyrus	11	4.8737	-18	50	-4	103
R	medial frontal gyrus	10	4.6301	15	56	8	51

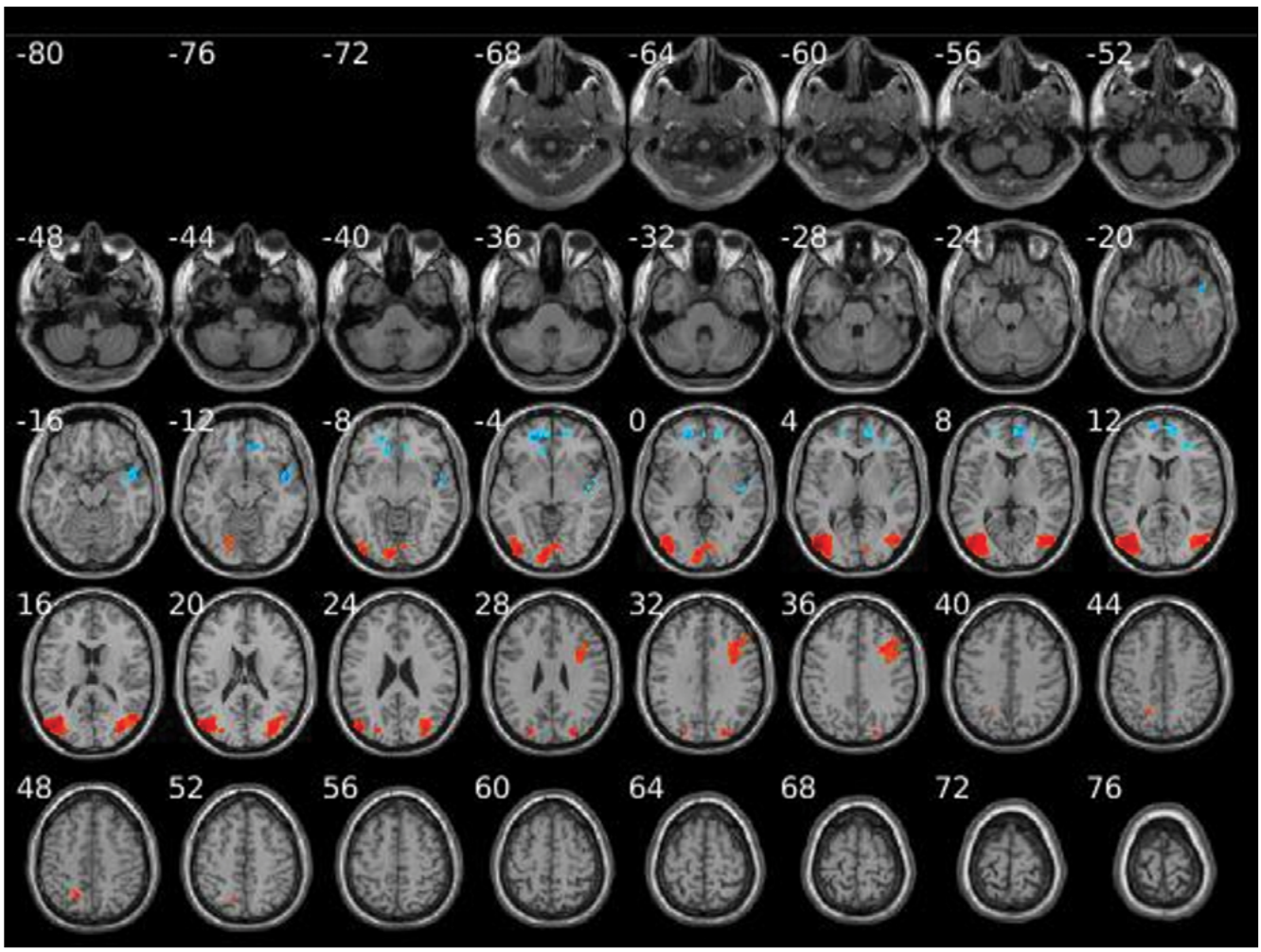

Fig. 3. Brain regions showing differential response to neutral stimuli during positive > negative sessions (red), and negative > positive sessions (blue).

Table I). In contrast, activation in the superior temporal gyrus (STG), and bilateral medial frontal gyrus (MFG) was higher for NEU pictures in the NEG compared to POS session[1].

Experiment 2 (EEG)

Subjective ratings of emotional state revealed that the mood induction did not affect the arousal reported by subjects (NEG: mean=0.42, SD=0.11; POS: mean=0.43, SD=0.10). However, reported valence differed significantly between the sessions (NEG: mean=-0.20, SD=1.03; POS: mean=0.15, SD=1.04; *t32*=3.02; *P*=0.005).

Cluster analysis revealed two clusters that showed significant differences in activation for neutral pictures following negative *vs.* positive mood induction. For the POS>NEG contrast, early activation (30-90 ms from stimulus onset) was observed in the medial and right occipital cortex (cluster mass=341.9, critical mass=314.5, sensor-level and cluster-level alphas were set to 0.05). For the NEG>POS contrast, activation was observed in the right inferior frontal gyrus and partially in the anterior right superior temporal gyrus during the 406-496 ms window (cluster mass=1023.3, critical mass=851.5 for sensor-level and cluster-level alpha set to 0.05). Cluster are depicted in Fig. 4.

[1] *To rule out the possibility that reported effects result from sustained activity related to processing of emotional pictures, we performed additional analyses. We compared effects of the reported contrasts with the effects of contrasts reflecting perception of emotional pictures. Specifically, we made 2 comparisons of 4 different contrasts: 1) a comparison of contrast of neutral pictures in positive sessions > neutral pictures in negative sessions with a contrast of perception of positive pictures > perception of negative pictures and 2) a comparison of contrast of neutral pictures in negative sessions > neutral pictures in positive sessions with contrast perception of negative pictures > perception of positive pictures. Both comparisons did not reveal any common effects, confirming that the reported results reflect changes in processing of neutral pictures rather than a post-effect of emotional picture processing.*

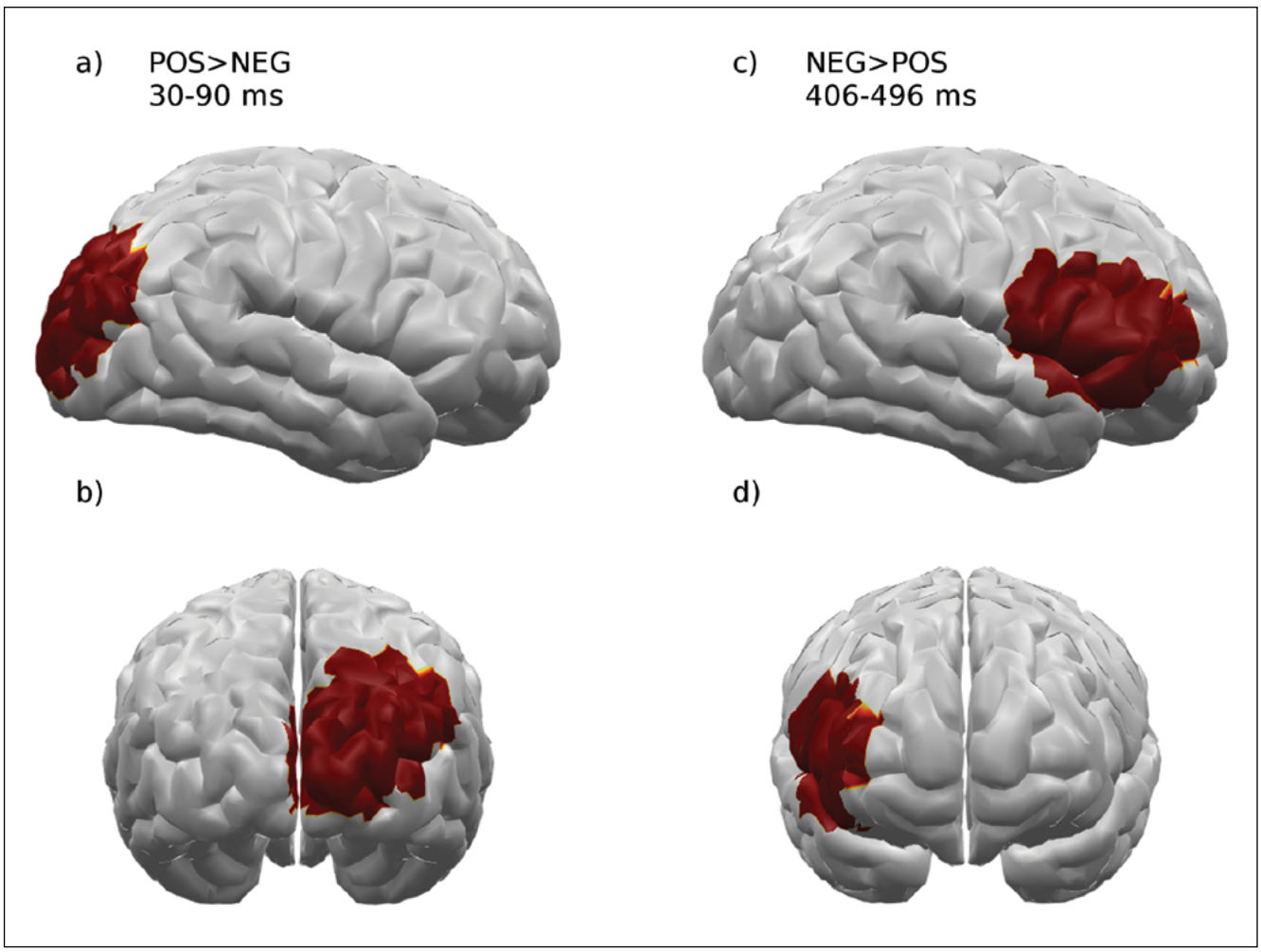

Fig. 4. EEG clusters showing significant main effect of session: a) the right occipital cluster (POS>NEG session; right and rear view, respectively); c-d) the right frontotemporal cluster (NEG>POS session; right and frontal view, respectively).

DISCUSSION

The study investigated the influence of positive and negative mood on processing of non-emotional, centrally presented stimuli. Using both EEG and fMRI methods, we showed that prior induction of mood affects activation of specific brain areas during processing of neutral pictures. In particular, negative mood was associated with relatively greater activity in the regions of the prefrontal cortex and the right temporal cortex, whereas positive mood was related to relatively higher activity in occipital sites. To our knowledge, this is the first study to demonstrate that affective experience influences brain activation during processing of neutral pictures in healthy subjects.

Our analysis from both experiments concerned two opposite contrasts which compared processing of neutral pictures after induction of a positive *vs.* negative emotional state. Contrary to our expectations, both fMRI analysis and EEG source localization data collected during similar experiments revealed higher activation of occipital visual areas during perception of neutral stimuli that followed a positive as compared to negative mood induction (i.e., POS>NEG sessions). In particular, fMRI analysis showed higher activation in bilateral middle occipital gyrus, lingual gyrus, and precuneus for POS>NEG. Similarly, EEG source localization method showed higher activation in a broad, right occipital area for POS>NEG. Taken together, these results suggest that positive mood intensified activation of visual areas in response to neutral pictures. Activity in visual areas may serve as a marker of increased perceptual processing of neutral stimuli in positive compared to negative sessions.

The high temporal resolution of EEG allowed us to infer the possible time dynamics of this modulation. Since the effect was observed in the very early phases of stimuli processing (i.e., before the stimulus

valence is likely to be fully determined), we conclude that sensory areas remain under a tonic top-down influence which modulates their functioning. This is consistent with our hypotheses and in agreement with previous studies examining the effects of mood on processing of peripheral stimuli. In those studies, mood affected the early (but not late) stages of perceptual processing (Moriya and Nittono 2011, Vanlessen et al. 2013). Taken together, these results suggest that emotional state can have a tonic impact and transiently change the reactivity of the perceptual system. Changes in the perceptual system appear to be more generalized, and are evident irrespective of stimuli valence or location.

As hypothesized, we observed higher neural activation in negative compared to positive conditions. However, the observed effects were evident in different brain regions than initially hypothesized. In both procedures, the NEG>POS session contrast again revealed higher activity of the prefrontal and temporal cortex. Specifically, fMRI analysis showed greater activation of the bilateral medial prefrontal cortex (MPFC) and right superior temporal gyrus (STG) for negative compared to neutral sessions. EEG analysis revealed higher activation only in the right anterior STG. The MPFC area is known to play an important role in modulating and inhibiting response to affective stimulation. Its activation is often associated with suppression of emotional responses (e.g. fear extinction) and with recruiting different kinds of implicit defense mechanism that serve to protect a subject from the impact of negative content (Hänsel and von Känel 2008, Roy et al. 2012). As such, higher activation of MPFC together with attenuated activity in the occipital cortex could reflect a control mechanism that serves to protect individuals against potential negative impact of external stimuli (for example, in situations in which a negative affective state is induced). Similarly, activity in the STG is often reported to increase when experiencing and controlling negative stimuli. Importantly, such control influences might be triggered only by the negative stimuli itself without any instruction to regulate emotions; this is considered an implicit form of emotional regulation (Gyurak et al. 2011, Silvers et al. 2014).

Taken together, our results may reflect a mechanism protecting against negative stimulation. This protective mechanism may be due to the fact that our experiments took place in the relatively safe and comfortable context of a laboratory environment. We may assume that such conditions do not require increased reactivity to negative stimuli, as they do not signal any potential threat. Hence, individuals experiencing prior negative stimulation may attenuate sensory processing to limit exposure to potential negative content. On the other hand, extant findings from the literature suggest that positive stimulation promotes greater 'openness' to external stimulation. Increased activation observed in sensory areas in our procedures may be related to the phenomenon of 'positive bias', which has been reported in similar laboratory conditions (Grzybowski et al. 2014). Similarly, a number of studies have shown a so-called 'congruency effect', i.e. positive and negative moods promote the processing of positive and negative stimuli, respectively (Jiang et al. 2007, Grzybowski and Wyczesany 2016). However, there are also reports showing the opposite effect; that negative mood decreases the processing of negative stimuli (Ellenbogen et al. 2002). We assert that these discrepancies may be due to experimental conditions or other factors, which could result in the recruitment of mechanisms underlying emotional control. Given that stimuli in our study were passively viewed and were task irrelevant, processing of the stimuli could be spontaneously attenuated in negative conditions at no detriment to experimental demands. Another factor which also could account for the observed effects was the bottom-up characteristics of our neutral stimuli. In particular, we have previously shown that in favorable conditions, a current affective state can trigger a global 'defense' mechanism which serves to improve well-being by altering the processing of incoming stimuli.

To our knowledge, this is the first study to show that a preceding mood manipulation impacts the processing of low-motivational (i.e., NEU) stimuli in healthy subjects. Based on results of a previous study examining processing of neutral stimuli in a group of anxious patients, we would expect an increase in processing of neutral stimuli (Gmaj et al. 2016). Here, we observed a *less* intense processing of neutral stimuli in negative mood comparing to positive mood in healthy subjects. Thus, control mechanisms might differ in anxious *vs.* healthy individuals. For example, anxious and depressive patients are often characterized by a lack of control influences from the prefrontal cortex to emotional parts of the brain (Kim and Hamann 2007, Kim et al. 2011), and often display a propensity to orient attention towards threatening stimuli (unless an avoidance strategy is used; Koster et al. 2006). Impaired top-down control from prefrontal areas is also linked to ruminative tendencies and focusing on negative thoughts related to one's autobiographical past (Ferdek et al. 2016). Therefore, it is possible that our results reflect a mechanism of controlling external stimuli in healthy subjects, and that this mechanism works differently in anxious individuals and is a symptom of their disorder. As such, future studies should test this hypothesis by comparing healthy and anxious individuals.

The present results may hold implications for everyday functioning of healthy individuals. Our results suggest that perception of neutral stimuli, which are frequently encountered in, everyday situations might change based on current affective state. During positive mood states, it may be beneficial to boost processing of the environment, letting in more visual input from the outer world. Conversely, during negative mood states, it may be adaptive to diminish perceptual processing. This attenuation may serve as a defense mechanism that protects us from potentially unpleasant stimuli, and may be adaptive in perceived safe contexts. Anxious individuals may not activate such a defense mechanism often enough because they are more likely to perceive relatively neutral conditions or situations as threatening and, consequently, as more negative. Indeed, previous studies show that patients suffering with anxiety disorders show a bias in their perception and are more likely to interpret stimuli as negative (Constans et al. 1999).

A few limitations and future directions of the study should also be mentioned. First, our design was not counterbalanced, which could affect the results. However, repetition of sessions may partly ameliorate any ordering effects. Second, subjects across the two experiments were not homogeneous. In particular, while only female subjects participated in the fMRI procedure, both male and female subjects participated in the EEG procedure. There are data showing that defensive tendencies against negative stimuli are more frequently observed in women as compared to men, and that regulation is more likely to be focused on appetitive content in men than in women (Bradley et al. 2001). Given that these sex differences could influence the implicit regulation of emotions, they should be taken into account in future studies. Future studies should also compare anxious individuals with healthy subjects. As such, the relationship between anxiety disorder and the proposed mechanism of control influences from the prefrontal cortex needs to be confirmed. Another concern is that the brain activation attributed in our study to perception of neutral stimuli may be the result of experiencing a particular mood rather than reflecting changes in perception per se. The design of both study procedures, however, rules out this possibility. In particular, during the EEG procedure, the signal was baseline corrected to the pre-stimulus period; thus, only differences related to perception were analyzed. During the fMRI procedure, we performed additional analyses comparing observed effects with the effects related to perception of emotional pictures (during which subjects reported altered mood states). Given that no similarities across these two analyses were found, it is unlikely that our results reflect those related to the mood induction. This additional analysis also suggests that observed effects do not reflect sustained activity related to processing of emotional pictures.

To conclude, the present study demonstrated that in a relatively comfortable, non-threatening situation, processing of neutral stimuli in healthy subjects is less intense after a negative as compared to a positive mood induction. We interpret these results as the effect of an implicit modulatory mechanism which tunes perceptual processing. In particular, in non-threatening settings (such as a laboratory environment), negative mood induction may induce a transient perceptual defense to block out non-relevant information. Our fMRI and EEG results indicate that the prefrontal cortex is a putative initiator of this mechanism.

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