Accepted Manuscript

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PII: S0010-9452(12)00370-X

DOI: 10.1016/j.cortex.2012.12.013

Reference: CORTEX 961

To appear in: *CORTEX*

Received Date: 15 May 2012

Revised Date: 12 October 2012

Accepted Date: 11 December 2012

Research report

"Emotions Guide Us": Behavioral and MEG correlates

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<u>Abbreviated form of the title:</u> Emotional salience in peripheral vision

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Number of pages: 38

Number of figures and tables: 4/1

Abbreviated form of the title: 30/42 characters including punctuation and spaces.

Number of words: Abstract (233/300), Introduction (1314), Discussion (1809).

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A B S T R A C T

Affectively salient stimuli are capable of capturing attentional resources which allows the brain to change the current course of action in order to respond to potentially advantageous or threatening stimuli. Here, we investigated the behavioral and cerebral impact of peripherally presented affective stimuli on the subsequent processing of foveal information. To this end, we recorded whole-head magnetoencephalograms from twelve participants while they made speeded responses to the direction of left- or right-oriented arrows that were presented foveally at fixation. Each arrow was preceded by a peripherally presented pair of pictures, one emotional (unpleasant or pleasant), and one neutral. Paired pictures were presented at 12° of eccentricity to the left and right of a central fixation cross. We observed that the participants responded more quickly when the orientation of the arrow was congruent with the location of the previously presented emotional scene. Results show that non-predictive emotional information in peripheral vision interferes with subsequent responses to foveally presented targets. Importantly, this behavioral effect was correlated with an early (~135msec) increase of left fronto-central activity for the emotionally congruent combination, whose cerebral sources were notably located in the left orbitofrontal cortex. This study suggests that the prior spatial distribution of emotional salience, like physical salience, grabs attentional resources and modifies the performance in the center of the visual field. Thus, these data shed light on the neurobehavioral correlates of the emotional coding of visual space.

Keywords: emotion, attention, peripheral vision, international affective picture system, magneto-encephalography

1. Introduction

Similar to physically salient stimuli (Yantis and Jonides, 1990), affectively salient stimuli are capable of capturing attentional resources and disrupting ongoing goal-oriented processing (LeDoux, 2000; Öhman and Mineka, 2001; Reeck and Egner, 2011; Vuilleumier and Huang, 2009). Indeed, because affective cues have strong adaptive significance, the brain has the ability to change the current course of action in order to respond to potentially advantageous or threatening stimuli (Corbetta et al., 2008; Vuilleumier, 2005). Lately, a growing body of research suggests that emotional stimuli are still selected in peripheral vision despite its poor acuity (Bayle et al., 2011; Calvo et al., 2008; Liu and Ioannides, 2010), even when these stimuli are presented at high degrees of eccentricity (Rigoulot et al., 2008, 2011, 2012), and though they are unexpected (Hung et al., 2010) or not consciously perceived (Bayle et al., 2009). Thus, it is likely that emotionally laden stimuli that appear in peripheral vision can interfere with a task that is currently occurring in central vision.

Visual perception is constrained by the properties of the retina (see Livingstone and Hubel, 1987; 1988; Nassi and Callaway, 2009; Wandell, 1995). The fovea encompasses the central 2° of the visual field, and it contains a high proportion of cone photoreceptors. It has a high spatial resolution and is thought to be at the origin of the parvocellular system. This system conveys high-spatial frequency (HSF) information that is ultimately relayed to the ventral stream (Baizer et al., 1991; Dacey and Petersen, 1992; Stephen et al., 2002). As stimuli appear farther away from the center of the visual field, the object details fade; however, the temporal resolution of object perception improves. The peripheral retina contains a high proportion of rod photoreceptors and appears to be mainly related to the magnocellular system, which rapidly conveys low-spatial frequency (LSF) information to the dorsal stream (Baizer et al., 1991; Dacey and Petersen, 1992; Lee et al., 1997; Purpura et al., 1988; Stephen et al., 2002). To deal with these spatiotemporal resolution differences between the central and the peripheral areas of the visual field, objects are sequentially selected by either overt or covert spatial attention, i.e. with or without foveal capture (Calvo et al., 2008). In fact, spatial attention can be oriented endogenously by top-down mechanisms depending on the goals of the observers and exogenously by bottom-up mechanisms triggered by behaviorally relevant stimuli, which are unexpected or salient (Chica et al., 2013; Corbetta and Shulman, 2002).

Many studies have suggested that exogenous spatial cues orient attention toward emotional stimuli, which can influence subsequent visual processing (Vuilleumier, 2005; Vuilleumier and Huang, 2009). For instance, studies using dot-probe tasks have shown that judging the orientation of probes presented in the same parafoveal locations where brief stimuli had previously been presented, is more rapid and/or accurate when the initial stimuli are emotional rather than neutral (e.g., Armony and Dolan, 2002; Brosch et al., 2008; Frewen et al., 2008; Lipp and Derakshan, 2005; MacLeod et al., 1986; Mogg and Bradley, 1999; Phelps et al., 2006; Pourtois et al., 2004; Santesso et al., 2008). Moreover, although attentional biases that favor emotional stimuli have been frequently associated with the detection of threatening events, it appears that emotionally arousing stimuli modulate the allocation of spatial attention independently of their valence (Anderson, 2005; Vogt et al., 2008; Vuilleumier and Huang, 2009). It has been postulated that this phenomenon relies on rapid interactions between the cortical visual areas and the affective anterior network, which is mainly composed of the amygdala, the temporal pole, and the orbitofrontal cortex (OFC; Barrett and Bar, 2009; Rudrauf et al., 2008; see also Pessoa and Adolphs, 2010; Tamietto and de Gelder, 2010). Increasing evidence shows that projections from the amygdala to the sensory cortices provide an effective mechanism for enhancing the processing of emotional events, which could operate in parallel with influences from fronto-parietal systems (Vuilleumier, 2005). In this context, the OFC constitutes another possible way of mediating emotional influence on attentional systems because of its bidirectional connections to the amygdala and its projections to parietal and lateral prefrontal areas (Cavada et al., 2000; Vuilleumier, 2005).

The early processing of the affective value of visual stimuli could rely on rapid, coarse representations of these stimuli that are extracted from LSF information (Alorda et al., 2007; Pourtois et al., 2005; Vlamings et al., 2009; West et al., 2010; see also Bocanegra and Zeelenberg, 2009, 2011; Phelps et al., 2006). In particular, during the parallel extraction of other visual features, the OFC might generate affectively laden predictions on the basis of the "gist" of the scene that are then integrated into the processing that occurs in the ventral stream (Bar, 2003; Bar et al., 2006; Barrett and Bar, 2009; Kveraga et al., 2007a, 2007b), which is strongly related to central vision, as mentioned above. Furthermore, given the privileged association between peripheral vision and the magnocellular system, affective predictions elicited by OFC are likely to influence where to attend and may contribute to the preferential orienting toward emotional stimuli when occurring in the visual periphery. Consequently, we hypothesized that peripherally presented emotional stimuli could interfere with the goal-directed processing of foveal information by inducing a spatial response bias when judging the orientation of a central arrow.

In the present study, we therefore looked for behavioral traces of this putative interference by measuring reaction times and the associated neuronal hallmarks by analyzing whole-head magnetoencephalogram (MEG) data. Our question was as follows: is endogenous attention influenced by exogenous attention to emotional stimuli, in a manner that is independent of gaze shift? To address this issue, pairs of simultaneous prime pictures were presented at 12° of eccentricity to the right and left of a central fixation cross. In each pair, one picture was emotional, and one was neutral. After the offset of each pair, the fixation cross was briefly replaced with an arrow. We hypothesized, first, that the participants would indicate the orientation of the arrow more quickly when it was congruent with the location of the emotional stimulus than when it was not, and second, that this behavioral bias is associated with an early increase in the activity level of the OFC.

2. Methods

2.1. Participants

Twelve healthy students were recruited for the present study (mean age 26 ± 3 years; 7 females), all of whom were right-handed (Hécaen, 1984), had normal or corrected to normal vision and lacked any history of neurological or psychiatric disorders, or drug consumption. All of them provided informed consent, and each participant was submitted to psychological tests that evaluated anxiety (State-Trait Anxiety Inventory, A and B; Spielberger et al., 1983) and depression (BDI-II, Beck Depression Inventory; Beck et al., 1996) to ensure that these conditions did not affect task performance. Every participant who was included in this study scored below 45 on the State-Trait Anxiety Inventory and below 11 on the Beck Depression Inventory; these scores are consistent with typical norms. The study was approved by the ethics committee of the Université de Montréal, and it was conducted in accordance with the Declaration of Helsinki. All of the experiments were performed at the MEG laboratory of the Centre de Recherche en Neuropsychologie et Cognition (CERNEC, Université de Montréal).

2.2. Materials

Given the differences usually observed between men and women in the processing of emotional stimuli (Bradley et al., 2001; Collignon et al., 2010), emotional and neutral pictures from the international affective picture system (IAPS; Lang et al., 2008) were selected according to gender. More precisely, for each sex, we selected a set of 200 pictures by considering the normative valence and arousal ratings provided for men and women. As a result, 104 pictures were included both for men and women while the others pictures were specific to men or women. Each gender-based set comprised two subsets of emotional stimuli, 50 unpleasant (U) and 50 pleasant (P), as well as two subsets of 50 neutral stimuli (N1 and N2). To control the emotional parameters of the selected pictures, we used linear and quadratic contrasts to compare standardized IAPS valence and arousal ratings. Linear contrasts of valence ratings (on a scale of 0 to 9 in which 0 indicated a very unpleasant picture and 9 indicated very pleasant picture) were used to compare the U and P picture categories. Quadratic contrasts of arousal ratings (on a scale of 0 to 9 in which 0 indicated very calm and 9 indicated very arousing) were used to compare the emotional pictures (unpleasant and pleasant) with the neutral pictures (N1 and N2; D'Hondt et al., 2010; Hot et al., 2006). The valences of U and P pictures differed (means valence ratings were U = 2.55, N1 = 5.12, N2 = 5.09, P = 7.38 for women, and U = 2.52, N1 = 4.99, N2 = 5.00, P = 7.40 for men; *ps* <.05), but the picture sets were equally arousing relative to each other (mean arousal ratings were U = 5.93, P = 5.94 for women, and U = 6.11, P = 6.13 for men; *ps* > .05) and were more arousing than N pictures (means were N1 = 2.95, N2 = 3.05 for women, and N1 = 2.88, N2 = 2.88 for men, *ps* <.05). No significant differences in either the arousal or valence ratings of the pictures were observed between N1 and N2 sets (*ps* > .05). Moreover, no significant gender-based differences in either the arousal or valence ratings of the pictures were observed (*ps* > .05). The numbers of pictures depicting faces, animals, objects, landscapes, and human beings were counterbalanced across U, N1, N2, and P sets. These sets were homogenized (Image J Software) in terms of their major physical characteristics, which included the mean luminance values, the standard deviation of the luminance (i.e., contrast index), spatial frequencies, and color saturation levels (red, green, blue). ANOVAs that were performed to analyze these characteristics did not reveal any differences between U, N1, N2, and P scenes that were shown to men or to women (*ps* > .05). The pictures were further tested for complexity, which was indexed in terms of the number of bytes, and the percentage of surface occupied by human faces (Calvo and Lang, 2005) and no difference was observed between U, N1, N2, and P sets that were shown to men or to women (*ps* > .05).

From these pictures, we built four kinds of "prime" pairs: 100 pairs with a U picture in the left visual field and a N picture in the right visual field ("U+N1" and "U+N2"), 100 pairs with a N picture in the left visual field and a U picture in the right visual field ("N1+U" and "N2+U"). Two other sets of 100 pairs were obtained by combining P and N pictures in the same way. Of note, one same N picture from N1 set or N2 set was therefore presented with a given U picture as many times than with a given P picture. Importantly, each picture that appeared on one side of the screen in a given "prime" pair was the mirror picture of the same picture that was presented on the opposite side of the screen in a different "prime" pair. Thus, the various elements of any given picture were equidistant from the fixation point when it was projected in either the left or the right visual hemifield (IrfanView Software; see Bryson et al., 1991). We computed differences between the emotional and neutral pictures of prime pairs for each emotional value and physical parameter that has been mentioned above. No significant differences were observed between the "U+N", "N+U", "P+N", and "N+P" conditions (*ps* > .05).

The total of the 400 "prime" pairs was presented twice, once in a congruent condition, once in an incongruent condition (see 2.3. Experimental procedure). The angular sizes of the pictures were 16° (horizontal) x 12° (vertical), and the center of each picture projected at 12° of eccentricity relative to the central fixation cross (Presentation V13, Neurobehavioral Systems). The target was either a left arrow ("<") or a right arrow (">"), and it had an angular size of 2° in both the horizontal and vertical dimensions. The central cross and arrows were black (Red = 0, Green = 0, Blue = 0) and the background of the screen was grey (Red = 128, Green = 128, Blue = 128). Testing was conducted under dimly lit conditions, and the screen was located at a viewing distance of 45 cm.

2.3. Experimental Procedure

The experiment consisted of one 10-trial practice block that was followed by 4 experimental blocks, each of which comprised 200 trials, for a total of 800 trials. Each trial began by the presentation of a "prime" pair during 500 msec (Fig. 1). An arrow (either left or right) replaced the fixation cross for a 150 msec period following a random interval (100, 150, 200, 250 or 300 msec) that began at the offset of the prime pair. Finally, the cross reappeared for an inter-stimulus interval (ISI) ranging between 1000 and 2000 msec. The location of the emotional picture in "prime" pairs was either congruent (50% of the trials) or not (the other 50% of the trials) with the direction of the arrow that replaced the central fixation cross. Each block contained 50 counterbalanced presentations of each pair condition ("U+N", "N+U", "P+N", and "N+P") in a pseudo-random order (i.e. one given "prime" pair and its "mirrored" version were never successively presented across an experimental session).

Moreover, the congruence condition was counterbalanced across pair conditions and experimental blocks.

The participants were instructed to keep their gaze on the cross in the center of the screen throughout the course of the experiment without moving the eyes at any time and to indicate the direction of the arrow as quickly as possible by pressing either the left or right button of a response-box. The participants were instructed to press the left button for the left arrow ("<") and the right button for the right arrow (">") using the index and the middle fingers. The hand used by each participant changed for each block and was counterbalanced across participants.

INSERT FIGURE 1 NEAR HERE

2.4. Behavioral Data

Data regarding both the reaction times (RTs) for each response and the percentage of correct responses (CRs) in the task were gathered using the two-button box controlled by the presentation software. CRs were used as a measure of accuracy. To reduce the influence of outliers, trials with RTs that were more than 3 standard deviations longer than each participant's mean RTs were excluded (Mogg et al., 2008), which represented 1.2% of the total number of trials, all participants included. ANOVA that was performed on the number of trials did not reveal any difference between experimental conditions ($p > .05$).

2.5. MEG Data

Head coils were placed on the nasion and on the left and right pre-auricular points prior to scanning for continuous head localization recording. The locations of these coils and the head-shape of each participant were digitized using a 3D digitizer (Fastrak Polhemus Inc., Colchester, VA). The position of the participant's head relative to the 271 MEG sensors was recorded before each experimental session and again after each session. Magnetic fields were measured using a 275-channel whole-head magnetometer (CTF MEG 275, CTF Systems) at a sampling rate of 600 Hz. Only 271 MEG sensors were used during the experiment due to technical issues with 4 of the channels. Electrocardiogram was monitored by two silver chloride electrodes placed on the left and the right collarbones, in order to check for any artefact in the ERF responses due to cardiac activity and correct the MEG signal if necessary. Vertical and horizontal electro-oculograms were also recorded allowing us to control on-line any ocular movements or blinks. A camera that is installed inside the MEG room was directed to the eyes of the participants, which also helped us to control any eye movement.

Third-order gradient noise reduction (computed with the CTF software) was applied to the recorded MEG signals, which were then baseline-corrected on the basis of the mean activity during the 100 msec prior to the target (i.e. arrows) onset. Trials on which the MEG sensor position differed by more than 5 mm, which indicated head movement, were automatically removed. Trials in which there had been eye movements were excluded from the final analysis after visual inspection of the oculograms (DataEditor, CTF Systems). This control was important for verifying that the participants remained focused on the fixation cross during the experiment. Trials were also rejected offline because of muscular (e.g., eye blinks) or electromagnetic artifacts. We did not apply any cardiac correction, as the visual examination of our data showed no contamination by the cardiac activity. All of the remaining trials (97 ± 2% of the trials across all conditions) were band-pass filtered from 0.1 to 55 Hz. Averaged event-related magnetic fields (ERFs) for each condition, each participant, and each of the 271 sensors were calculated over a 100 msec period (baseline) before and 500 msec after the target (i.e. arrows) onset.

First, the neuromagnetic data were subjected to a spatiotemporal principal component analysis (stPCA, detailed procedures are reported in Spencer et al., 2001); this type of analysis has proven to be an efficient tool for synthesizing the spatial and temporal dimensions of electrophysiological recordings (Pourtois et al., 2008 for ERP data; D'Hondt et al., 2010 for MEG data). Two successive PCAs were computed on baseline-corrected MEG waveforms, after the application of third-order gradient noise reduction and rejection of trials with head movements or ocular artefacts; these PCAs were used to provide scores that reflected the amplitudes of the ERFs at specific locations (spatial factors, or SFs, that were extracted during spatial PCA) and specific latencies (temporal factors, or TFs, that were extracted during temporal PCA) in response to the arrows that were presented. In a first step of the analysis, a spatial PCA (sPCA) was performed that used the MEG sensors (271) as dependent variables and that considered time points, participants and conditions (arrow, congruence, and emotional valence) as observations (Varimax rotation, SPSS V. 15 software). The sPCA identifies groups of highly correlated sensors and redistributes them into a smaller number of linear combinations (Varimax rotation, SPSS V. 15 software) that are referred to as spatial factors (SFs, Pourtois et al., 2008). Each SF represents a specific spatial configuration of brain activation, and the factor loading corresponds to the degree to which the SF contributes to the values of the original variables (i.e., how much the spatial factor accounts for the magnetic field that was recorded at each sensor). These spatial configurations can be visualized with topographic maps of factor loadings (Cartool software, Denis Brunet)[1], and they are usually defined by considering sensors with the highest factor loadings (D'Hondt et al., 2010; Rigoulot et al., 2008, 2011). In addition, sPCA scores reflect the contribution that each SF makes to each variable—i.e., specific time point, arrow, congruence, and emotional valence condition—for each participant. The various factor scores indicate the contribution of the SF to the magnetic fields observed for each original waveform, and these scores can be analyzed with regular statistical tests (Pourtois et al., 2008). SF scores were subsequently considered to be "virtual" ERFs, and their corresponding time series (300 time points, 500 msec duration at a sampling rate of 600 Hz) were subjected to temporal PCA (tPCA) in which participants and conditions (arrow, congruence, and emotional valence) were considered observations. tPCA identifies groups of points with high temporal correlations and redistributes these groups of points into new linear combinations (Varimax rotation, SPSS V. 15) called temporal factors (TFs; Pourtois et al., 2008). tPCA loadings correspond to the contribution of a given TF to each SF at each time point. Thus, TFs determine SF activity at specific latencies, generally by considering the highest factor loadings (D'Hondt et al., 2010; Rigoulot et al., 2008, 2011). Finally, the stPCA procedure in its entirety results in a set of factor scores that was used in the present study to compare the activity of various cerebral configurations (i.e., SFs) at specific latencies (i.e., for each TF) in response to each experimental condition. SFs and TFs were selected for these comparisons using the scree test (Cattell, 1966), which is a widely used method of determining the point at which the slope of the curve of decreasing eigenvalues becomes flatter. Only the factors that are located prior to this decline in slope are retained for further analysis.

Second, the Brainstorm software program was used to estimate the cortical current density at each time point in each condition and for each participant by means of a weighted minimum-norm estimation (wMNE) with standard Tikhonov regularization. This use of BrainStorm software package is documented, and the software itself is freely available for download online under the GNU General Public License (Tadel et al., 2011)[2]. For each participant, a noise covariance matrix was computed on the basis of the 100 msec baseline prior to target (i.e. arrows) onset using the single trials from which the average files were computed. Surface head models were computed by means of an overlapping spheres model (Huang et al., 1999), and source reconstruction was constrained to the cortical mantle of a generic brain model extracted from the standard "MNI/Colin27" brain template (Collins et al., 1998) defined by the Montreal Neurological Institute. Prior to this step, MEG sensor locations were coregistered to the MNI/colin27 template, thanks to an iterative algorithm implemented in the Brainstorm software, using the digitized head points and aligning the fiducial points obtained during acquisition. Finally, we applied a z-score procedure to the source reconstruction data with a 100 msec baseline prior to target (i.e. arrows) onset. This operation substracts the average and divides by the variability of the baseline. The goal is to increase the visibility of the significant effects by reducing the weight of the sources that have a strong variability in the baseline.

2.6. Statistical analyses

Repeated-measures ANOVAs were performed on the percentages of CRs and the RTs of the CRs of participants that used arrow (< or >), congruence (congruent, incongruent) and emotional valence (unpleasant, pleasant) as within-subject factors. A significance level of 5% (two-tailed) was selected. The same analyses of variance were also applied to individual stPCA scores for each SF and TF pair. Then, the individual source reconstructions that had been obtained for the congruent and incongruent conditions were subtracted and were subjected to a one-sample t-test against baseline (Brainstorm software). A Student's t-statistic that exceeded an alpha level of .001 (Bonferroni correction for multiple comparisons with a control in time and space) was used to define greater activation in response to congruent conditions relative to activation in response to incongruent conditions. Finally, we conducted a search for behavioral correlates of the cerebral effects that had been demonstrated in the results of the ANOVAs by computing Bravais-Pearson correlation coefficients between the individual values that corresponded to these effects.

3. Results

3.1. Behavioral Results

The mean CR rate was very high (98% ± 1; Tab. 1), and the analyses of variance did not reveal any significant effect of any of the experimental conditions ($p > .05$). An ANOVA was also conducted on the RTs of the CRs, and it revealed that there was a significant main effect of congruence ($F(1,11) = 7.8$; $p < .05$; $\eta_p^2 = .41$; Fig. 2). The mean RTs of the participants were shorter in congruent conditions compared with incongruent conditions; however, no significant effects of other experimental conditions were observed ($p > .05$).

INSERT TABLE 1 AND FIGURE 2 NEAR HERE

3.2. MEG Results

3.2.1. stPCA

Applying sPCA to the data from the 271 MEG sensors used in the present study yielded 18 SFs that, taken together, described 96.7% of the spatial variance in the dataset. tPCA was then used to group the temporal dimensions of the dataset; 300 time points were assigned to 16 TFs, and these TFs accounted for 97.0% of the variance in the data. Using the scree test (Cattell, 1966), 12 SFs (which accounted for 93.1% of the variance) and 9 TFs (which accounted for 91.9% of the variance) were selected for use in further analyses of variance.

A 2 (Arrow: <, >) x 2 (Congruence: congruent, incongruent) x 2 (Valence: unpleasant, pleasant) ANOVA revealed a significant main effect of congruence in the left fronto-central component (indicated by the maximum factor loadings for component SF01, which accounts for 34.4% of the spatial variance; Fig. 3A) at 135 msec (indicated by the maximum factor loading for component TF07, which accounts for 2.8% of the temporal variance; Fig. 3B). Scores for the congruent conditions were more positive than scores associated with the incongruent conditions ($F(1,11) = 5.9$, $p < .05$; $\eta_p^2 = .35$; Fig. 3C), and no influences of any other factors were observed ($p > .05$).

INSERT FIGURE 3 NEAR HERE

3.2.2. wMNE

We were interested in identifying the sources associated with the significant difference in neuromagnetic activity between congruent and incongruent conditions revealed by the stPCA. To this end, we computed a one-sample t-test against baseline (n = 12, $p < .001$, Bonferroni correction with control in time and space; Fig. 3D) on the resulting contrasts. This analysis revealed that at 135 msec, there was significantly increased activity in the left orbital parts of the inferior (44 vertices, $t = 10.34$) and middle (42 vertices, t = 10.26) frontal gyri. At this latency, activity was also observed in the right precuneus (13 vertices, $t = 11.26$), the right cuneus (53 vertices, $t = 13.10$), the right calcarine fissure (59 vertices, $t = 5.36$), the left inferior parietal cortex (56 vertices, $t = 14.47$), and in the left middle (29 vertices, $t = 6.19$) and superior (82 vertices, $t = 10.84$) occipital cortices.

3.3. Correlation

Bravais-Pearson correlation coefficients were computed using the individual values of the cerebral and the behavioral effects that had been evidenced by the analyses of variance. The difference in RTs between the congruent and incongruent conditions was correlated with the difference in stPCA scores in the left fronto-central component (SF01) at 135 msec (TF07; r (10) = -.585; p < .05; Fig. 4.) between the congruent and incongruent conditions. Thus, the greater the activation in an individual's left fronto-central region for the congruent condition relative to the level of activation in the incongruent condition, the more rapid his or her behavioral response was.

INSERT FIGURE 4 NEAR HERE

4. Discussion

We recorded whole-head MEGs from healthy participants who had been asked to determine the orientation of an arrow that appeared at fixation after being exposed to two pictures that were presented simultaneously in the periphery. The peripheral picture in one hemifield was an emotional one, and the picture in the other hemifield was neutral. We found that participants responded more quickly when the location of the peripherally presented emotional scene was congruent with the direction of the central arrow that followed it. We also showed that this behavioral bias was correlated with a similar congruence effect in a left fronto-central MEG component at 135 msec. At the same latency, statistical analyses performed on source reconstructions of the MEG signals revealed effects, notably at the level of the left OFC, that were specific to congruence between the locations of emotional scenes and the directions of the arrows. Given the controls that were applied to the physical and semantic parameters of the pictures that we selected for use in this study, the observed effect of congruence can only result from the emotional content of the pictures. Thus, these results evidence that emotional salience in peripheral vision induces a bias in the subsequent processing of foveal information.

At the behavioral level, the current study revealed that the speed with which observers were able to judge the orientation of a central arrow was affected by the congruence of the direction of the arrow and the location of a previously presented emotional scene. This shows that despite the relatively poor visual acuity in peripheral vision, affective stimuli are processed preferentially in comparison to neutral stimuli, which is consistent with findings from recent studies (e.g., Bayle et al., 2011; Rigoulot et al., 2011). Moreover, the response bias to foveal information induced by an attentional capture in peripheral vision is consistent with the necessity to react to relevant stimuli, whether they are positive or negative, even when attention is not primarily directed toward them. Previous studies using dot-probe tasks have suggested that emotionally salient stimuli in the periphery can induce an exogenous orienting of attention. In these tasks, the visual selection of a parafoveal probe is facilitated by the emotional value of the preceding visual stimulus on the basis of a common spatial location (e.g., Brosch et al., 2008; Pourtois et al., 2004). Nevertheless, contrary to dot-probe tasks, the congruence effect observed in our study depends on the compatibility between the side of the hemifield primed by peripherally presented emotional stimuli and the side indicated by the probe (left or right arrow) appearing in foveal vision rather than its actual location. Furthermore, the peripheral location of emotional stimuli in our study was totally non-predictive of the direction of the central arrow. Thus, to the best of our knowledge, this work is the first to show that the exogenous orienting of attention by task-irrelevant affective cues in peripheral vision can disrupt the function of endogenous attention directed toward the processing of foveal information. This novel result may reflect the way in which affectively salient stimuli in the peripheral visual field are able to capture attentional resources dedicated to the analysis of foveal input.

In everyday life situations, this type of attentional capture generally leads to a saccadic capture that allows for a better perception of potentially advantageous or threatening stimuli. In agreement with this, Nummenmaa et al. (2006) used an eye-tracking method to assess attentional orientation and engagement with emotional scenes, and they found that the probability of fixating on an emotional picture, regardless of whether it was pleasant or unpleasant, was greater than the probability of fixating on neutral pictures. According to Calvo et al. (2008), even though the specific content of emotional or neutral scenes is not processed in peripheral vision, a coarse impression of the scene may be extracted, and that impression may then lead to selective attentional orienting. This is in agreement with our finding that the congruence effect that we observed in the present study was not modulated by the emotional valence of the stimuli. Hence, stimuli do not need to be evaluated as being either negative or positive to capture attention; rather, they only need to be arousing (Anderson, 2005; Vogt et al., 2008; Vuilleumier and Huang, 2009). This assumption also concurs with the precocity of arousal impact on the activity of visual areas during perception of emotional scenes as revealed by ERP and MEG studies (D'Hondt et al., 2010; Flaisch et al., 2008; Junghofer et al., 2006; Peyk et al., 2008; Schupp et al., 2003).

At a cortical level, the activity that was observed in the left early fronto-central component (135 msec) was greater for the congruent condition than the incongruent condition. Interestingly, the spatial and temporal characteristics of this component were similar to those of the N1 component that has been recorded in response to any kind of visual stimulus in ERP studies. The N1 component consists of a complex of at least three separate subcomponents that are associated with current flows over frontal (peaking at approximately 140 msec), parietal (150–160 msec), and occipital (170–190 msec) scalp areas (Clark and Hillyard, 1996). It has been shown that the amplitude of the N1 component is influenced by selective attention, and it may reflect a sensory gain control mechanism (Luck et al., 2000; Rugg et al., 1987). In fact, in visuo-spatial cueing paradigms, the amplitude of the N1 component represents a benefit that is derived from correctly allocating attentional resources and is greater in response to stimuli in attended locations compared with unattended ones (Hillyard et al., 1998; Luck et al., 1994). Because previous studies have shown that emotional stimuli elicit greater N1 amplitudes than neutral stimuli (Foti et al., 2009; Keil et al., 2001), it is plausible that emotional stimuli are able to capture attentional resources more effectively than non-affective stimuli. This notion is also in agreement with the results of the present study, demonstrating that affective cues in peripheral vision may have induced an allocation of attentional resources to the stimulated location that led to the observed increase in the amplitude of the early fronto-central MEG component when the location of an affective stimulus was congruent with the direction indicated by the arrow. The lateralization of the observed emotional bias to the left hemisphere may be linked to encoding-related neural activity, which has frequently been reported as being lateralized to the left hemisphere (Cabeza and Nyberg, 2000; Tulving et al., 1994). The lateralization of encoding activity is most probably because human subjects tend to use verbal strategies when processing a wide variety of stimuli, including nonverbal ones (Frey and Petrides, 2000).

At the latency of the congruence effect observed on the activity of the left early fronto-central component (135 msec), source reconstructions have provided evidence of activity that is specific to this effect in the left OFC, the bilateral occipital cortices, and in parietal regions. It is interesting to note that the frontal sub-component of the N1 component has been associated with either a distributed set of sources that are located in the frontal cortex or with one or several deep posterior generators that project toward frontal scalp locations (Clark et al., 1995). Moreover, activity in the ventral prefrontal regions of the cortex has been observed in response to emotional distractors (Fichtenholtz et al., 2004; Yamasaki et al., 2002). These cortical areas are certainly involved in the anticipation of emotional consequences in the planning of future behaviors, and they have been shown to take part in decision-making processes (Damasio, 1994). In addition, some authors have recently confirmed that not only is there a convergence of information regarding rewarding and aversive stimuli in the OFC (Morrison and Salzman, 2009), but the OFC also plays roles in the assignment of behavioral significance to a stimulus, the prioritization of attentional selection, and in behavioral control (Desimone and Duncan, 1995; Diekhof et al., 2011). Although occipital activity may be linked to enhancement in target processing in the congruent condition (e.g., Armony and Dolan, 2002; Brosch et al., 2008; Pourtois et al., 2004), increased parietal activation has also been observed in response to emotional stimuli or during spatial-orienting tasks in which neutral targets are preceded by emotional cues (Armony and Dolan, 2002; Keil et al., 2005; Pourtois et al., 2006). Finally, it has been suggested that a ventral fronto-parietal network is involved in directing attention to salient events, and this network interacts with a dorsal fronto-parietal system, the activity of which is modulated by the detection of stimuli and is involved in preparing and applying goal-directed mechanisms for selecting both stimuli and responses (Corbetta and Shulman, 2002; Corbetta et al., 2008).

The preferential processing of emotional scenes in peripheral vision may modulate the selection of higher-level representations. This modulation may include imposing an affective bias on the activity of prefrontal regions (Miller and Cohen, 2001), which in turn influences sensory processing and response selection (Vuilleumier, 2005). The affective bias observed in the present study could result from affective predictions generated by the OFC (Barrett and Bar, 2009) in the following manner: the extraction of the gist of an emotional scene from the low-spatial frequency (LSF) information conveyed by magnocellular pathways to the OFC may have influenced decisions regarding where to attend, and ultimately influenced the responses that were made during the further processing of the arrows. The increase in the activity in the visual cortices, as observed in the present study, might also reflect an enhancement of visual input following congruent emotional stimuli, that results from top-down signals that originate in affective anterior regions (Barrett and Bar, 2009; Pessoa, 2010; Rudrauf et al., 2008; Vuilleumier, 2005). When the locations of emotionally salient stimuli are congruent with the directions of the arrows, spatial orienting toward emotional scenes probably affects executive control mechanisms that are involved in determining behavioral outcomes (Pessoa, 2009) and that are ultimately responsible for faster reaction times.

Finally, we found that the higher activity observed in the left early fronto-central component for the congruent condition compared to the incongruent one was significantly correlated to the behavioral effect on reaction times. This finding indicates that emotional salience in peripheral vision modulates both the early activity in the left fronto-central areas of the brain and the speed of behavioral responses to subsequent targets in foveal vision in a similar manner. Hence, we showed that when individuals are engaged in a task that is taking place at the center of the visual field, the spatial distribution of emotional salience induces a spatial response bias. Independently of its relevance to the ongoing behavior, the location of a potential negative or positive stimulus in the visual space may be coded by the OFC from a coarse representation of inputs occurring in peripheral vision. Therefore, this study supports the idea that peripheral vision serves as a warning system favoring particularly salient signals of high adaptive relevance.

Acknowledgments

This work was supported by grants from the Ministère de la Recherche, France (F.D.), the Rotary Foundation (F.D.), the Programme International de Collaboration Scientifique (PICS) of the CNRS (H.S, M.L. groups grant) and the Centre International de Lille 1 (CIL, H.S.), the Fonds de Recherche du Québec-Santé (FRQS, group grant), the Canada Research Chair Program (CRCP, M.L., F.L.), the Canadian Institutes of Health Research (CIHR, M.L., F.L.), and the Natural Sciences and Engineering Research Council of Canada (NSRECC, M.L., F.L.). The Cartool software program was programmed by Denis Brunet of the Functional Brain Mapping Laboratory, Geneva, Switzerland, and is supported by the Center for Biomedical Imaging (CIBM) of Geneva and Lausanne.

Role of the funding sources and conflicts of interest

All authors report no competing financial interests or potential conflicts of interest, and no financial relationships with commercial interests. The funding sources did not exert any editorial direction or censorship on any part of the experiment.

Footnotes

[1] http://brainmapping.unige.ch/Cartool.htm

[2] http://neuroimage.usc.edu/brainstorm

Figure captions

Fig. 1 – Sequence of events in a trial. A trial begins with the simultaneous presentation of two pictures (International Affective Picture System; Lang et al., 2008) for a duration of 500 msec; in this example, an emotional picture is presented to the left of a central fixation cross, and a neutral picture is presented to the right. After the offset of these two pictures, the cross is presented alone for a period that varies randomly from trial to trial (100, 150, 200, 250 or 300 msec), termed the stimulus onset asynchrony (SOA, i.e., the delay between the pictures and the onset of the target). Then, the detection target about which the observer is asked to make a judgment (an arrow) appears for a 150 msec interval. For this trial, the location of the emotional picture (on the left of the fixation cross) is congruent with the direction of the arrow (also left). Finally, the cross reappears for an inter-stimulus interval (ISI) of between 1000 and 2000 msec in duration.

Fig. 2 – Congruence effect on behavioral data. Mean reaction times of the participants (n=12) for the congruent and incongruent conditions (* indicates p < .05). Error bars denote standard errors corrected for between-subject variability (Cousineau, 2005).

Fig. 3 – Congruence effect on event-related magnetic field (ERF). (A) Topographic maps of the factor loadings for SF01 (the corresponding percentage of variance accounted for by SF01 is specified). From the left to the right, lateral left, dorsal and lateral right views. (B) Factor loadings of the temporal factor TF07 (the corresponding percentage of variance accounted for by TF07 is specified). The green dashed bar indicates the latency (revealed by the maximum factor loading of the specified TF) for which the significant congruence effect was observed. The Y-axis is unitless. (C) Mean factor scores of TF07 for SF01 according to congruence condition (* indicates *p* < .05). The Y-axis is unitless. Error bars denote standard errors corrected for between-subject variability (Cousineau, 2005). (D)

Difference in the computed wMNE results between the congruent and incongruent conditions (Student's t-test of signal vs. baseline after correcting for multiple comparisons, *p* < .001) at 135 msec (threshold at 80 vertices). Source reconstructions are constrained to the cortical mantle of a generic brain model extracted from the standard "MNI/Colin27" brain template. "F" indicates the frontal orientation and "L" indicates the left orientation.

Fig. 4 – Significant Bravais-Pearson correlation coefficients for congruence effects between reaction times (RT; y-axis, in msec) and event-related magnetic field (ERF; x-axis, unitless). The difference in RTs between the congruent and incongruent conditions (i.e., congruence effect) was correlated with the same difference in stPCA scores in the left fronto-central component (SF01) at 135 msec. Thus, the greater the activation in an individual's left fronto-central component (SF01) at 135 msec (TF07 scores) for the congruent condition relative to the level of activation in the incongruent condition, the more rapid his or her behavioral response was.

Table 1. Behavioral measures. CRs: mean correct response rates (SD); RTs: mean reaction times (SD).

CRs in %			
Arrow	Emotional valence	Congruence	
		Congruent	*Incongruent*
<	*Unpleasant*	98 (2)	98 (2)
	Pleasant	98 (2)	98 (2)
>	*Unpleasant*	98 (1)	99 (2)
	Pleasant	98 (1)	98 (1)
RTs in msec			
Arrow	Emotional valence	Congruence	
		Congruent	*Incongruent*
<	*Unpleasant*	414 (65)	425 (81)
	Pleasant	420 (74)	424 (75)
>	*Unpleasant*	419 (77)	423 (80)
	Pleasant	419 (82)	424 (82)

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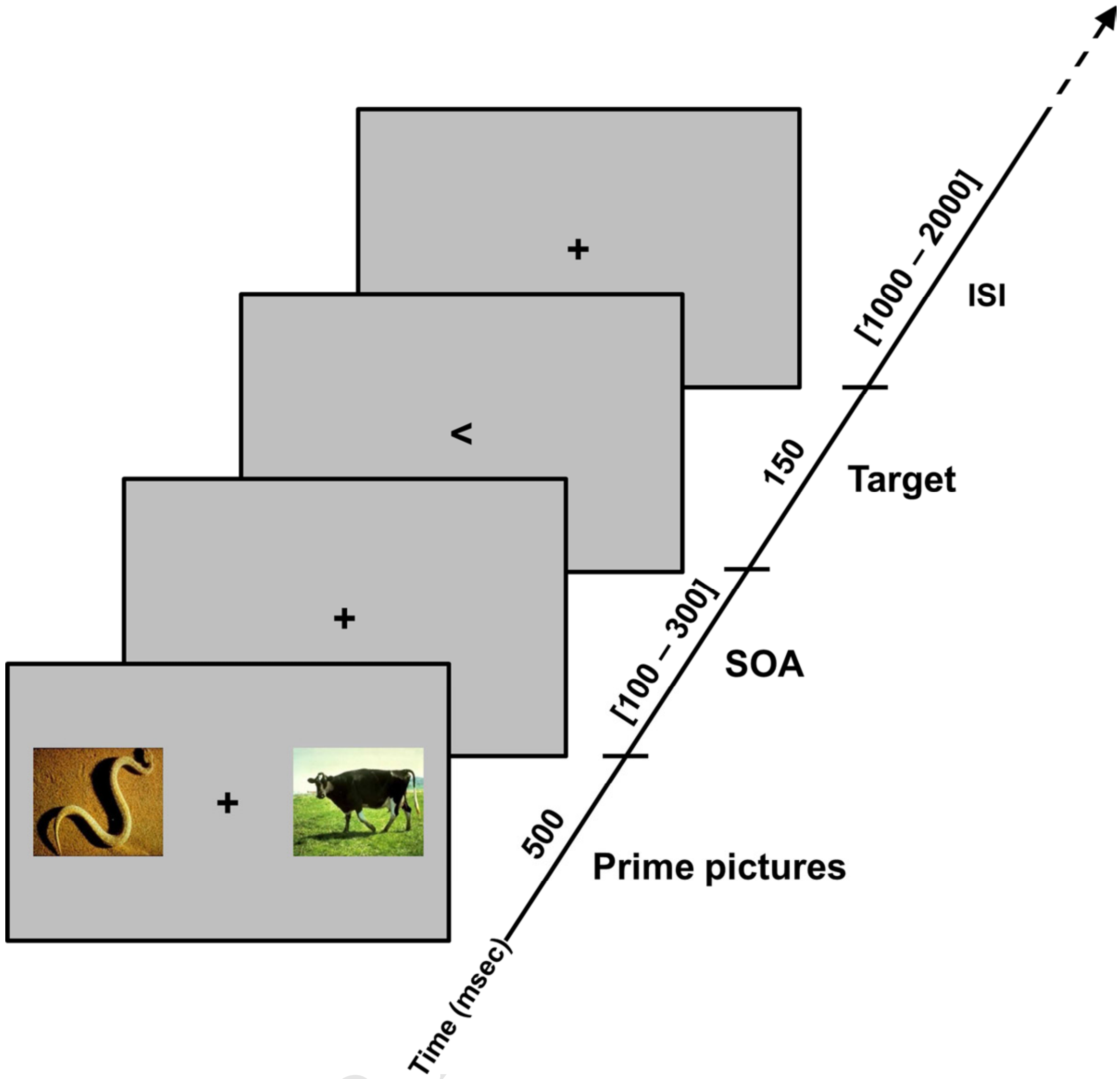
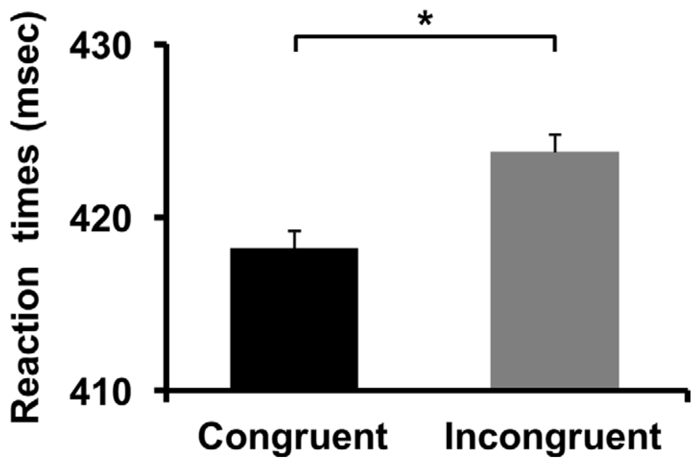
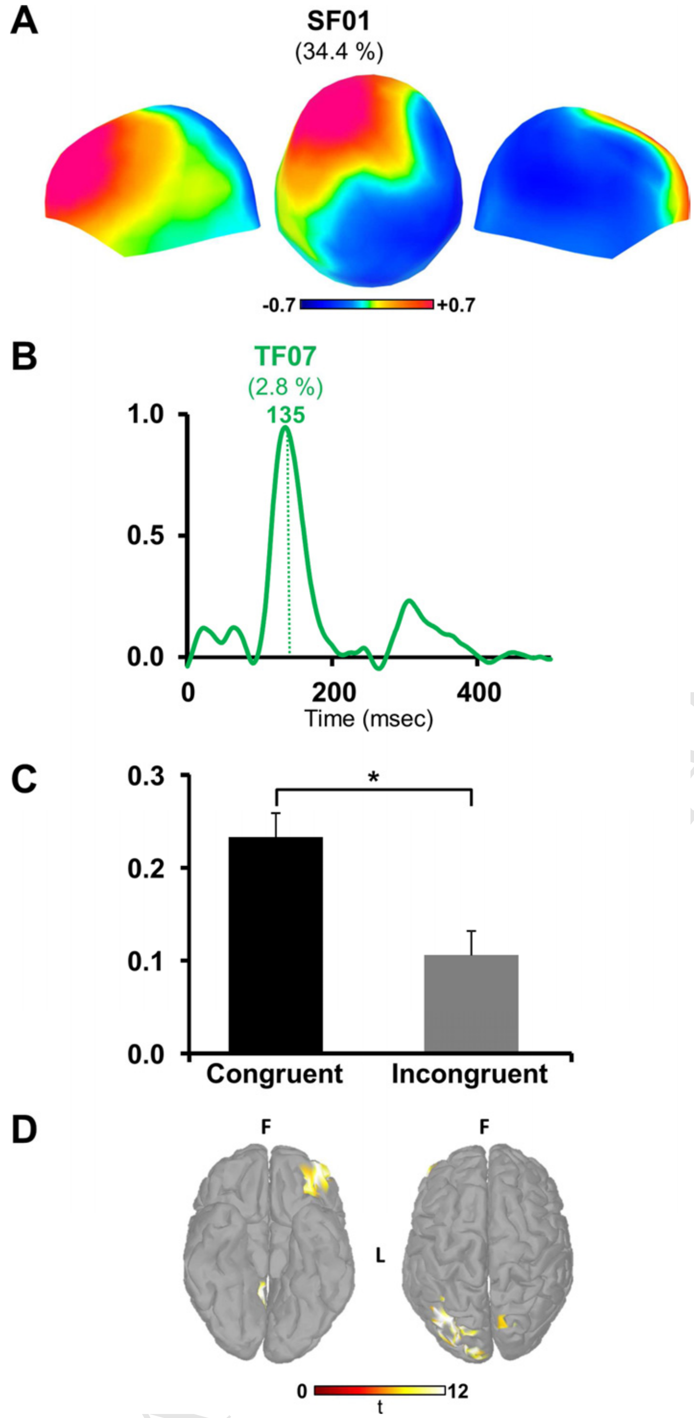
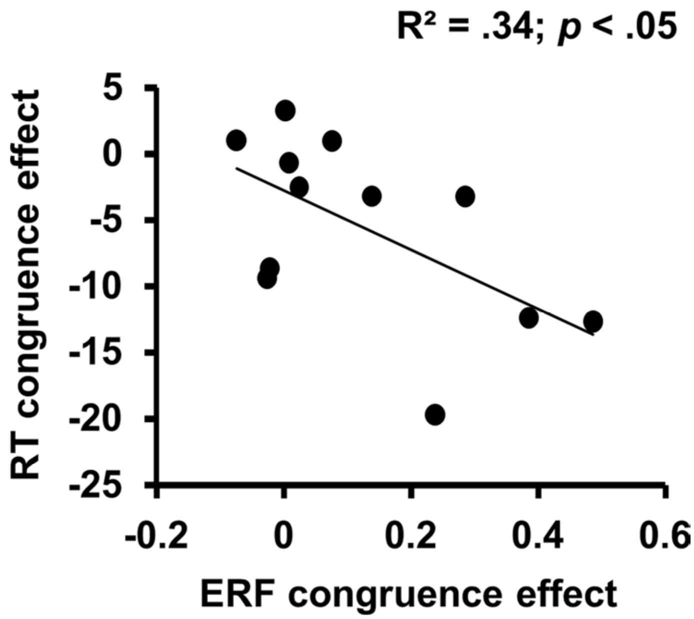


+
<
+
+
Time (msec)
500
Prime pictures
[100 – 300]
SOA
150
Target
[1000 – 2000]
ISI



*
430
420
410
Reaction times (msec)
Congruent
Incongruent


A
SF01
(34.4 %)
-0.7
+0.7
B
TF07
(2.8 %)
135
1.0
0.5
0.0
0
200
400
Time (msec)
C
0.3
0.2
0.1
0.0
*
Congruent
Incongruent
D
F
F
L
0
12
t



R² = .34; p < .05
5
0
-5
-10
-15
-20
-25
RT congruence effect
-0.2
0
0.2
0.4
0.6
ERF congruence effect