RUNNING HEAD: Threat and Looming Stimuli

Threat Modulates Neural Responses to Looming Visual Stimuli

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Abstract

Objects on a collision course with an observer produce a specific pattern of optical expansion on the retina known as looming, which in theory exactly specifies the time-to-collision (TTC) of approaching objects. We recently demonstrated that the affective content of looming stimuli influences perceived TTC, with threatening objects judged as approaching sooner than non-threatening objects. Here, we investigated the neural mechanisms by which perceived threat modulates spatiotemporal perception. Participants judged the TTC of threatening (snakes, spiders) or non-threatening (butterflies, rabbits) stimuli, which expanded in size at a rate indicating one of five TTCs. We analysed visual-evoked potentials (VEPs) and oscillatory neural responses measured with electroencephalography (EEG). The arrival time of threatening stimuli was underestimated compared to non-threatening stimuli, though an interaction suggested that this underestimation was not constant across TTCs. Further, both speed of approach and threat modulated both VEPs and oscillatory responses. Speed of approach modulated the N1 parietal and oscillations in the beta band. Threat modulated several VEP components (P1, N1 frontal, N1 occipital, EPN and LPP) and oscillations in the alpha and high gamma band. The results for the high gamma band suggest an interaction between these two factors. Previous evidence suggests that looming stimuli activate sensorimotor areas, even in absence of an intended action. Our results show that threat disrupts the synchronization over the sensorimotor areas that are likely activated by the presentation of a looming stimulus.

Introduction

Protecting the body from potentially threatening objects is among the most critical functions of the visual system. Looming (i.e., rapidly approaching) objects represent one such cue to threat that requires a rapid defensive or evasive response. Indeed, looming stimuli elicit stereotyped fear responses in monkeys (Schiff, Caviness, & Gibson, 1962), human infants (Ball & Tronick, 1971), and adults (King et al., 1992). In theory, the rate of optical increase in the size of the retinal image as an object approaches exactly specifies the time-to-collision (TTC), independent of object size or distance (Gibson, 1979). Traditionally looming has been viewed as a purely optical cue to collision, regardless of the content of the approaching stimulus (Schiff et al., 1962; Ball & Tronick, 1971; King et al., 1992). This view is consistent with the idea that the processing of looming relies on low-level, and largely sub-cortical, mechanisms.

In contrast, two recent studies have demonstrated that perceived TTC is affected by the semantic content of looming stimuli (Brendel et al., 2012; Vagnoni, Lourenco, & Longo, 2012). In the study of Vagnoni and colleagues, the participants completed a TTC task in which a visual stimulus expanded in size over one second and then disappeared. After the stimulus disappearance, the participants had to imagine the stimulus continuing to approach and judge when it would have made contact with their body. Threatening objects (snakes and spiders) were judged as arriving sooner than non-threatening objects (butterflies and rabbits). Further, the magnitude of this effect was correlated with self-reported fear of snakes and spiders, such that people who were more fearful of these stimuli underestimated their arrival time more than those who were less fearful. The precise nature of this modulation, however, remains unclear.

In this study, we therefore investigated the cortical mechanisms underlying this modulation by measuring visual-evoked potentials (VEPs) and evoked oscillatory responses

induced by looming visual stimuli. Several studies have investigated VEPs associated with visual processing of emotionally-laden stimuli (e.g., Olofsson, Nordin, Sequeira, & Polich, 2008). Differential neural activity related to the affective valence of pictures begins as early as 100 ms after stimulus onset and persists for the next 1000 to 2000 ms (Codispoti, Ferrari, & Bradley, 2007; Olofsson & Polich, 2007). We were specifically interested in whether and how emotion modulates neural responses to looming images. We asked participants to make TTC judgments of looming visual stimuli. We manipulated both the rate of image expansion, consistent with one of five TTCs, and the emotional content of the stimulus (i.e., threatening, non-threatening). Our previous work showed that threat influences looming judgments, with the arrival time of threatening images underestimated relative to non-threatening images (Vagnoni et al., 2012). In this study we expand on this work by asking about the neural basis of the underestimation effect of threatening stimuli. Does threat modulate the visual mechanisms involved in calculating TTC, or does it alter visual processing by some other mechanism that affects TTC judgments?

Methods

Participants

Nineteen members of the Birkbeck community (10 female) between 19 and 36 years of age (M = 24.4, SD = 4.9) participated for payment or course credit. Participants were generally right-handed as assessed by the Edinburgh Inventory (M: 41.9, range: -100 – 100; 3 participants were left handed) (Oldfield, 1971). During the recruitment, participants with phobia to one of the four categories (snakes, spiders, butterflies, and rabbits) used were discarded. Before starting the experiment, the participants read the information about the study and gave written informed consent to take part in this experiment. Procedures were approved by the local ethics committee and were in accordance with the 2013 WMA Declaration of Helsinki.

Materials

Stimuli were the same as used in our previous study (Vagnoni *et al.*, 2012), namely 160 colour photographs collected from the internet, 40 from each of the four categories. Images were cropped and resized using Adobe Photoshop CS5 (Adobe Systems, San Jose, CA). This resulted in images (400 pixels wide, 250 pixels high) in which the animal took up the entire image. Backgrounds from the original photographs were replaced with a homogenous grey colour (identical to the background of the experimental script).

Procedure

Participants sat at a table approximately 40 cm in front of a 19-inch monitor (120 Hz refresh rate). The distance between the participants and the monitor was checked during the experiment (measures were taken during the breaks between blocks). Stimulus presentation

and data collection were controlled by a custom MATLAB (Mathworks, Natick, MA) script using the Cogent Graphics toolbox (developed by John Romaya at the Wellcome Department of Imaging Neuroscience, University College London). On each trial, the stimulus increased in size across 120 frames (i.e., one second), consistent with one of five TTCs (3.0, 3.5, 4.0, 4.5, and 5.0 s after the onset of the first frame). The width of the stimulus on the first frame was either 400 or 500 pixels (15.1° or 18.9° visual angle), giving the impression that it was at two different distances. It seems, from our previous results (Vagnoni et al., 2012), that participants judged bigger stimuli as closer and smaller as farther). We cannot exclude, however, that the stimuli were perceived of different size and at the same distance. Starting image size was manipulated so that actual TTC was not perfectly correlated with the size of the image on the final frame. After the 120th frame, the image was replaced by a blank background. There were a total of 320 trials divided into 8 blocks of 40 trials each. Each block included one repetition of each combination of TTC (5 levels), stimulus category (4 levels), and initial image size (2 levels). The order of trials within each block was randomized. The 40 images from each category were randomly assigned to trial types and each image was used exactly twice for each participant. After the participant responded on each trial, the next trial began after a random inter-trial interval of 500-1000 ms. Between blocks the participant was allowed to take a short break if he/she wished. The next block started whenever the participant was ready.

Participants were all instructed that they would see objects expanding in size as if they were approaching and that they would disappear after a while. They were told that their task was to imagine the object continuing to approach at the same rate and to press the button when they judged that the object would have made contact with their body.

Fear ratings for each of the four categories were collected by modifying the Fear of Spiders Questionnaire (Szymanski & O'Donohue, 1995), as in our previous study (Vagnoni *et*

al., 2012). The 18 items on this questionnaire ask participants to indicate their agreement or disagreement with statements indicating fear or anxiety related to spiders. Example items include: "If I saw a spider now, I would feel very panicky." and "I now would do anything to try to avoid a spider." The 18 statements were modified for each of the other stimulus categories by replacing the word "spider" with either "snake", "butterfly", or "rabbit". Participants rated their agreement or disagreement with each statement using a 7-point Likert scale, where a score of +3 indicated strong agreement with the statement (i.e., high levels of fear) and -3 indicated strong disagreement (i.e., low levels of fear). The 72 items were presented in random order using a custom MATLAB script.

EEG data collection

A SynAmps 2 amplifier system and SCAN 4.3 software (Neuroscan, El Paso, TX, USA) were used to record EEG (electroencephalography) data. Twenty-six scalp Ag-AgCl electrodes were recorded (FP1, FPz, FP2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2) according to the 10–20 international electrode placement system. The active reference electrode was placed on the nose and the ground electrode was placed on the chin. Electrode impedances were kept below 3 KΩ. The horizontal electroculogram was recorded from electrodes placed near the outer canthi of each eye, and the vertical electroculogram was recorded from electrodes placed above and below the right eye. The EOG data was collected using the same amplifier. EEG signals were amplified and digitized at 1000 Hz.

Event-related potential (ERP) analysis

The EEG data were analysed with EEGLAB (Delorme & Makeig, 2004; http://sccn.ucsd.edu/eeglab/). Data were re-referenced to the average of all of the sensors and

digitally low-pass filtered (0-30 Hz). The EOG (electrooculogram) data was collected using the same amplifier as the EEG and all digitization and preprocessing was identical for both types of data. Epochs, time-locked to the visual stimulus presentation, were extracted from the raw EEG data from -0.1 s before to 2 s after the stimulus onset. Epochs containing severe artefacts were rejected by visual inspection. Further artefacts were discarded using blind source separation with independent component analysis (Jung *et al.*, 2000) collapsing across experimental conditions. In total, 3.8% of trials were discarded (on average 12 out of 320 trials).

We focused our analysis on VEPs known, in the literature, not only as being linked to visual processing but also modulated by the emotional content of the stimulus:

The P1 is interpreted as an index of attention allocation in the extrastriate visual cortex. This component seems to be modulated by the emotional content of the stimulus being larger for negative, relative to positive, stimuli. The modulation of the P1 by the emotional content of stimuli suggests that positive and negative stimuli receive different amounts of attention very early in the information processing stream (Smith *et al.*, 2003; Carretié *et al.*, 2004; Cobb & Dawson, 1960; Eason *et al.*, 1969; Van Voorhis & Hillyard, 1977; Luck *et al.*, 1994). The P1 was evaluated as the activity at the left (O1, PO7, P7) and right (O2, PO8, P8) occipital–parietal recording sites in the time window between 115-135 ms after stimulus onset (Michalowski *et al.*, 2009; Smith *et al.*, 2003).

In the literature, we found three different N1 components: an early frontal component and two late components, one that peaks across the parietal recording sites and another that peaks across the occipital recording sites (Luck, 2005). Given that the N1 seems to be influenced by several characteristics of the stimulus, including colour (Anllo-Vento & Hillyard, 1996), location (Martinez *et al.*, 2006), perceived motion (Lorteije *et al.*, 2008) and emotional content (Hart *et al.*, 2012; Carretié *et al.*, 2004; Foti *et al.*, 2009) and given that we

were interested in both the influence of the emotional, as well as the temporal characteristics of the stimuli, we analysed all the different components of N1. The N1 early component was evaluated as the activity at the frontal recording sites (F7, F3, FZ, F4, F8) between 110-135 ms (Hart *et al.*, 2012) after stimulus onset. The N1 late parietal component was evaluated as the activity at the parietal recording sites (P7, P3, Pz, P4, P8) in the time window between 150-200 ms (Hart *et al.*, 2012; Bailey *et al.*, 2012). Given the latency and the scalp distribution of this component we believe that what we have called the N1 parietal, following the classification of Luck (Luck, 2005), represents what in the literature is referred to more commonly as N2 (Heinrich *et al.*, 2005) or N160 (Kremláček *et al.*, 2004). Moreover, in the literature, the scalp location of motion-onset VEP amplitude depends on the character of the motion stimulus. While linear motion mainly activates human MT (middle temporal visual area) analogues in the occipito-temporo-parietal cortex (Kubová *et al.*, 1990), radial motion (''expansion/contraction'') produces maximum responses in the centro-parietal cortex (Kremláček *et al.*, 2004; Langrová *et al.*, 2006) and it is for this reason that we looked at the parietal N1 expecting a modulation of this component by the characteristics of the perceived motion of the stimuli.

The N1 late occipital was evaluated as the activity at the left (PO7, PO3, O1) and right (PO8, PO4, O2) occipital – parietal recording sites at the window time between 155-185 ms after stimulus onset (Hart *et al.*, 2012; Bailey *et al.*, 2012).

There are two components that are thought to index the greater attention that we pay to emotional relative to neutral stimuli (i.e., motivated attention, Lang et al., 1997): the EPN and the LPP (Nordström & Wiens, 2012). The EPN reflects a transient negativity over the posterior region of the scalp between 200 and 300 ms after stimulus onset. Emotional (e.g., both unpleasant and pleasant), compared with neutral, pictures elicit an increase in this component (Hajcak & Dennis, 2009). The early posterior negativity (EPN) selects for further

processing of affectively arousing stimuli (Olofsson *et al.*, 2008). The EPN was evaluated as the activity at the occipital– parietal recording sites (T7, P7, PO7, PO3, O1, Oz, POz, T8, P8, PO8, PO4, O2) at the time window between 200-300 ms after stimulus onset (Nordström & Wiens, 2012; Bailey *et al.*, 2012; Michalowski *et al.*, 2009; Hajcak & Dennis, 2009).

The late positive potential (LPP) is represented by a long-lasting elevated ERP positivity to arousing pictures (Amrhein *et al.*, 2004; Cuthbert *et al.*, 2000; Ito *et al.*, 1998a,b; Keil *et al.*, 2002; Mini *et al.*, 1996; Olofsson & Polich, 2007; Palomba *et al.*, 1997; Schupp *et al.*, 2000). This component indexes the sustained increase in attention toward emotional stimuli. The LPP before stimulus offset was evaluated as the activity at the central recording sites (Cz, Pz) from 400-1000 ms after stimulus onset. The LPP after stimulus offset was evaluated as the activity at the central recording sites (Cz, Pz) at time window 1400-1800 ms after stimulus onset (Hajcak & Nieuwenhuis, 2006; Nordström & Wiens, 2012; Bailey *et al.*, 2012; Hajcak & Olvet, 2008; Ito *et al.*, 1998b; Cacioppo *et al.*, 1994; Michalowski *et al.*, 2009; Hajcak & Dennis, 2009).

Time-frequency analysis

Analyses of EEG oscillations were conducted using SPM8 (http://www.fil.ion.ucl.uk/spm/software/spm8/). We started the time-frequency analysis over from the raw, unfiltered data. We performed the blind source separation with independent component analysis (Jung *et al.*, 2000) then we divided the file according to the condition. A complex Morlet wavelet decomposition of the EEG signal with seven wavelet cycles using a variable time window length was performed across a 2–40 Hz frequency range, in steps of 1 Hz for the alpha, beta and theta bands. Regarding the high gamma band, the frequency range was 70-190 Hz and the wavelet decomposition was performed in steps of 10 Hz. The wavelet decomposition was performed for each trial, sensor, and participant. The power at each

frequency was logarithmically rescaled (LogR in SPM8) for a baseline period defined as the 1 s before the onset of the stimulus. Time–frequency data were averaged across trials of the same trial type to produce an average time–frequency map for each sensor and for each condition.

We focused our analysis on the alpha (8–13 Hz) and beta (15–25 Hz) bands at the posterior sites because previous studies have shown the modulation of alpha band due to the emotional content of the stimuli (Aftanas *et al.*, 1996a) and the modulation of beta band due to the temporal characteristics of the stimulus (van der Meer *et al.*, 2008). van der Weel (van der Weel & van der Meer, 2009) found that infants' looming related brain activity is characterised by theta oscillations (4-7 Hz) , further, there are several evidences about the modulation of high gamma band (70-190 Hz) during perceptual binding and multisensory integration (Quinn *et al*., 2014), we then analysed also these frequency bands. Repeated measures ANOVAs were performed on alpha, beta, theta and high gamma power. We averaged the mean amplitude of the alpha power over the posterior channels (O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P3, Pz, P4, P8); the beta power on the same electrode sites as the alpha power (O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P3, Pz, P4, P8); the theta power over the occipital channels (O1, Oz, O2); the high gamma on the central (C3, Cz, C4) and occipital (PO7, O1, Oz, O2, PO8) channels comparing the different stimulus category (threatening, non-threatening) and actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s). In the task used, the stimulus was visible for 1 second and then disappeared. After the stimulus disappearance, the participants had to imagine it still approaching them and to judge its arrival time. Given the task structure, we divided the analysis into three periods: the first period in which the stimulus was visible (500-1000 ms), the period in which the stimulus disappeared (1000-1500 ms) and then the period in which the stimulus was not visible but imagined (1500-2000 ms).

It is reasonable to expect any effects of stimulus, and its characteristics, to change according to these different stages.

Statistical analysis

Regarding the P1, a repeated measures ANOVA was run on the mean amplitude with stimulus category (threatening, non-threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), hemisphere (left, right) and channel (O1/2, PO7/8, P7/8) as the within-subjects factors.

Regarding the early (frontal) N1, a repeated measures ANOVA was run on the mean amplitude with stimulus category (threatening, non-threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), hemisphere (left, right) and channel (F3/4, F7/8) as the within-subjects factors.

Regarding the N1 that peaks over the parietal channels, a repeated measures ANOVA was run on the mean amplitude with stimulus category (threatening, non-threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), hemisphere (left, right) and channel (P3/4, P7/8) as the within-subjects factors.

Regarding the N1 that peaks over the occipital channels, a repeated measures ANOVA was run on the mean amplitude with stimulus category (threatening, non-threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), hemisphere (left, right) and channel (O1/2, PO3/4, PO7/8) as the within-subjects factors.

The mean voltage data of the EPN was analysed with a repeated measures ANOVA with stimulus category (threatening, non-threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), hemisphere (left, right) and channel (O1/2, PO3/4, PO7/8, P7/8, T7/8) as the within-subject factors.

The mean voltage data of the LPP (both before and after the stimulus disappearance) was analysed with a repeated measures ANOVA with stimulus category (threatening, non-

threatening), actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), and channel (Cz, Pz) as the within-subjects factors.

The mean amplitude of power in the alpha and beta bands was averaged over the posterior channels (O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P3, Pz, P4, P8). The selection of the channels was made in accordance with the literature. Indeed Krause *et al.* (2000) showed the influence of the emotional content of the stimulus on alpha band in the posterior electrodes while van der Meer *et al.* (2008) showed, over the same channels, the influence of motion's characteristics on beta band.

Regarding the analysis of the theta band, we selected the occipital channels (O1, Oz, O2) according to the work of van der Weel *et al.* (2009) where it is shown a modulation of theta power by the temporal structure of looming stimuli.

Moreover the high gamma was analysed on the central (C3, Cz, C4) and occipital (PO7, O1, Oz, O2, PO8) channels following the study of Quinn *et al.* (2014) on perceptual binding and multisensory integration.

In all the frequency band's analyses we compared the different time periods: during stimulus presentation (500-1000 ms), the period immediately after the stimulus disappearance (1000-1500 ms), and the post stimulus period (1500-2000 ms); stimulus category (threatening, non-threatening); and actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s).

Results

Behavioural Responses

Mean fear ratings were higher for snakes (-.19) and spiders (-.66) than for butterflies (-2.13) and rabbits (-2.08), $t(17) = -5.34$, $p < .001$. This provides a check on our manipulation of how threatening the different types of stimuli were.

To identify outliers, we calculated the Z-score for each TTC judgment, separately for each participant and level of actual TTC. Trials with Z-scores greater than +3 or less than -3 were considered outliers and excluded from analyses (0.8% of trials). An analysis of variance (ANOVA) was run on mean TTC judgments including actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s), stimulus category (threatening, non-threatening), and initial stimulus size (400, 500 pixels wide) as within-subjects factors. Figure 1 shows the behavioural results. There was a significant effect of actual TTC, $F(4, 72) = 32.06$, $p < .0001$, with responses increasing monotonically with actual TTC. There was also a marginal effect of stimulus category, $F(1, 18) = 4.19$, $p = .055$, with TTC being reduced for threatening compared to non-threatening stimuli, consistent with previous results (Brendel *et al.*, 2012; Vagnoni *et al.*, 2012). There was also a marginally significant interaction between these factors, $F(4, 72) = 2.43$, $p = .056$. It seems that threatening stimuli, relative to the non-threatening, were not underestimated for all the time-to-collisions. The pattern of this interaction is not linear given that the underestimation of threatening stimuli does not increase, nor decrease, with the increase, or decrease, of time-to-collision. Moreover, no such interaction was apparent in our previous experiments using this paradigm (Vagnoni et al., 2012). Finally, there was also a significant effect of initial stimulus size, $F(1, 18) = 8.27$, $p < .02$, with shorter judgments following presentation of larger, than smaller, images.

To isolate variance specifically related to individual differences in fear of the threatening stimuli, we regressed fear ratings for threatening on ratings for non-threatening, and calculated the residuals. Similarly, for TTC judgments, we regressed mean judgments for threatening stimuli on judgments for non-threatening stimuli and calculated the residuals. The residuals estimated how much more afraid of snakes and spiders a participant was than would have been predicted by their fear of butterflies and rabbits. In the case of TTC judgments, the residuals estimated how much earlier a participant judged the arrival time of threatening

stimuli than would have been predicted by their TTC for non-threatening stimuli. The residuals for fear and TTC judgments were significantly negatively correlated, $r(17) = -.621$, $p < .005$, indicating that people who reported more fear of snakes and spiders, relative to their fear of butterflies and rabbits, showed larger underestimation of TTC of these threatening stimuli. These results replicate our previous findings (Vagnoni et al., 2012).
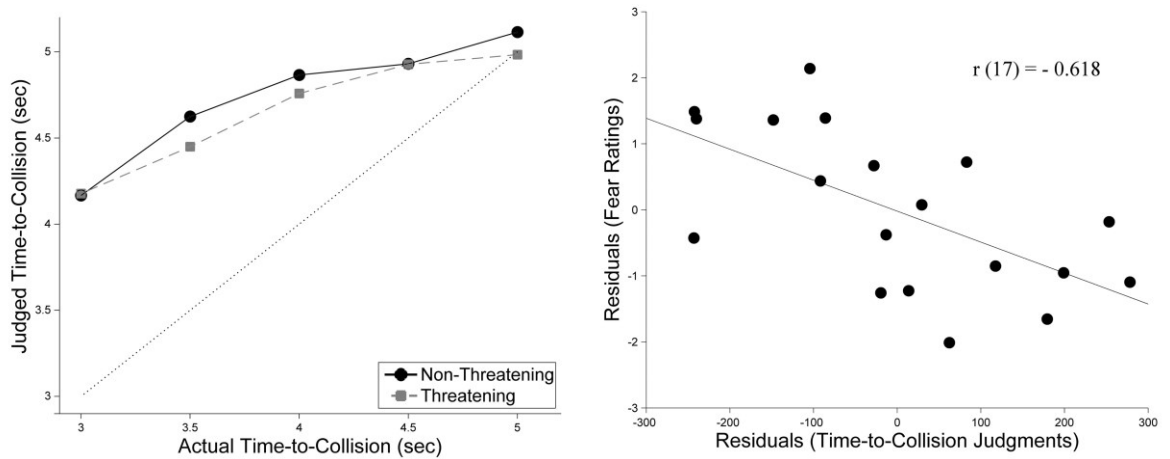

Figure 1: Left panel: judged TTC as a function of actual TTC. Judgments increased monotonically as a function of actual TTC for non-threatening (butterflies and rabbits) and threatening (snakes and spiders) stimuli. The light grey dotted line indicates veridical judgments. There was a clear bias to underestimate TTC for threatening compared to nonthreatening stimuli. Right panel: scatterplot showing relation of TTC judgments and fear. For both TTC judgments and fear ratings, variance specifically related to the threatening stimuli was isolated by calculating the residuals regressing scores for threatening on those for non-threatening stimuli. These residuals were significantly negatively correlated, indicating that greater fear was associated with increased tendency to underestimate TTC.

VEPs

The VEPs analysis was focused on components found in the literature being modulated by the emotional content of the visual stimuli or by the motion characteristics. This section is organised according to the latency of the component analysed, starting from the earlier components to the later ones.

P1 and N1. The P1 amplitude was modulated by the emotional content of the stimulus, with decreased amplitude for threatening compared to non-threatening stimuli, $F(1, 18) = 24.71$, $p < .001$ (Figure 2). This main effect was explained by a significant interaction between stimulus category and channel, $F(2, 36) = 26.524$, $p < .001$, which appeared as a gradient with the difference between threatening and non-threatening stimuli being more marked on the occipital channels, $t(18) = -6.07$, $p < .001$ (M for threatening = 1.32 µV, SE = 0.64; M for non-threatening = 2.86 µV, SE = 0.60), relative to the occipito-parietal channel, $t(18) = -3.61$, $p < .005$ (M for threatening = 3 µV, SE = 0.50; M for non-threatening = 3.62 µV, S.E. =0.52), and no difference between threatening and non-threatening on the parietal channels, $t(18) = -.21$, $p = 0.836$ (M for threatening = 2.73 µV, SE = 0.42; M for non-threatening = 2.75 µV, SE = 0.41). Finally, there was a significant effect of hemisphere, with the P1 being enhanced over the right hemisphere, $F(1, 18) = 10.08$, $p < .01$. We did not find an interaction between stimulus category and TTCs, $F(4, 72) = 1.37$, *n.s.* The effect of stimulus category, hemisphere and the interaction between stimulus category and channel imply that emotional stimuli are processed differently, especially on the posterior sites.

Our results showed that also the early frontal N1 was modulated by the emotional content of the stimulus, being decreased when threatening stimuli were presented, $F(1, 18) = 25.86$, $p < .001$ (Figure 3). The ANOVA showed a significant effect of TTC, $F(4, 72) = 2.75$, $p < .05$ and an interaction between channel and TTC, $F(4, 72) = 2.77$, $p < .05$. These effects were modulated by a significant three-way interaction between stimulus category, channel and TTC, $F(4, 72) = 2.83$, $p < .05$. Given this three-way interaction, we performed separate ANOVAs for threatening and non-threatening stimuli. For threatening stimuli there was a significant main effect of TTC, $F(4, 72) = 3.59$, $p = .01$. The amplitude of the N1 frontal changed according to the different TTCs but not in an obvious way. The amplitude was less negative for TTC equal to 3.0 s (M = -0.87 µV, SE = 0.50) relative to the amplitude for TTC

equal to 3.5 (M = -1.83 μV, SE = 0.38) and 4 (M = -1.78 μV, SE = 0.36). The mean

amplitude for TTC equal to 4.5 was -1.2 μV (SE = 0.44) and -1.4 μV (S.E. = 0.40) for TTC

equal to 5.0 sec. Therefore the amplitude did not increase nor decrease according to the TTC.

Regarding the ANOVA performed on non-threatening stimuli, we did not find any significant

result. It seems that threatening and non-threatening stimuli are still, after the P1, processed

differently.

The late N1 parietal increased in amplitude as approach speed increased, $F(4, 72) =$

3.07, $p < .05$ (Table 1). This pattern broke down, however, for the slowest stimulus; indeed

the amplitude of the N1 parietal increased when stimuli with a TTC of 5 seconds were

presented. We found a significant effect of hemisphere, $F(1, 18) = 6.55, p < .05$ so that the

amplitude across the left hemisphere was less positive, and a significant interaction between

stimulus category and channel, $F(1, 18) = 14.63, p < .002$, and a significant three-way

interaction between stimulus category, hemisphere and channel, $F(1, 18) = 6.20, p < .05$, but

critically no significant interactions involving TTC. To investigate the three-way interaction

we performed separate ANOVAs for each hemisphere. For the left hemisphere we found a

significant interaction between stimulus category and channel $F(1, 18) = 7.15, p = .01$, with

the mean amplitude when threatening stimuli were presented being more negative (M = 0.26

μV, SE = 0.58) relative to when non-threatening were presented (M = 0.75 μV, SE = 0.50) on

channel P3 and the reverse pattern on channel P7 (threatening: M = -0.35 μV, SE 0.66; non-

threatening: M = -0.46 μV, SE 0.56). Regarding the right hemisphere we found a significant

interaction between stimulus category and channel $F(1, 18) = 21.61, p < .01$, with the mean

amplitude when threatening stimuli were presented being less positive than when non-

threatening were presented on channel P4 (for the threatening M = 0.95 μV, SE = 0.44; for

the non-threatening M = 1.48 μV, SE = 0.53) and the reverse pattern on channel P8 (for the

threatening M = 1.29 µV, SE = 0.64; for the non-threatening M = 0.88 µV, SE = 0.80). This

pattern suggests that perceived threat shifts activations more laterally.

Actual TTC (sec)	Non-threatening	Threatening	Averaged Non-threatening and Threatening
3	0.473 (1.94)	0.157 (2.17)	0.315 (2.02)
3.5	0.451 (2.22)	0.679 (2.10)	0.565 (2.11)
4	0.934 (2.00)	0.433 (1.77)	0.684 (1.81)
4.5	1.024 (1.96)	0.705 (1.53)	0.865 (1.81)
5	0.809 (1.88)	0.448 (1.75)	0.629 (1.75)

Table 1. The mean (with SD) peak amplitude (µV) of the N1 parietal in response to the five different TTC (sec)

for non-threatening (second column), threatening (third column) and for the average of non-threatening and

threatening stimuli (fourth column).

The N1 occipital was modulated by the emotional content of the stimulus, enhanced

for threatening relative to non-threatening stimuli, $F(1, 18) = 15.12$, $p < .002$ (Figure 2). We

found a significant interaction between stimulus category and channel, $F(2, 36) = 7.05$, p

$= .003$, and a significant interaction between stimulus category, hemisphere, and channel, $F(2,$

$36) = 3.29$, $p < .05$. When threatening stimuli were presented on the screen, the amplitude of

the N1 was more positive in the right hemisphere compared to the left, but only for the

posterior-occipital channels (PO8 M = 2.07 µV, SE = 0.79; PO7 M = 1.19 µV, SE = 0.87).

Moreover, we found a significant interaction between TTC and channel, $F(8, 144) = 2.26$, p

$< .05$. This interaction is not interpretable given that the amplitude does not increase or

decrease according to the increase or decrease of the TTC. Indeed the amplitude became

more positive for stimuli with a TTC of 3.5 (in O1-O2 M = 1.56 µV, SE = 0.81; in PO3-PO4

M = 1.57 µV, SE =0.93; in PO7-PO8 M = 1.63 µV, SE = 0.93), 4 (in O1-O2 M = 1.57 µV,

SE = 0.74; in PO3-PO4 M = 1.49 µV, SE =0.74; in PO7-PO8 M = 2.06 µV, SE = 0.81), 4.5

(in O1-O2 M = 1.73 µV, SE = 0.74; in PO3-PO4 M = 1.81 µV, SE =0.78; in PO7-PO8 M =

2.02 µV, SE = 0.79) compared to the amplitude when stimuli with a TTC of 3.0 (in O1-O2 M

= 1.21 µV, SE = 0.78; in PO3-PO4 M = 1.22 µV, SE =0.85; in PO7-PO8 M = 1.46 µV, SE =

0.82) or 5.0 (in O1-O2 M = 1.14 µV, SE = 0.71; in PO3-PO4 M = 1.28 µV, SE =0.79; in

PO7-PO8 M = 1.73 µV, SE = 0.81) were presented. However we did not find an interaction

between stimulus category and TTC, $F(4, 72) = 1.05$, *n.s.*

In summary, these results show how emotion affects the early stages of stimulus

processing; modulating the brain activity within 100-150 ms, the characteristic latency of the

P1. Regarding the N1, we identified three different sub-components: the frontal, the parietal

and the occipital component. The occipital was strongly influenced by the emotional content

of the stimulus and more on the occipital channels than on the occipito-parietal ones. The N1

frontal was clearly influenced by the emotional content of the stimulus, being reduced as a

threatening stimulus was presented. Regarding this component, we did find an interaction

involving both the stimulus category and the speed of approach but it is difficult to draw

conclusions from this interaction. Indeed, when we explored it more deeply with separate

ANOVAs, one for each stimulus category, the only significant effect that we found was a

main effect of TTC when a threatening stimulus was presented. Finally, the N1 parietal

showed an interesting pattern, with its amplitude modulated by the speed of approach of the

stimuli. This component was also modulated by the stimulus category and hemisphere, with

the activity shifted more laterally when a threatening stimulus was presented. However, we

did not find any significant interaction between speed of approach and stimulus category.

EPN and LPP. Regarding the EPN, our results showed a significant effect of stimulus

category $F(1, 18) = 12.48$, $p < .005$ (Figure 2), a significant effect of channel, $F(4, 72) =$

56.48, *p* < .0001 and a significant interaction between stimulus category and channel, *F*(4, 72) = 8.95, *p* < .0001, with the amplitude being significantly less positive when a threatening stimulus was on the screen for channels O1 and O2, *t*(18) = -3.53, *p* < .005, channels PO3 and PO4, *t*(18) = -3.82, *p* < .002, channels PO7 and PO8, *t*(18) = -2.09, *p* = .051, channels T7 and T8, *t*(18) = -2.82, *p* < .02, but not for channels P7 and P8, *t*(18) = -1.33, *n.s.*

For the LPP (calculated before the stimulus disappearance i.e. 400-1000 ms) we found a significant interaction between channel and stimulus category, with a significant difference between threatening and non-threatening only in Cz, *F*(1, 18) = 9.01, *p* < .01, with the amplitude being more positive when threatening stimuli were presented. For the LPP post-stimulus (calculated after the stimulus appearance i.e. 1400-1800 ms) we found a significant effect of channel *F*(1, 18) = 9.454, *p* = .007, and a significant interaction between stimulus category and channel with the LPP being enhanced for threatening stimuli in Cz, *F*(1, 18) = 7.12, *p* < .02 (Figure 4).
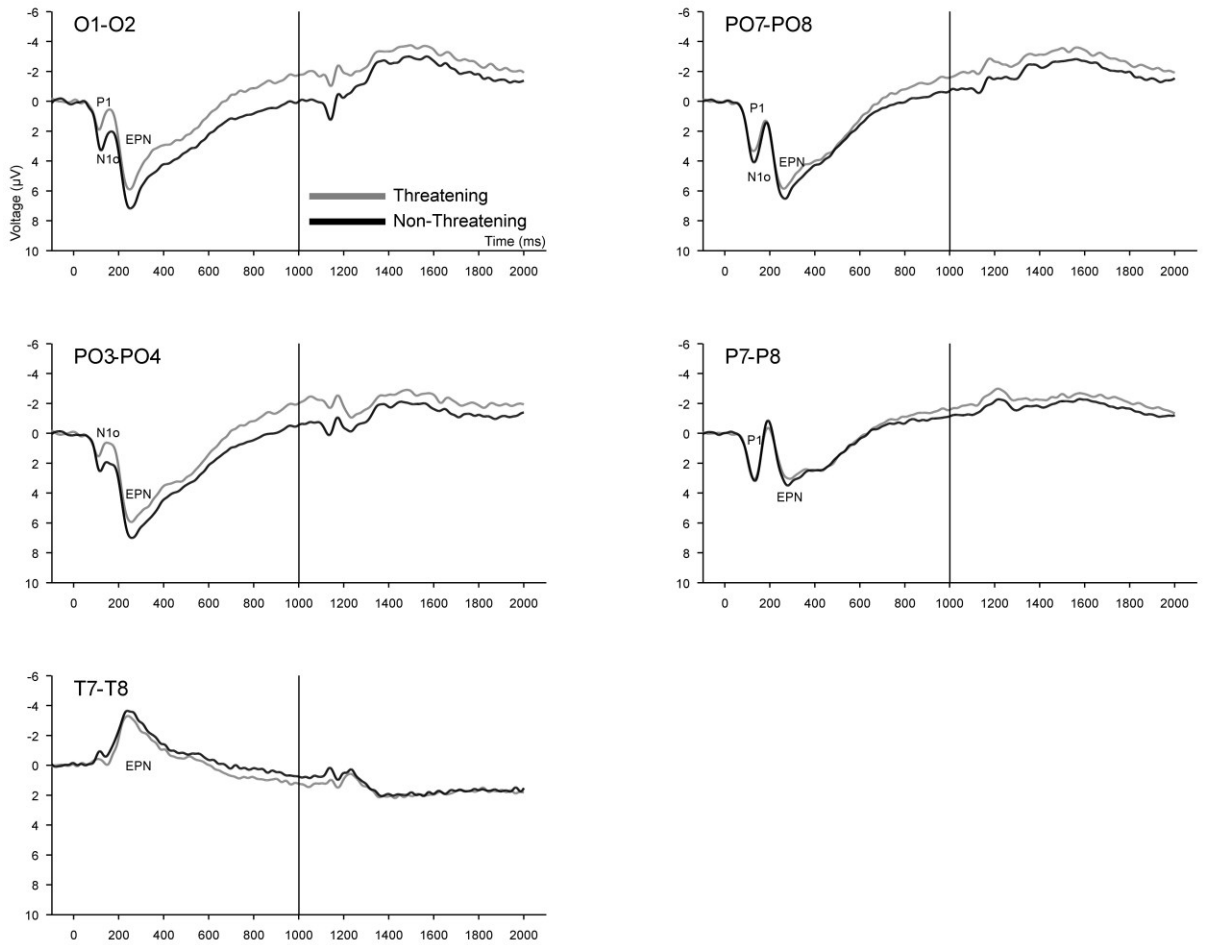
Figure 2. Averaged VEP waveforms at occipital (O1-O2), occipito-parietal (PO3-PO4; PO7-PO8), parietal (P7-P8) and temporal (T7-T8) electrodes. The earliest positive-going (downward) deflection is the P1, which is smaller for threatening stimuli than non-threatening stimuli. The difference between threatening and non-threatening stimuli is more marked on the occipital channels (O1-O2) relative to the occipito-parietal (PO7-PO8) channel and no difference between threatening and non-threatening on the parietal channels (P7-P8). The second, negative-going (upward), deflection is the N1 occipital, which is less positive for threatening relative to non-threatening stimuli. The third one is the EPN, which is less positive for the threatening stimuli relative to the non-threatening stimuli. The EPN is significantly less positive when a threatening stimulus was on the screen for channels O1 and O2, channels PO3 and PO4, channels PO7 and PO8, channels T7 and T8, but not for channels P7 and P8. These three components were clearly modulated by the emotional content of the stimuli. The black vertical line at 1000 ms represents the stimulus disappearance.
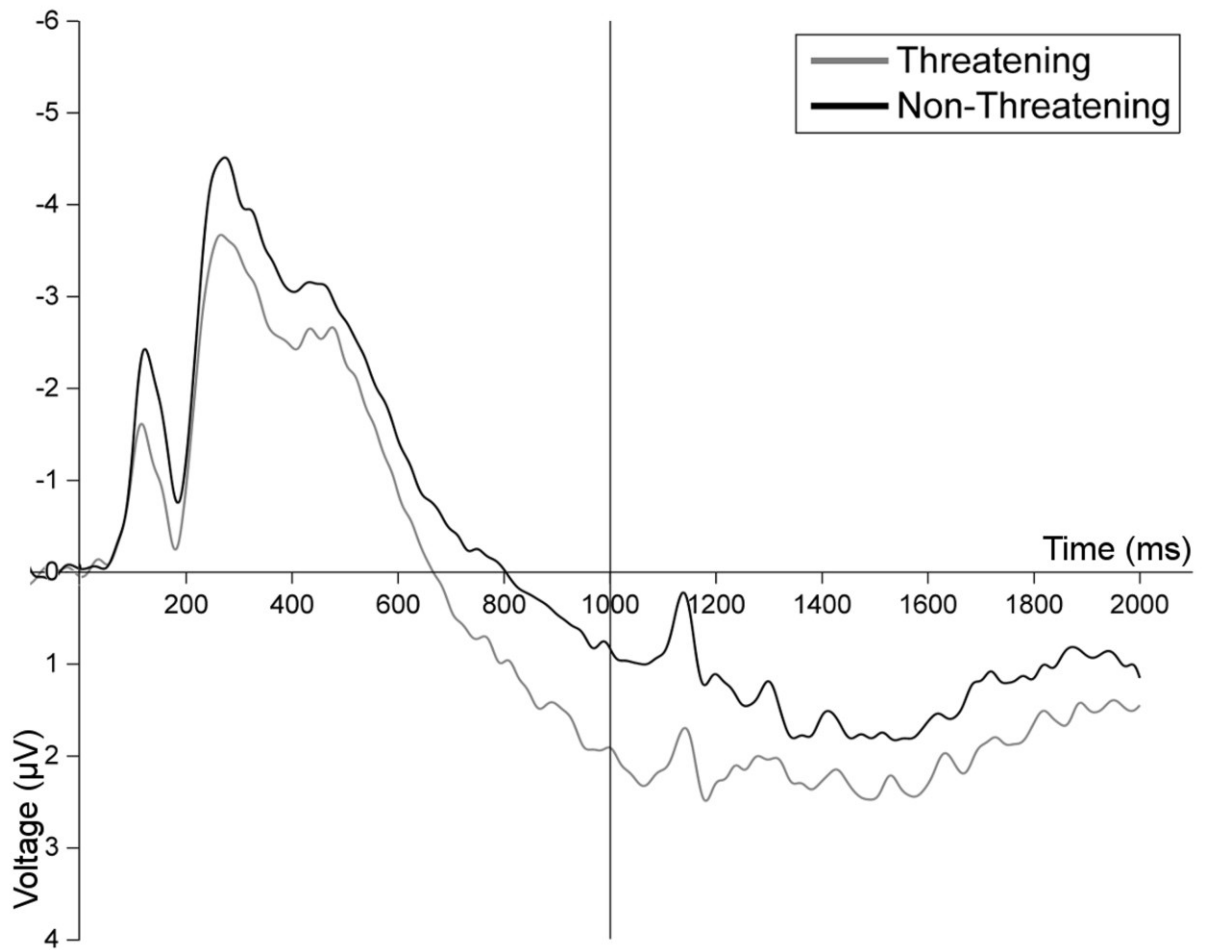
Figure 3: Averaged VEP waveforms at the frontal electrodes (F7, F3, FZ, F4, F8). The upward going deflection between 110-135 ms is the N1 frontal, which is decreased for threatening, relative to non-threatening, stimuli. The black vertical line at 1000 ms represents the stimulus disappearance.
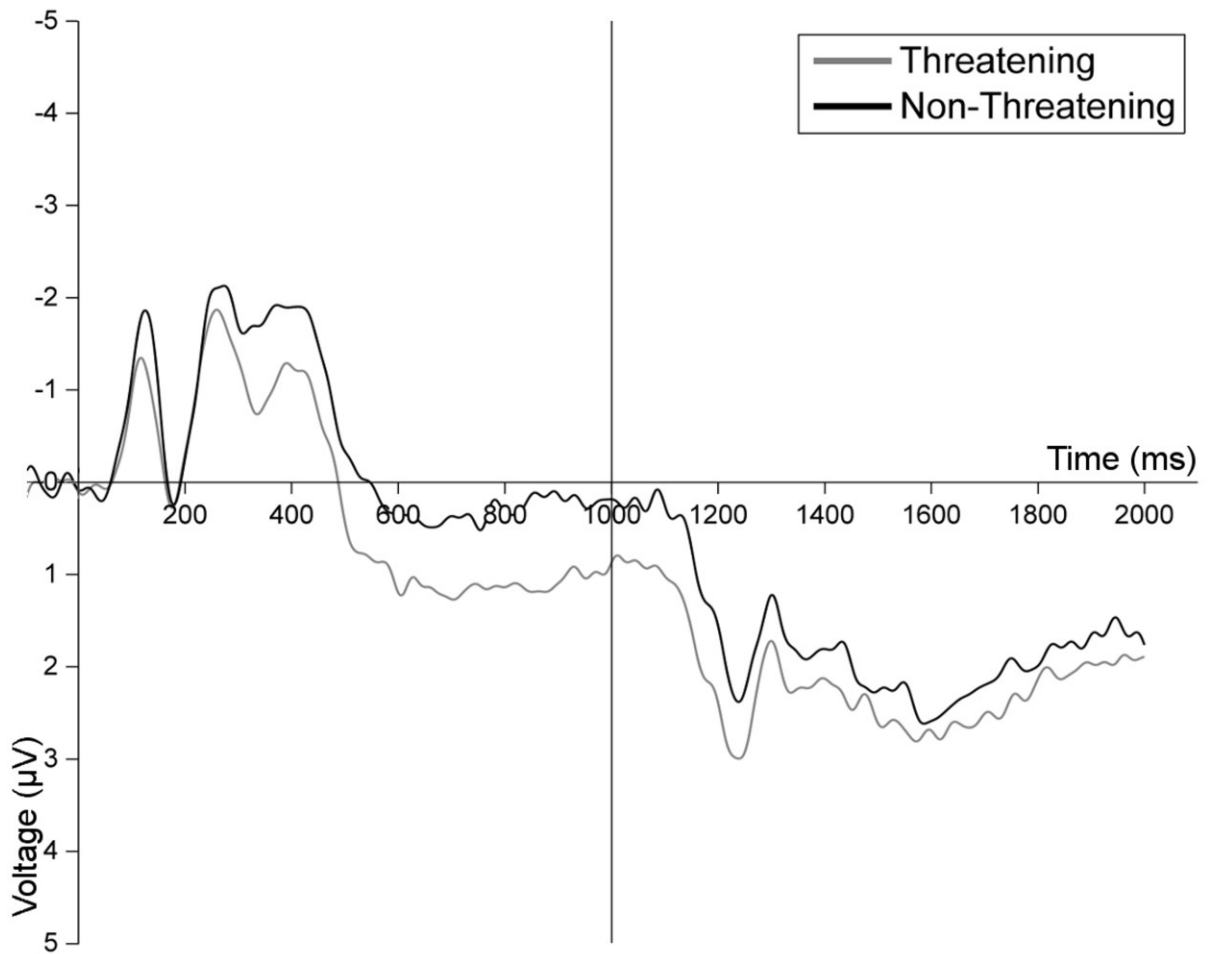
Figure 4: Averaged VEP waveforms at Cz. The LPP is clearly enhanced for threatening, relative to non-threatening, stimuli both before and after the stimulus presentation (black vertical line at 1000 ms).

Stimulus-induced oscillations

Alpha band (8–13 Hz). The ANOVA on the average of alpha power showed a significant effect of time period, $F(2, 36) = 20.52$, $p < .001$, with less desynchronization during the third time period (first time period M = -2.97 μV, S.E. = 0.53; second time period M = -2.22 μV, S.E. = 0.42; third time period M = -0.98 μV, S.E. = 0.24). There was also a significant main effect of stimulus category, $F(1, 18) = 9.66$, $p < .01$, with more desynchronization during the presentation of threatening relative to non-threatening stimuli (Figure 5). The interaction between time period and stimulus category was not significant,

$F(2, 36) = 2.32$, p = 0.11. Moreover, there was no significant effect of actual TTC, $F(4, 72) = 1.62$, *n.s.*, nor the interaction between stimulus category and TTC, $F(4, 72) = 2.03$, *n.s.*

Beta band (15–25 Hz). The ANOVA on the averaged beta power revealed a significant effect of time period, $F(2, 36) = 25.90$, $p < .001$, actual TTC, $F(4, 72) = 2.73$, $p < .05$, and the interaction between time period and actual TTC $F(8, 144) = 2.84$, $p < .01$. The effect of stimulus category, however, was not significant, $F(1, 18) = 3.13$, $p = .094$ (Figure 5), nor did it interact with the other factors.

Given the presence of the time period effect, we ran separate ANOVAs for each time period. The ANOVA for the first time period (between 500 and 1000 ms) revealed no significant effect of stimulus category, $F(1, 18) = 1.99$, $p = .175$ (Figure 5); but a significant effect of actual TTC, $F(4, 72) = 5.02$, $p < .002$ (Table 2) so that the desynchronization of the beta band increased as the time-to-collision decreased (mean amplitude beta band for time-to-collision equal to 3.0 M = -1.67 µV, S.E. = 0.23; for time-to-collision equal to 3.5 M = -1.42 µV, S.E. = 0.21; for time-to-collision equal to 4.0 M = -1.34 µV, S.E. = 0.21; for time-to-collision equal to 4.5 M = -1.28 µV, S.E. = 0.23; for time-to-collision equal to 5.0 M = -1.42 µV, S.E. = 0.22). There were no other significant effects.

We further investigated whether beta power changes as a function of TTC. We calculated the regression coefficient, regressing the averaged beta power across posterior sites (O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P3, Pz, P4, P8), on the five actual TTCs. Our results show that during the period in which the stimulus is visible (500-1000 ms) beta activity over posterior sites changes as a function of TTC, specifically there was more de-synchronization as the TTC decreases (*slope* = 0.115, *t(17)* = 3.49, $p = .002$).

Actual TTC (sec)	Non-threatening	Threatening	Averaged Non-threatening and Threatening
3	-1.649 (1.17)	-1.642 (0.97)	-1.645 (1.02)
3.5	-1.361 (0.94)	-1.496 (0.92)	-1.428 (0.91)
4	-1.249 (0.85)	-1.433 (1.12)	-1.341 (0.92)
4.5	-1.297 (1.03)	-1.267 (1.07)	-1.282 (1.01)
5	-1.328 (1.01)	-1.531 (1.05)	-1.429 (0.97)

Table 2. The mean (with SD) amplitude (μV) of the beta power in response to the five different TTC (sec) for non-threatening (second column), threatening (third column) and for the average of non-threatening and threatening stimuli (fourth column).

Theta band (4–7 Hz). The ANOVA on the average of theta power did not show a significant effect of time period, $F(2, 36) = 0.51$, *n.s.,* nor of stimulus category, $F(1, 18) = 0.34$, *n.s.,* nor of actual TTC, $F(4, 72) = 0.37$, *n.s.,* nor of the interaction between stimulus category and actual TTC, $F(4, 72) = 1.56$, *n.s*

High gamma band (70-190 Hz). Regarding the ANOVA performed on central electrodes, we found a significant interaction between time period and stimulus category, $F(2,36) = 4.52$, $p = 0.01$. To further investigate this interaction we performed separated ANOVA, one for each time period. The only significant effect was the effect of stimulus category during the second time period $F(1,18) = 6.45$, $p = 0.02$. After the presentation of threatening stimuli, there was clearly more desynchronization on high gamma band.

Regarding the ANOVA performed on occipital channels, with time period (500-1000 ms, 1000-1500 ms, 1500-2000 ms), stimulus category (threatening, non-threatening) and

actual TTC (3.0, 3.5, 4.0, 4.5, 5.0 s) as within-subjects factors, there were no significant effects.

Thus, we found an effect of TTC on beta oscillations limited to the period that the stimulus was visible on the screen, in contrast to the effect of threat on alpha oscillations, which continued throughout the period during which participants imagined the stimulus continuing to approach. Regarding the high gamma band, we found an effect of threat soon after the disappearance of the visual stimulus only over the central electrodes and not over the occipital ones.

The results from the analysis of the theta band were not statistically significant.
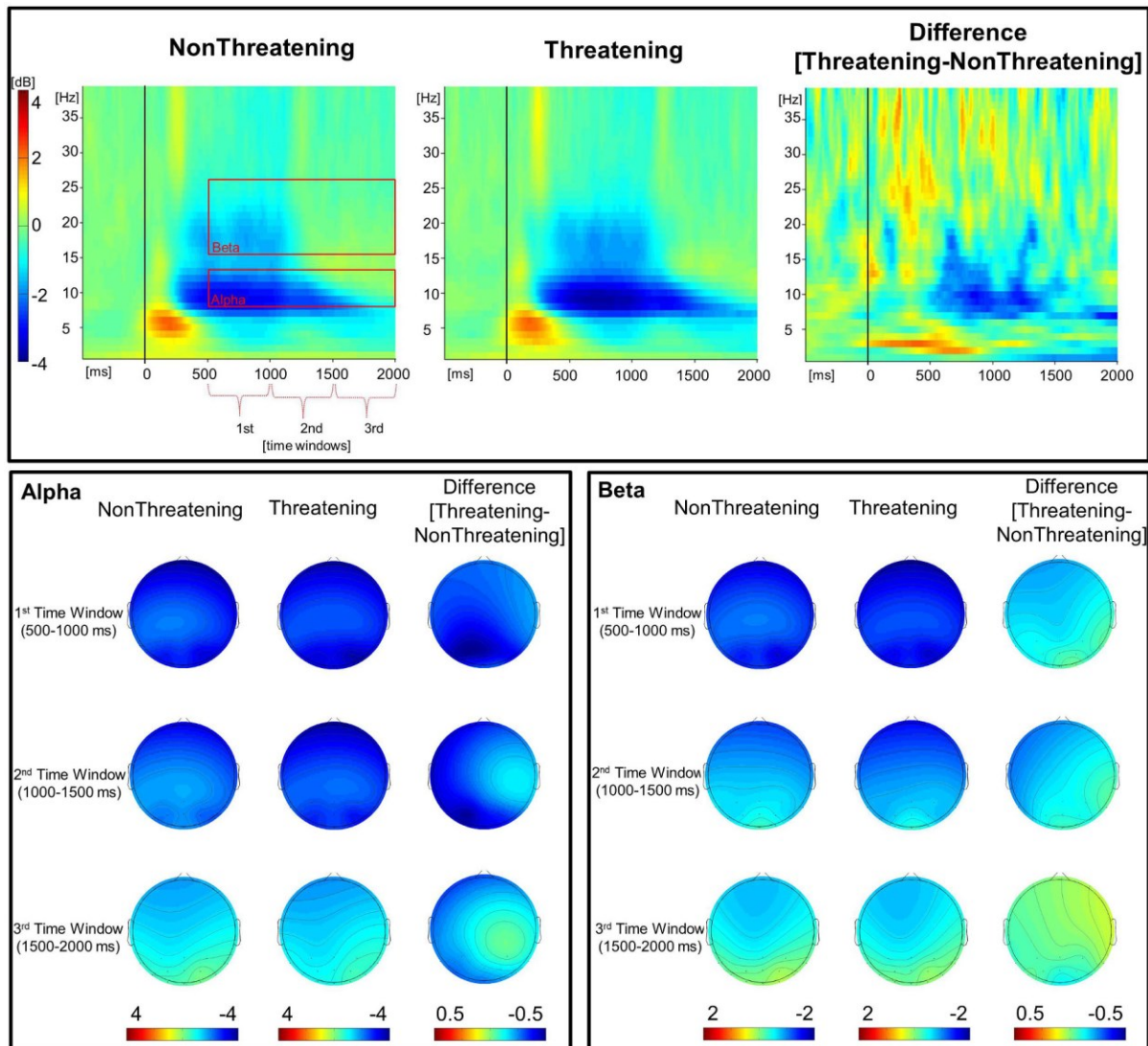
Figure 5: The colour maps represent the grand mean time–frequency representations of EEG spectral power over the occipito-parietal electrodes (O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P3, Pz, P4, P8). Baseline-rescaled responses were averaged across all subjects. The colour maps represent average oscillatory power during the 3 periods 500-1000 ms, 1000-1500 ms, 1500-2000 ms in the alpha (8–13 Hz) and beta (15–25 Hz) bands. In the first panel the colour map on the left represents the grand mean for non-threatening stimuli, the second represents the grand mean for threatening whereas the third one the grand mean of the difference between threatening and non-threatening stimuli. The brackets specifies the three different periods while the two red square the frequency bands. On the left of the lower panel there are the topographical maps representing the alpha band for the non-threatening, threatening and the difference between threatening and non-threatening during the three different time periods. On the right of the lower panel is represented, instead, the topographical maps for the beta activity. It is clear from the figure that alpha activity is modulated by the emotional content of the stimulus. This difference is sustained across the three different time-periods (although the difference is less

robust during the third period). The beta band, in contrast, is unaffected by the emotional content of the stimulus at any time period.

Discussion

We investigated neural responses to threatening and non-threatening looming stimuli with different TTCs. Both speed of approach and threat modulated several aspects of visual processing, measured both with VEPs and event-related oscillations. We found also components (like the N1 frontal and the N1 parietal) modulated by both the speed of approach and the emotional content of the stimulus but, critically, we did not find any meaningful interaction between these two factors. Indeed, the N1 frontal seems to be modulated both by the semantic content of the stimulus and the speed of approach but in an uninterpretable way. When threatening stimuli were on the screen the amplitude of this component was modulated by the different time-to-collision but the amplitude did not increase nor decrease according to them making difficult to draw any conclusions.

These results have implications for understanding the modulation of perceived TTC by threat recently reported in the literature (Brendel *et al.*, 2012; Vagnoni *et al.*, 2012). In particular, they suggest that threat does not modulate the mechanisms involved in interpreting the optical expansion specifying looming. Rather, these results suggest that threat may produce a separate bias in the visual system.

The behavioural results partially replicated previous findings: the arrival time of threatening stimuli is underestimated relative to the arrival time of non-threatening stimuli (Brendel *et al.*, 2012; Vagnoni *et al.*, 2012), but not in all time-to-collision conditions. Moreover, the magnitude of this underestimation is related to individual differences in fear for the threatening stimuli used in this study (snakes and spiders). We found a significant correlation between trait fear ratings and TTC judgments indicating that threatening stimuli are perceived as making contact sooner than non-threatening stimuli especially for those who

are fearful of snakes and spiders. This correlation shows that the actual fear of threatening stimuli can modulate the strength of the underestimation bias for threatening stimuli.

The influence of emotion on neural processing of visual stimuli

The VEP analysis showed that both the emotional content of the stimulus as well as the speed of approach modulate the timing and amplitude of short, middle and long latency components. The P1 is modulated by the emotional content of the stimuli with a smaller P1 when threatening stimuli are presented. Given that the P1 is most often interpreted as being an index of attention allocation in extrastriate visual cortex (Smith *et al.*, 2003), these results suggest that positive and negative stimuli are receiving different amounts of attention very early in the information-processing stream. Zajonc (1980) and others have suggested that the role of emotion is to focus our information processing resources on, and guide our behavioural responses to, important stimuli. Clearly, being able to differentiate threatening from non-threatening stimuli already within the first 100 ms is useful to engage in a fast and appropriate response. The faster we can separate negative from positive stimuli, the faster we can engage an appropriate response strategy, and the more successful we will be in responding to the world (Smith *et al.*, 2003). There is evidence, in the literature, of P1 modulation by the emotional content of stimuli (Smith *et al.*, 2003; Carretié *et al.*, 2004), though less clear is the direction of this modulation. Indeed, if on one hand there is evidence showing a larger P1 for negative relative to positive stimuli (Smith *et al.*, 2003; Carretié *et al.*, 2004), on the other there are demonstrations of the opposite pattern (Begleiter *et al.*, 1967, 1969).

Begleiter et al. (1967, 1969) elicited ERPs with neutral visual stimuli that were affectively conditioned by using words of unpleasant, neutral, and pleasant valence. The authors found that if participants were not notified of an association between words and

figures just before the ERP session, the amplitude was lowest for unpleasantly conditioned stimuli, whereas the opposite pattern was obtained from subjects that were aware of the presence of an association between words and figures.

Affective VEP findings show a great deal of variability across studies in the early latency range. Different mixes of stimulus valence categories and arousal levels might induce processing differences that have not yet been investigated systematically. Even the varying number of stimulus repetitions could further modulate these affective VEP effects (Olofsson *et al.*, 2008).

Regarding the N1 component, we found an interesting pattern with the N1 frontal and occipital being influenced by the emotional content of the stimulus and the N1 parietal being modulated by speed of approach. Indeed we found a smaller mean amplitude of N1 early frontal (Bailey *et al.*, 2012) and a greater amplitude of the N1 occipital when threatening stimuli were presented. Likewise, the results on the N1 parietal are consistent with previous evidence (Lorteije *et al.*, 2008) with the component increasing in amplitude for faster stimuli.

The EPN represents the process of selecting emotional arousing stimuli for further processing (Dolcos & Cabeza, 2002; Schupp *et al.*, 2004). Consistent with that interpretation, our results show that the EPN is enhanced for the threatening stimuli. The LPP is represented by a long-lasting elevated ERP positivity to arousing pictures (Amrhein *et al.*, 2004; Cuthbert *et al.*, 2000; Ito *et al.*, 1998a,b; Keil *et al.*, 2002; Mini *et al.*, 1996; Olofsson & Polich, 2007; Palomba *et al.*, 1997; Schupp *et al.*, 2000). According to several authors, the LPP reflects the allocation of attentional resources to salient events (Nordström & Wiens, 2012). Carretié and colleagues (2006) presented affective picture stimuli during a non-affective discrimination task. An increase in VEP amplitude at 680 ms following stimulus onset was present for unpleasantly arousing stimuli. In line with these findings, our results show greater mean amplitude of the LPP following the presentation of threatening stimuli. Our results highlight

that the nature of the stimulus – particularly its semantic content – is able to modulate the LPP even after it has disappeared. These findings are especially interesting in relation to the interpretation given by several authors that the LPP is involved in memory formation (Olofsson *et al.*, 2008; Palomba *et al.*, 1997; Azizian & Polich, 2007; Karis *et al.*, 1984; Paller *et al.*, 1988; Dolcos & Cabeza, 2002).

Several authors contend that the analysis of event related synchronization and de-synchronization can help to uncover the dissociation between the neural correlates of the processing of different types of emotional stimuli (Aftanas *et al.*, 1996a; 1996b; 2001; Krause *et al.*, 2000). Aftanas and colleagues (1996a) investigated the event-related desynchronization (ERD) of alpha components in an affective task. Positive and negative emotions were evoked by winning and losing certain amounts of money in a gambling situation while measuring ERD to positive and negative feedback stimuli. The authors found a left frontal activation to the positive feedback stimuli and right frontal activation to the negative feedback stimuli. This effect was restricted to the upper (i.e. 10-12 Hz) alpha band. These findings are evidence in favour of a specific role of frontal hemispheric asymmetries in valence discrimination. This study (Aftanas *et al.*, 1996a) showed that the ERD is able to evidence relatively small differences in emotion processing and appears to be a suitable method with which to study emotion. Therefore, desynchronization in the upper alpha band is associated with semantic processes (Aftanas *et al.*, 2001; Pfurtscheller & Lopes da Silva, 1999) and is influenced by the emotional content of the stimulus in the posterior electrodes (Krause *et al.*, 2000). A growing literature shows that the de-synchronization of the alpha band is not only linked to processes of external attention such as alertness/vigilance and expectancy but might also be associated with perceptual and cognitive processes (Aftanas *et al.*, 2001; Basar *et al.*, 1999; Doppelmayr *et al.*, 1998; Klimesch, 1999). In the present study, threatening stimuli, compared to non-threatening stimuli, induced de-synchronization in the alpha band. We

found that the effect of the stimulus's emotional content on alpha activity began approximately 500 ms after the stimulus presentation and continued until well after the stimulus had disappeared. This suggests that the difference in the processing of the emotional content begins when the stimulus is recognized and is maintained even when the stimulus is not visible (Aftanas *et al.*, 2001). Moreover, the effect of emotion on the high gamma band is present soon after the disappearance of the stimulus only on the central channels. Looming objects contain optical information that could directly specify an action. The action might be an interception (catch) or a defensive response (block), but in either case, the looming stimulus toward the body specifies how rapid that response should be (Field & Wann, 2005). Field and Wann (2005) demonstrated using fMRI that the TTC task, compared to an inflation judgment and closure gap task, produces specific activity in sensorimotor areas. Interestingly, these activations correspond closely to networks previously identified for reaching and grasping (Field & Wann, 2005). Likewise, Billington and colleagues (2001) found sensorimotor responses to looming, relative to static or receding stimuli, that suggest that there is motor preparation in response to an approaching object, even though execution is not intended, underlining the direct and impelling nature of looming events. Obviously, in our case we cannot exclude an initial preparation of the response given that we asked the participant to perform an action (to press the keyboard key). From our results, it seems that threat can disrupt the synchronization of the gamma band that is linked to the actual execution of an action (Ball, 2008) or, perhaps, to the preparation of action due to the simple perception of a looming stimulus (Field & Wann 2005; Billington *et al*., 2011).

Looming related brain activity

In addition to modulation by the emotional content of stimuli, we found neural responses that scaled with the speed of object approach. The first analysis was focused on

specific VEPs and showed that the mean amplitude of the N1 parietal increased with approach speed.

The analysis of oscillation bands has been used, as well as the VEPs analysis, to investigate the perception of moving stimuli (Piantoni *et al.*, 2010; van der Meer *et al.*, 2008). Piantoni and colleagues conducted an EEG experiment to directly compare neural signatures in illusory motion reversal (IMR) and binocular rivalry (BR), a well-studied form of rivalry. The authors found that both IMR and BR show large changes in power in the beta range (14–30 Hz) at the time of a perceptual switch. More importantly, during a stable percept, beta power correlates with the probability of a perception. From their findings, it is clear that beta power associated with veridical motion perception was higher than the power during illusory motion perception. The authors proposed that the amplitude of synchronized beta activity reflects the size of currently active neural coalitions, with less likely percepts associated with smaller coalitions. In our case, instead, the de-synchronization of beta activity increases as the speed of approach increases.

van der Meer and colleagues (2008) compared the influence of structured optic flow and random visual motion to static dots on neural oscillations and found that while infants showed an induced decrease in the amplitudes in the theta band, adults showed an induced increase in the beta band. Therefore, in their experiment van der Meer and colleagues showed that the presentation of stimuli representing the optic flow increased beta-band activity in adults. Starting from these findings, the clear link between beta oscillations and the perception of motion, we investigated the influence of different TTC on beta band. Our findings show that, when the stimulus is visible, beta activity changes as a function of the TTC: de-synchronization increases as objects approach more quickly.

Implications for understanding emotional modulation of looming

The main purpose of this work was to find the neural correlates of the influence of emotion on TTC judgments. We found a modulation of emotion on several components (P1, N1 frontal, N1 occipital, EPN and LPP) and power band (alpha band). Moreover, we found a modulation of the calculation of the speed of approach on other different components (N1 parietal) and power band (beta band). Although we did not find any component or power band modulated by the interaction of these factors, we did find an interesting pattern regarding the modulation of high gamma band. This frequency band was modulated by the semantic content of the stimulus over sensorimotor areas. There is evidence of the activation of the sensorimotor areas by the simple presentation of looming stimuli (Field & Wann 2005; Billington *et al.*, 2011). Threat seems to disrupt the synchronization of the high gamma band over the areas linked to the preparation of an action. This is the only result that could be linked to the neural basis of an interaction. Indeed all the other ones represent more two biases that seem to run in parallel without interacting with each other. Recently, de Vignemont and Iannetti (2015) proposed a dual model of peripersonal space, based on a clear functional distinction between bodily protection and goal-directed action. The authors argue that the two functions of peripersonal space require distinct sensory and motor processes that obey different principles. On the one hand, our results are in line with this differentiation, given that we presented a set of results showing how emotion influences the processing of visual stimuli and another set depicting looming related brain activity. But, on the other hand, we have to keep in mind that just the simple detection of an approaching object is interpreted as a cue for threat. Moreover, the modulation of the high gamma band by threat seems to suggest the existence of an interaction between the sensorimotor activation linked to the action preparation and the stimulus content.

In our behavioural findings, there is not a clear interaction between the effect of stimulus category and time-to-collision. The underestimation bias for the threatening stimuli

does not increase, nor decrease, with the increase, or decrease, of the time-to-collision. It seems more that the underestimation of TTC of threatening compared to non-threatening stimuli may be the result of two different biases: we underestimate the TTC of an approaching stimulus because we interpret it as a cue for threat. In addition to this, the emotional effect makes the underestimation even stronger without interfering with the actual perception of the characteristics of the expansion.

Several nuclei operating at the subcortical level, however, could be involved in the processing of emotional visual stimuli and could have an important role on the modulation of emotion on visual perception. For example, it has been claimed that the role of the pulvinar is to integrate information from visual areas determining the biological relevance of a stimulus (Pessoa & Adolphs, 2010). Because both biological relevance (Pessoa & Adolphs, 2010) and temporal characteristics of looming stimuli (Billington *et al.*, 2011) are processed in subcortical areas future research should consider these nuclei. Indeed, Billington and colleagues (Billington *et al.*, 2011) have found that the superior colliculus and the pulvinar nucleus of the thalamus respond to looming, in addition to cortical regions associated with motor preparation. These authors also implicated the anterior insula in making timing computations for collision events.

Acknowledgments

Abbreviations

BR, binocular rivalry; EEG, electroencephalography; EPN, early posterior negativity; ERD, event-related desynchronization; ERP, event related potential; IMR, illusory motion reversal; LPP, late positive potential; MT, middle temporal visual area; TTC, time-to-collision; VEP, visual evoked potentials.

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