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Electrophysiological spatiotemporal dynamics during implicit visual threat processing

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ABSTRACT

Numerous studies have found evidence for corticolimbic theta band electroencephalographic (EEG) oscillations in the neural processing of visual stimuli perceived as threatening. However, varying temporal and topographical patterns have emerged, possibly due to varying arousal levels of the stimuli. In addition, recent studies suggest neural oscillations in delta, theta, alpha, and beta-band frequencies play a functional role in information processing in the brain. This study implemented a data-driven PCA based analysis investigating the spatiotemporal dynamics of electroencephalographic delta, theta, alpha, and beta-band frequencies during an implicit visual threat processing task. While controlling for the arousal dimension (the intensity of emotional activation), we found several spatial and temporal differences for threatening compared to nonthreatening visual images. We detected an early posterior increase in theta power followed by a later frontal increase in theta power, greatest for the threatening condition. There was also a consistent left lateralized beta desynchronization for the threatening condition. Our results provide support for a dynamic corticolimbic network, with theta and beta band activity indexing processes pivotal in visual threat processing.

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1. Introduction

Quickly processing threatening objects present in the environment is vital for survival. In humans, this initial response is mediated through the limbic system, which includes phylogenetically ancient pathways (LeDoux, 1998; Phelps & LeDoux, 2005). However, there are tightly intertwined interactions between cognitive and emotional processes in that threatening information can modulate early attentional allocation (Carretie, Hinojosa, Martin-Loeches, Mercado, & Tapia, 2004). Consequently, emotional stimuli reflexively engage corticolimbic systems and these contemporaneous processes influence perception and promote adaptive behavior (Bradley, 2009; Ferrari, Bradley, Codispoti, & Lang, 2011).

Processing of threatening visual stimuli involves various complex functions including sensory processing, attention, decision making, and memory. In the last decade a growing number of studies have utilized emotionally evocative stimuli, characterizing

* Corresponding author. *E-mail addresses*: bld095020@utdallas.edu (B.L. DeLaRosa), jhart@utdallas.edu (J. Hart Jr.). various attributes of these stimuli (Lang, Bradley, & Cuthbert, 1999). Two key factors commonly assessed are valence and arousal. Valence refers to the direction of behavioral activation according to the motivational system that is activated, appetitive (toward pleasant emotion) or the defensive (away from unpleasant emotion). Valence modifies allocation of attentional resources and can heighten sensory processing of environmental cues; this occurs at both early and late stages of visual processing (Lane, Chua, & Dolan, 1999). Arousal is orthogonal to valence and refers to the intensity of the emotional activation (Lane et al., 1999; Lang et al., 1999).

Electrophysiological markers have been used to probe processing of emotionally evocative stimuli, revealing a possible processing bias for threatening stimuli. For instance, many early eventrelated potentials (ERP), such as frontal N1, suggest that attention is more readily oriented toward threatening information. However, some posit that the arousal dimension of stimuli recruits attentional mechanisms, and that the frontal N1 potential reflects arousal influences and not basic affective recognition in general (Olofsson, Nordin, Sequeira, & Polich, 2008). More recently it has been shown that when arousal influences are controlled for there is still a processing bias for threatening stimuli over positive







stimuli, suggesting selective processing for threatening stimuli (Sun, Sun, Wang, & Gong, 2012).

Compared to the number of studies that use traditional ERP analysis to study brain responses to threatening stimuli (for review see Olofsson et al., 2008), there are relatively few studies using event-related spectral perturbations (ERSP), a complementary approach (Makeig, 1993). The utility of ERSP for studying neural network activity is based upon strong evidence for oscillatory dynamics as a mechanism of information processing in the brain (Buzsaki, 2006; Cannon et al., 2013; Uhlhaas et al., 2009; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Womelsdorf et al., 2007). Theta activity is of particular interest because studies show oscillations in this frequency band relate to both encoding and retrieval threat processes. To illustrate, in animal models encoding of threat results in increased theta activity between neurons in the lateral amygdala and the CA1 region of the hippocampus (Bienvenu, Busti, Magill, Ferraguti, & Capogna, 2012; Pape, Narayanan, Smid, Stork, & Seidenbecher, 2005; Seidenbecher, Laxmi, Stork, & Pape, 2003), and during emotional arousal neurons in the amygdala produce theta activity (Paré, Collins, & Pelletier, 2002). Furthermore, cortical theta activity also indexes semantic retrieval (Hart et al., 2013), with theta topography being determined by the semantic properties of the object (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008), and fMRI studies show that threat is a feature within visual semantic object memory (Calley et al., 2013).

Electrophysiological studies utilizing threat paradigms report heterogeneous topography in regards to theta oscillations, and resolving this discordance is of interest. Some studies have reported increased posterior theta synchronization for threatening visual stimuli (Aftanas, Reva, Varlamov, Pavlov, & Makhnev, 2004; Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2001a; Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2002; Sun et al., 2012), while others have reported larger frontal theta synchronization (Balconi, Brambilla, & Falbo, 2009). One possible explanation for the previously reported posterior or frontal topographical theta activity in processing threatening or negatively valenced visual stimuli could be that the different paradigms used stimuli that elicited different levels of arousal (high and low). Some investigators have posited that emotionally laden stimuli are initially processed by the amygdala in an automatic and nonconscious manner (without the need of attention) by bypassing the neocortex (Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010). On the other hand, the prefrontal cortex may play a key role in threat processing given its role in integrating information, especially in relation to memory processes, through various connections with other cortical and subcortical areas (Miller & Cohen, 2001). Since corticolimbic theta activity is involved in both the encoding and retrieval step of visual object processing, controlling for arousal influences appears to be an important consideration in clarifying this issue to better understand threat processing.

While the majority of studies regarding electrophysiological aspects of threat processing have focused on theta activity, delta, alpha, and beta power changes may also index relevant neural processes; subsequently, should be investigated for a more encompassing understanding of threat processing. To illustrate, positron emission tomography (PET) studies show a metabolic relationship between frontal cortical delta and subcortical thalamic activity, and in EEG studies it is argued that the functional significance of delta is related to motivational processes (Alper et al., 2006; Knyazev, 2012; Knyazev, Slobodskoj-Plusnin, & Bocharov, 2009). Also, frontal delta power increases have been observed in response to highly arousing images but not to low-arousal images (Balconi et al., 2009). Alpha activity reflects selective cortical inhibition, which plays a role in signal amplification, and recently has been shown to play a specific role in affective attention (Uusberg,

Uibo, Kreegipuu, & Allik, 2013). Beta activity, purportedly representing cortico-cortical local information processing (Jensen et al., 2005), has been associated in studies with a negativity bias. For example, there is early beta activity in visual cortices in response to negative images (Güntekin & Başar, 2010; Keil, Stolarova, Moratti, & Ray, 2007). Furthermore, studies considering patterns of delta and beta activity have been linked to both vigilant and avoidant responses to threat (Putman, 2011; Putman, Arias-Garcia, Pantazi, & van Schie, 2012).

The overarching aim of this study is to utilize data-driven statistical techniques to elucidate spectral, spatial, and temporal electrical patterns during an implicit threat processing task. One goal of this study is to control the arousal dimension, allowing for isolation of the valence component, and investigate theta power changes during implicit threat processing. We predict that there will be early differential theta power changes for the emotionally valenced stimuli, and that with arousal influences controlled for, there will be greater theta power changes in posterior occipital regions for the threatening stimuli compared to the non-threatening stimuli. In addition, we will utilize data driven statistical techniques to characterize delta, alpha, and beta band power changes for an encompassing account of visual threat processing.

2. Materials and methods

2.1. Participants

Thirty-two healthy, right-handed adults between the ages of 19–30 years old (M = 24.01, 19 female) participated in the study. None of the subjects reported neurological impairments. The data from six subjects were excluded, either because of major movement artifact or excessive noise, or because they did not complete the task. Our final cohort thus comprised 26 subjects (19 female). Students were given course credit for a psychology course in exchange for participation. All gave informed consent prior to participation in accordance with the Institutional Review Board of The University of Texas at Dallas.

2.2. Stimuli

We used 90 colored pictures chosen from the International Affective Picture Set (IAPS) set of normed pictures as well as 22 additional pictures selected for the categories of combat scenes (N = 16) and weapons (N = 6) (Calley et al., 2013). These additional pictures were chosen to be of comparable visual complexity and resolution to the set from the IAPS. Each picture was then modified to create a matched, scrambled visual stimulus by randomizing the phase information and recombining it with the original picture's magnitude information (Haxby, Hoffman, & Gobbini, 2002).

The stimuli were derived from two groupings on the pleasantness scale (IAPS scales), one clustered at the pleasant end and the other at the unpleasant end of the scale. They were also chosen from a variety of categories.

The real pictures comprised eight groups of items from six different categories, as follows:

- 1a. Animals threatening (N = 16).
- 1b. Animals nonthreatening (N = 16).
- 2a. Nature scenes threatening (N = 8).
- 2b. Nature scenes nonthreatening (N = 8).
- 3a. Combat threatening (N = 16).
- 3b. Pleasant situations nonthreatening (N = 16).
- 4. Weapons threatening (N = 16).
- 5. Food nonthreatening (N = 16).

Importantly, arousal was not a confounding feature between the threatening (M = 3.23, SD = .39) and nonthreatening (M = 3.11, SD = .38) groups as overall arousal was not different between these two groups, (t(110) = 1.65, p = .10). A more detailed account of stimuli selection and ratings can be found in Calley et al. (2013).

2.3. Behavioral procedures

The 224 pictures of real and nonreal "scrambled" items were pseudo-randomized and presented individually using a Neuroscan system (Compumedics, Inc.) The stimuli were re-randomized and presented on a computer screen approximately 1 meter in front of the subject. Each stimulus was presented for 2700 ms, with a pseudo-random jittered inter-stimulus interval average of 2300 ms. Subjects were instructed to push a button under their right index finger to indicate that they perceived an item to be real (an item they recognized), and to push a button under their right middle finger for a nonreal item (a scrambled image).

2.4. Behavioral analysis

Two subjects were excluded from the behavioral analysis because of equipment problems; however, they remained in the ERSP analysis because we had verification that they were performing the task as they had appropriate reaction times and accuracy rates in the condition where the response system was working. Reaction times and accuracy rates were analyzed to investigate differences between task explicit processing of the real versus scrambled images, and implicit processing of the threatening versus the non-threatening images.

2.5. EEG recording

Continuous EEG was recorded from a 64-electrode Neuroscan Quickcap using Neuroscan SynAmps2 amplifiers and Scan 4.3.2 software with a reference electrode located near the vertex. Data were sampled at 1 kHz with impedances typically below 10 k Ω . Additionally, bipolar electrooculogram (EOG) was recorded from two electrodes to monitor blinks and eye movements (positioned vertically at the supraorbital ridge and lower outer canthus of the left eye). The continuous EEG data were offline high-pass filtered at 0.5 Hz and low-pass filtered at 30 Hz using a finite impulse response (FIR) filter.

2.6. EEG pre-processing

We analyzed the EEG using scripts developed in our lab that implement functions from EEGLAB version 12 (http:// www.sccn.ucsd.edu/eeglab, Delorme & Makeig, 2004) running under Matlab 7.11.0 (The MathWorks, Inc.). Preprocessing consisted of down-sampling to 512 Hz, removing data recorded from poorly functioning electrodes, and correcting for stereotyped artifacts including eye blinks, lateral eye movements, muscle, line noise, and heart rate using the "Runica" algorithm (with the 'extended', 1 option, Delorme & Makeig, 2004; Jung et al., 2000), an implementation of the logistic infomax independent component analysis algorithm of Bell and Sejnowski (1995). Stereotyped artifacts were identified by visual inspection of the spatial and temporal representation of the independent components. Continuous data were then segmented into 2 s non-overlapping epochs spanning from 500 ms before to 1500 ms after the presentation of the visual stimuli. Epochs containing high amplitude, high frequency muscle noise, and other irregular artifacts were removed. Only trials to which the subject responded correctly and those without artifacts were subjected to further analysis, retaining on average 75% of all epochs. Lastly, missing electrodes were interpolated and data were re-referenced to the average reference (Junghöfer, Elbert, Tucker, & Rockstroh, 2000).

2.7. Event-related time-frequency analysis

To assess changes in spectral power that occur after stimuli presentation, we calculated event-related spectral perturbations (ERSP; Makeig, 1993) using the new*timef* function of EEGLAB toolbox. Thirty linearly spaced frequencies from 1 to 30 Hz were estimated using hanning FFT tapering in 50 time windows (-384 to 895 ms). We performed single-trial baseline correction using the prestimulus interval as baseline (Grandchamp & Delorme, 2010).

2.8. STAT-PCA

We utilized an extension of STAT-PCA, a data-driven statistical technique, which incorporates both inferential statistics and data reduction (Spence, Brier, Hart, & Ferree, 2013). More specifically, a mixed-effects general linear model (GLM) was used to assess differences between each of the conditions (threat, nonthreat, and scramble), and a principal components analysis was used to reduce data dimensions for interpretation of statistical results.

Log normalized squared absolute values at each space, time, frequency point (STF) were calculated and used as input for the inferential stage of STAT-PCA. Our experiment has one independent variable, condition, with three levels (threat, nonthreat, and scramble). The statistical model can be written as $P_{sck} = \mu + b_s + \gamma_c + \varepsilon_{sck}$ where *P* is the observed power at a given space-time-frequency point; $s = 1, \dots, 26$ subjects; $c = 1, \dots, 3$ conditions; and $k = 1, \dots, 3$ t_{sc} a variable number of trials in each subject and condition. This is a mixed-effects linear model with subjects as a random effect, b_s , and condition as a fixed effect, γ_c . F statistics for each STF point were calculated to assess the influence of the experimental conditions on log power, and planned *t*-contrasts were calculated from differences between the real and scramble conditions, as well as differences between the threatening and non-threatening conditions. Mean differences between conditions were masked by t-statistics that were significant at the 0.01 level. The linear models were implemented by the mixed procedure in SAS 9.2 (Cary, NC).

After the inferential stage, the masked mean difference estimates were stored as an STF array of 62 electrodes, 30 frequency bands, and 35 time points, which were submitted to a sequential or unfolding PCA. For this analysis, frequencies were subjected to PCA before space and time by reshaping the STF array into a matrix such that the columns indexed frequency and the rows indexed space and time. PCA was performed and returned a set of eigenvalues and eigenvectors (factor loadings), which were subjected to Parallel Analysis (Horn, 1965) to determine the number of factors to retain. This estimates the eigenvalues of a structure-free matrix, and only eigenvalues above the 95% confidence intervals of the null distribution were retained. The retained eigenvectors were varimax rotated and used to calculate the factor scores by projecting the original dataset onto the eigenvectors. The factor scores corresponding to each spectral factor were reshaped such that the columns index electrodes and the rows index time points. PCA was performed on this matrix and factor retention was determined. The resulting eigenvectors represent topographies and their corresponding factor scores represented the time courses (Ferree, Brier, Hart, & Kraut, 2009).

3. Results

3.1. Behavioral results

Reaction times for the real images (M = 872.59 ms, SD = 183.76 ms) were significantly longer compared to the

scrambled images (M = 756.90 ms, SD = 137.78 ms), (t(23) = 4.43, p < .001, one-tailed; Calley et al., 2013). Reaction times for the threatening images (M = 890.74 ms, SD = 197.13 ms) were not significantly longer compared to those for the non-threatening images (M = 854.91 ms, SD = 185.38 ms), (t(23) = 1.67, p = .10). There were not significant differences in accuracy in either the real (M = .93, SD = .09) versus scrambled (M = .92, SD = .11) (t(23) = -0.67, p = .51), or the threat (M = .93, SD = .10) versus non-threatening (M = .93, SD = .08) stimuli (t(23) = -0.52, p = .61).

3.2. Event-related time-frequency results real versus scramble

The contrast of the real images versus the scrambled images resulted in early widespread changes in occipital region electrodes. More specifically, four STF components were retained. The first STF component comprised early, 400–500 ms, alpha (peak 10–11 Hz) activity over bilateral occipital regions (Fig. 1a) The second STF component was very similar to the first in both time and topography, but had a spectral peak at 18 Hz (Fig. 1b). The third STF component was early, 50–200 ms, theta (peak 7 Hz) activity over occipital cortices (Fig. 1c). Finally, the fourth component was delta



Fig. 1. STAT-PCA results for the task condition, real versus scramble. (a–d) Space time frequency (STF) Component 1–4, spectral PCA loadings plotted from the first PCA (left); spatial PCA loadings plotted on topoplot from the second PCA (center); temporal PCA scores plotted as function of time (right). (a) STF Component 1 with a spectral peak at 11 Hz, spatially over bilateral occipital regions, temporally maximal around 400 ms. (b) STF Component 2 with a spectral peak at 18 Hz, spatially over bilateral occipital regions, temporant 3 with a spectral peak at 7 Hz, spatially over bilateral occipital regions, temporally maximal around 150 ms. (d) STF Component 4 with a spectral peak at 2 Hz, spatially over prefrontal regions, temporally maximal around 450 ms.

(peak 2–3 Hz) activity over prefrontal regions around 300–500 ms (Fig. 1d).

3.3. Event-related time-frequency results threat versus nonthreat

In the present study our primary focus was on the differences between the responses to stimuli perceived as threatening and the responses to the nonthreatening stimuli. The following results pertain to the resulting *t* statistics from the contrast of threatening versus nonthreatening images. The PCA decomposition was performed on the estimated mean difference matrix of the two conditions, threat versus nonthreat, masked at a significance level of 0.01. This yielded three STF components.

The first STF component is loaded in the theta band with a peak at 6 Hz. Spatially, this theta activity is left lateralized predominantly around FT7 and FC5. Temporally, this activity peaks at about 575 ms post stimulus (Fig. 2a). Spectrograms at FC5 and FT7 show that there is greater theta power for the nonthreatening condition about 500–600 post stimuli presentation (Fig. 2b).

The second STF component is loaded in the beta1 band with a peak at 18 Hz. Spatially, this beta activity is localized around FC3, with maximal activity around 475 ms post stimulus (Fig. 3a). Spectrograms at FC3 show that there is a larger decrease in beta power in the threat condition (Fig. 3b).

The third STF component is loaded in the theta band with a peak at 5 Hz. Spatially this theta activity has maxima over two regions, one frontal around FPZ and one posterior around 01. The time factor has three peaks, one early around 300 ms, the second around 475 ms, and the third around 650 ms (Fig. 4a). Spectrograms show that at electrode 01 there are early theta power changes from 200 to 500 ms after stimulus presentation with greatest power increase for the threat condition (Fig. 4c). Electrode FPZ shows theta power changes from 400 to 700 ms post stimulus, again with greatest power increase for the threat condition (Fig. 4b).



Fig. 2. STAT-PCA results for conditions threat versus nonthreat with corresponding spectrograms per condition. (a) Space time frequency (STF) Component 1, spectral PCA loadings plotted from the first PCA (left); spatial PCA loadings plotted on topoplot from the second PCA (center); temporal PCA scores plotted as function of time (right). STF Component 1 with a spectral peak at 6 Hz, spatially left lateralized, temporally maximal around 550 ms. (b) Spectrograms at FC5 for each condition, scramble, nonthreat, and threat, show greatest ERSP theta synchronization for the nonthreat condition corresponding to STF Component 1.



Fig. 3. (a) Space time frequency (STF) Component 2, spectral PCA loadings plotted from the first PCA (left); spatial PCA loadings plotted on topoplot from the second PCA (center); temporal PCA scores plotted as function of time (right). STF Component 2 with a spectral peak at 18 Hz, spatially maximal at FC3, temporally maximal around 475 ms. (b) Spectrograms at FC3 for each condition, scramble, nonthreat, and threat show greatest ERSP beta desynchronization for the threat-ening condition corresponding to STF Component 2.

4. Discussion

We investigated ERSP spatiotemporal dynamics during an object recognition task (real versus scrambled images) to help clarify the neural substrates of implicit visual threat processing. While controlling for arousal, we found various spatial and temporal differences for threatening compared to nonthreatening. This includes an early posterior increase in theta power, a later frontal increase in theta power, and a consistent left lateralized beta desynchronization, all greatest for the threatening condition.

4.1. Real versus scrambled images

We found spectral differences between the real versus scrambled images with greater theta and alpha power changes for the real images in occipital regions early after visual stimuli presentation. In addition, there was an early increase in delta power for the real images in the prefrontal cortices. The topography and timing of these spectral differences suggest that they are primarily due to basic visual processing of real versus scrambled, or meaningless, images. However, there is a confound of task imposed processing in that we asked the subjects to focus explicitly on distinctions between real and scrambled images. Recently, delta activity has been suggested to play a role in motivational processes (Knyazev, 2007; Knyazev, 2012), and while this assignment still remains speculative, the delta band changes we found may reflect the influence of the explicitly assigned task, as opposed to the properties of the stimuli that we were exploring.

4.2. Threat-theta

Spatially, various topographical patterns of EEG power changes, particularly within the theta band, have been associated with emotional/threatening stimuli (Aftanas et al., 2001a; Aftanas et al., 2002; Aftanas, Pavlov, Reva, & Varlamov, 2003; Balconi et al.,



Fig. 4. (a) Space time frequency (STF) Component 3, spectral PCA loadings plotted from the first PCA (left); spatial PCA loadings plotted on topoplot from the second PCA (center); temporal PCA scores plotted as function of time (right). STF Component 3 with a spectral peak at 5 Hz, spatially maximal at two locations FPZ and O1, temporally maximal at 3 time points, 300 ms, 475 ms, and 650 ms. (b) Spectrograms at FPZ for each condition, scramble, nonthreat, and threat, show greatest ERSP theta synchronization for the threatening condition at the later temporal maximum. (c) Spectrograms at O1 for each condition, scramble, nonthreat, and threat, show greatest ERSP theta synchronization for the threatening condition at the later temporal threat, show greatest ERSP theta synchronization for the threatening condition, scramble, nonthreat, and threat, show greatest ERSP theta synchronization for the threatening condition at the two earlier temporal maximums.

2009). Temporally, emotional stimuli (e.g. threatening or pleasant) have been proposed to be "privileged" in the competition for processing resources, are prioritized in perception, and impede other cognitive operations (Brosch & Grandjean, 2013; Sun et al., 2012). We show that viewing an object which is perceived as either threatening or nonthreatening results in an early (300-475 ms) increase in theta-band EEG power over the occipital lobes, with the greatest power changes for the threatening images. Also, we show that there is a later (600 ms) theta power increase over the frontal region for both threatening and nonthreatening images, again with the greatest theta increase for the threatening images. This is unlikely to be secondary to the arousal characteristics of the stimuli as the threatening and nonthreatening stimuli had comparable arousal ratings. The theta power increase is in keeping with the findings in animal studies that theta synchrony between the amygdala and hippocampus is associated with encoding of threat with a stimulus (Pape et al., 2005; Seidenbecher et al., 2003) and detectable in the amygdalo-hippocampal complex associated with fearful memory processing (Narayanan et al., 2007; Narayanan, Seidenbecher, Sangha, Stork, & Pape, 2007).

Due to limitations in interpreting spatial sources of cortical EEG signal, it is difficult to conclude whether or not the amygdala

directly influences the observed, presumed cortical activity. However, several studies provide support for such a conclusion, in that there is a role for the amygdala in mediating modulatory activity on sensory cortices (Amaral, Behniea, & Kelly, 2003; LeDoux, 1996; Phelps & LeDoux, 2005). For example, ERP's recorded from preoperative patients with medial temporal lobe epilepsy revealed that the magnitude of early (200 ms) and later cortical components (500-600 ms) in response to fearful faces systematically varied with degree of amygdala damage (Rotshtein et al., 2010). Other studies show that there is an automatic response to threat in the amygdala, irrespective of experimental manipulations of attentional diversion (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010). The amygdala activity reported in that study followed a distinct time course with early emotion modulation starting at 140 ms post-stimulus onset, and later modulation starting at 700 ms. Depth electrode potential studies show an early selective response to fear in the amygdala at about 200 ms with later responses recorded at occipital, temporal, and frontal cortices at 300-(Krolak-Salmon, Hénaff, Vighetto, 1000 ms Bertrand, Mauguière, 2004). In addition, intracranial electrophysiological data recorded from the human amygdala shows prominent theta frequency band changes during 200-500 ms while subjects are being presented with emotionally valenced stimuli (Meletti et al., 2012). These findings overall are consistent with the temporal and spatial dynamics found in the current study, with early posterior theta oscillations and later frontal theta oscillations during the implicit processing of threatening versus nonthreatening visual stimuli

We posit that the posterior theta EEG phenomena we observe relate to amygdalar activity, either directly or indirectly, and play a role in visual semantic memory. The theta power increases we are reporting are in the same frequency band as are the power increases between the amygdala and hippocampus when threat is first encoded as a salient feature of an object (Seidenbecher et al., 2003). Our previous fMRI study, utilizing the same paradigm, shows that threat is a feature in visual semantic memory (Calley et al., 2013), and EEG theta power increases index semantic memory retrieval (Bastiaansen et al., 2008). The posterior theta power may either be locally generated, triggered by theta synchronization from the amygdala that we cannot detect from scalp recording, or the amygdala triggers this occipital cortical theta response without generating an intrinsic theta rhythm on its own (Pape et al., 2001). In regards to the frontal theta activity, we suggest that frontal theta power may play a more modulatory role because of the later time course. For example, frontal theta is involved in prefrontal control and in overriding Pavlovian learning biases (Cavanagh, Eisenberg, Guitart-Masip, Huys, & Frank, 2013). Other studies have shown that frontal regions attenuate amygdala responses to threat (Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Rosenkranz & Grace, 2001).

The theta activity we recorded may be part of a coordinating corticolimbic network. For example, in the cognitive domain theta activity generally is indicative of an orienting function as EEG theta power typically increases with increasing task difficulty (Başar, 1999; Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Sakowitz, 2001). Furthermore, theta band activity plays a role in integrating neural activity in response to emotional stimuli across sub-cortical (amygdala) and cortical structures, both frontal and visual cortices (Knyazev, 2007; Lewis, 2005a; Lewis, 2005b; Maratos, Mogg, Bradley, Rippon, & Senior, 2009; Meletti et al., 2012; Paré et al., 2002). Cortical regions such as the medial prefrontal cortex (mPFC) play a prominent role in threat behavior as well as regulatory mechanisms. More specifically, the dorsal mPFC plays a role in both expression and encoding of threat, while ventral regions are linked to the inhibition of threat-related behavior (Courtin, Bienvenu, Einarsson, & Herry, 2013). Frontal theta is a sensitive index of prefrontal control and can reflect the application of top-down control (Cavanagh et al., 2013). Evidence suggests that the amygdala influences perceptual systems, possibly through white matter pathways (Catani, Jones, & Donato, 2003; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). Lastly, in multimodal models of semantic organization (Hart & Kraut, 2007; Hart et al., 2013) medial visual cortices show threat to be a feature in visual object memory (Calley et al., 2013), and the occipital theta found in the current study shows temporal dynamics expected for semantic memory retrieval. Taken all together, we associate different cognitive functions for the differing temporal and topographical theta power changes. Specifically, the early posterior theta detected may be a reflection of amygdalar-related activity and the later posterior theta may index semantic memory retrieval, while the frontal theta activity may serve a more modulatory role.

4.3. Threat-beta

We also consistently observed event related desynchronization (ERD) in the beta band with greater ERD for threatening compared to nonthreatening or scrambled images (Fig. 3b). Studies show that implicit processing of aversive, but not nonthreatening, stimuli is associated with activity in the dorsal (vision for action) processing stream, because perception of aversive stimuli may mandate rapid behavioral response (Knyazev et al., 2009). Other studies support the notion that this left lateralized beta ERD reflects part of the orienting reflex, a complex body response to externally presented stimuli including changes in heart rate, skin conductance, and motor preparation (Barry, 2006; Pavlov, 1927). To illustrate, early beta ERD reflects visually induced preparatory activity in motor cortex networks, and is often accompanied by changes in heart rate (Pfurtscheller et al., 2013). In addition, other studies have found short-lasting early (~500 ms) beta ERD after action-coded visual stimuli (Doyle, Yarrow, & Brown, 2005; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller, Scherer, Müller-Putz, & Lopes da Silva 2008; Ramautar, Romeiin, Gómez-Herrero, Piantoni, & Van Someren, 2013: Solis-Escalante, Müller-Putz, Pfurtscheller, & Neuper, 2012: Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Zhang, Chen, Bressler, & Ding, 2008), related to motor planning, response inhibition, and uncertainty. Overall, our data and others' support the idea that the orienting reflex is mediated by a network of activity which has evolved to increase the likelihood of survival upon encountering environmental items that are considered threatening (Bradley, 2009). As this is the first study, to our knowledge, to show such robust left lateralized beta band ERD during threat processing, this phenomenon merits further investigation.

4.4. Nonthreat-theta

Through data-driven statistical analysis we found a left lateralized theta power increase, greatest for the nonthreatening compared to the threatening conditions, around 500 ms. We suggest that this later theta activity is in response to the positive affect of the nonthreatening images, as left lateralized activity is associated with approach related motivation and is often found in response to pleasantly valenced stimuli (Aftanas et al., 2001b; Davidson, Pizzagalli, Nitschke, & Kalin, 2003). However, a potential limitation to this study is that the current cohort consisted of primarily women. Some have suggested that there are gender differences in processing affective images; however, to date, there has yet to be a systematic assessment of gender differences (Cahill, 2006; Fujita, Diener, & Sandvik, 1991; Kring & Gordon, 1998; Rozenkrants & Polich, 2008).

5. Conclusion

In conclusion, while previous studies have found either isolated posterior or frontal theta activity in response to threatening images, we found differential topographical theta power changes as a function of time. More specifically, when arousal influences were controlled for there was an early posterior increase in theta power for threatening compared to nonthreatening images and then a later frontal increase in theta power. We also found a consistent beta ERD in response to the threatening images. Thus, theta and beta band activity index processes that play a prominent role in coordinating information processing at different time scales. Previous studies suggest a role for subcortical structures in threat detection with a recent emphasis on cortical regions playing a more modulatory role, specifically in regards to theta activity. Our results support the conclusion for such a network in threat processing. In addition, our results support a multimodal account of semantic memory with threat as a feature in visual semantic memory. Evaluating this network and modifying its response properties may provide diagnostic or treatment value in individuals with disorders characterized by abnormal processing of stimuli perceived as threatening.

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