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Defensive engagement and perceptual enhancement

Andreas Keil[a,*], Margaret M. Bradley[a], Niklas Ihssen[b], Sabine Heim[c], Jaime Vila[d], Pedro Guerra[d], Peter J. Lang[a]

[a] NIMH Center for the Study of Emotion and Attention, University of Florida, Gainesville, FL, United States
[b] Bangor University, Bangor, UK
[c] Deutsches Institut für Internationale Pädagogische Forschung, Frankfurt/Main, Germany
[d] University of Granada, Granada, Spain

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ABSTRACT

We tested whether visual cortical sensitivity to external cues in the context of an acute defensive reaction is heightened or attenuated. A strong cardiac defense (fear) response was elicited by presenting an abrupt, loud acoustic stimulus following a 10-min period of quiescence. Electrocortical responses to aversive and neutral pictures following defensive stimulus onset were measured using dense-array EEG. Pictures were flickered at 12.5 Hz to evoke steady-state visual evoked potentials (ssVEP), which can be reliably extracted on the basis of single trials. Visual cortical activity indexing perceptual processing was substantially heightened when pictures were shown in temporal proximity to (i.e., 5 s after) the defense stimulus. Replicating previous studies, aversive visual stimuli were associated with enhanced ssVEP amplitude, compared to neutral stimuli. Acute defense facilitates visual perception of external cues and preserves accurate discrimination between threatening and safe cues.

1. Introduction

The acute defensive response to a threatening event prompts behavioral, physiological, and cognitive reactions that are essential to survival. The defense cascade model (Lang, Bradley, & Cuthbert, 1997), based on psychophysiological studies, converges with animal models (Davis, 1998) in suggesting a temporal sequence of defensive events, ranging from initial detection of a threat cue to a circa-strike phase, which involves fight or flight (Fanselow, 1994). It has been a matter of debate whether acute defensive engagement (i.e., in temporal proximity to the circa-strike phase) is accompanied by heightened sensitivity to external cues, or alternatively, by a focus on bodily processes and internal cues (Graham & Clifton, 1966).

Whereas traditional psychophysiological models have interpreted the initial phase of defense (characterized by a dramatic increase in heart rate) as indicating sensory "rejection" to facilitate internal processing or protect the individual from the aversive character of the external stimuli (Libby, Lacey, & Lacey, 1973), the defense cascade model (Lang et al., 1997; Lang & Bradley, 2010) predicts enhanced perceptual processing in the context of an acute defensive response. According to this view, emotions are founded on defensive (or appetitive) motivational circuits in the brain that developed early in evolutionary history to ensure the survival of individuals and their progeny. These motivational circuits are activated by environmental and memorial cues and initiate cognitive processes that enhance perception in the service of selecting an appropriate action.

Activation of the defense circuit reliably occurs following the presentation a loud, disruptive, unexpected auditory stimulus that is reliably characterized as aversive (Vila et al., 2007). This procedure prompts a cardiac defense response that includes an initial heart rate increase (up to 20 beats per min), followed by an initial deceleration, a second acceleration, and a final deceleration to baseline, over the course of a minute (Ramirez, Sanchez, Fernandez, Lipp, & Vila, 2005; Sanchez et al., 2009). This cardiac defense response is greatly attenuated if the eliciting stimulus is presented a second time (Mata, Rodriguez-Ruiz, Ruiz-Padial, Turpin, & Vila, 2009), limiting its use for neuroimaging studies that require trial averaging.

Here, we used the steady-state visual evoked potential (ssVEP), to measure visual cortical activity based on single trials of EEG data (Keil et al., 2008). The ssVEP is a continuous oscillatory brain response elicited by a visual stimulus that is rapidly brightness-modulated (flickered). The time-varying ssVEP amplitude indicates states of heightened cortical activation, such as when selectively attending to a stimulus (Müller et al., 2006), or when viewing intrinsically relevant stimuli such as affectively arousing pictures

* Corresponding author at: Department of Psychology and NIMH Center for the Study of Emotion & Attention, University of Florida, PO Box 112766, Gainesville, FL 32608, United States. Tel.: +1 352 392 2439; fax: +1 352 392 6047.
E-mail address: akeil@ufl.edu (A. Keil).

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(Moratti, Keil, & Stolarova, 2004). Localization and multi-modal neuroimaging studies suggest that the primary generators of this scalp-recorded signal are in lower tier visual cortices (Di Russo et al., 2006). Importantly, the ssVEP has been shown to be sensitive to fear system engagement as measured by means of heart rate changes (Moratti, Keil, & Miller, 2006).

In the present study, we flickered either unpleasant or neutral pictures, at varying intervals after the onset of a loud white noise stimulus that was unexpectedly delivered to participants after sitting in a dark room for 10 min. Flicker trains started either 5 or 20 s the loud noise, thus capturing (1) the peak of initial heart rate acceleration (i.e., at 5 s) with the subsequent deceleration and (2) the second heart rate acceleration/deceleration wave (i.e. at 20 s). Measuring ssVEPs in even closer temporal proximity to the defense stimulus (e.g., simultaneous onset of loud noise and flicker) was not feasible due to onset of the reflexive startle eyeblink and other motor components of the overt defense response evoked by the noise stimulus, which create artifacts in the EEG.

Based on previous work, we expected that unpleasant pictures would be associated with overall greater ssVEP spectral power as well as greater cardiac deceleration, compared to neutral pictures (Bradley, Codispoti, Cuthbert, & Lang, 2001; Keil et al., 2008; Lang, Greenwald, Bradley, & Hamm, 1993). To the extent that acute defense involves sensory rejection, we expected a decrease in the ssVEP response following noise onset and a failure of the ssVEP to discriminate among the neutral and unpleasant pictures. If acute defensive engagement includes heightening of perception and attention (Bradley et al., 2003; Phelps, Ling, & Carrasco, 2006), we expected maximum electrocortical facilitation as expressed in increased ssVEP power at the peak of the acute defense response.

2. Materials and methods

2.1. Participants

Twenty right-handed students (12 female) with normal or corrected-to-normal vision whose age ranged from 22 to 27 years (mean age 24.3 years) gave informed consent to participate in the study. They were given class credit for participation. Participants filled in the State-Trait Anxiety Inventory and the Beck Depression Inventory. On these measures, none of the participants scored outside the range normally seen in healthy student populations.

2.2. Stimuli and procedure

Four colored pictures (numbers 6570.1, 6570.2, 9635.1, 9635.2) were selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005) that were perceptually similar but different in emotional content. For instance, one pair included a picture showing a man holding a gun against his head (#6570.1), whereas its pair member showed the same person holding a hair dryer (#6570.2), with all other aspects of the picture remaining identical; the second pair showed a burning barrel (#9635.1) and its pair a person engulfed in flames (#9635.2). Foveal luminance of all stimuli was adjusted to be 42 cd/m^2, as measured with a Minolta luminance meter.

Pictures were presented on a 19 inch screen from a LCD projector with a vertical refresh rate of 75 Hz, subtending a visual angle of 10° horizontally and 7° vertically. A fixation point was marked in the center of the screen and was present throughout the experiment. The critical pictures were presented 5 and 20 s following defense onset on each of two defense trials. Each picture was presented for 4800 ms in a flickering mode at a rate of 12.5 Hz (thus containing 60 on/off cycles), with the picture shown for 40 ms, followed by 40 ms black screen during each cycle. Complexity was measured as entropy using Matlab software and was matched such that the small differences in picture entropy favored the unpleasant picture in one pair (entropy of 6.5 and 6.4), and the neutral picture in the other pair (entropy of 7.2 and 7.1).

The four pictures presented across the two defense trials comprised a novel presentation of each of the four pictures in the stimulus set; each defense trial comprised an aversive and a neutral version of the picture pair. The order of picture content on the first defense trial was counterbalanced across participants (e.g., aversive–neutral, neutral–aversive), with the specific picture occurring in each condition (e.g., 6570.1, 9635.1) also counterbalanced across subjects. The order of picture content on the second defense trial was always opposite to that experienced on the first defense trial (e.g., aversive–neutral on 1st trial; neutral–aversive on 2nd).

A third picture was presented temporally distant (45 s post-noise onset) from the noise stimulus that was identical to the first picture presented on that defense trial. This was done to determine whether the normal difference in the ssVEP between aversive and neutral pictures can be observed in this single-trial study.

The defense stimulus was an intense, loud burst of auditory white noise (98 dB, 1000 ms duration, and virtually instantaneous rise time). It was presented first following 10 min of quiet rest by the participant, and then again following a second 10-min rest period.

2.3. Electrophysiological recordings

EEG was recorded continuously from 129 electrodes using an Electrical Geodesics™ system and digitized at a rate of 250 Hz, using Cz as a recording reference. Impedances were kept below 50 kΩ, as recommended for the Electrical Geodesics high input-impedance amplifiers. A subset of EGI net electrodes located at the outer canthi as well as above and below the right eye was used to determine the horizontal and vertical electrooculogram. All channels were preprocessed on-line by means of 0.1 Hz high-pass and 100 Hz low-pass filtering. Offline analysis sampled epochs of 5400 ms (400 ms pre-, 5000 ms post-onset of the flickering pictures) obtained from the continuously recorded EEG. In a first step, data were low-pass filtered at a frequency of 30 Hz (24 dB/octave) and then submitted to eye movement and blink correction in BESA software (Ille, Berg, & Scherg, 2002). No trials were discarded. The validity of the remaining, corrected, data were further examined by visually inspecting the vertical and horizontal EOG as computed from a subset of the electrodes that were part of the electrode net. The average reference was used for all analyses.

Heart rate was measured from electrocardiogram recorded with a BioPac bioamplifier using three disposable snap electrodes. Sensors were placed at the medial left and right forearms, and the electrocoardiogram was digitized at a rate of 200 Hz, constrained by filters between .1 and 50 Hz. Heart rate changes over time were obtained by detecting R-waves using a Schmitt trigger and converting inter-beat intervals into beats per min (bpm) values for .5 s bins, as proposed by Graham (1978). This method uses weighting of the temporal distance of heart beats to a given time bin (here: 0.5 s) to yield a continuous function of heart rate estimates for subsequent time bins. The mean baseline (averaged across 2 s prior to defense stimulus onset) bpm value was subtracted from the heart rate time series to result in a waveform reflecting heart rate change from the pre-noise baseline over time.

2.4. Procedure

Participants were greeted and instructed that they would sit in a dark chamber for about 30 min, during which they would hear noises and view pictures. Subsequently, they gave written informed consent and none withdrew from the study. After application of the EEG electrode array and heart rate sensors, participants sat in the dark chamber for 10 min, with no task. Then, the defense stimulus was presented over standard headphones and the first set of three pictures presented. This was followed by a second 10-min quiet period and presentation of the second set of pictures. All procedures were approved by the local institutional review board and were in line with the Declaration of Helsinki.

2.5. Extraction of ssVEP

The ssVEP has the same fundamental frequency as the flickering stimulus (Regan, 1989). Thus, the 12.5 Hz Fourier components representing stimulus-locked oscillations for each single trial were extracted by means of a time-locked moving average procedure (Keil et al., 2003). ERP studies with IAPS pictures have provided abundant evidence that viewing emotionally arousing pictures is associated with strong visual evoked potentials (P1 and N1), followed by pronounced P3 and late positive complex waveforms. To avoid contamination with these initial ERPs, a 400–4800 ms post-stimulus part of each epoch was used for these analyses. For each single trial, the data segment was treated as follows: a 400 ms window (containing 5 cycles of ssVEP) was shifted across the epoch in steps of 80 ms, and the potential within the shifting windows in the time domain was averaged, resulting in a 400 ms segment containing 5 cycles of the 12.5 Hz ssVEP and reflecting an average across 50 sliding windows (Fig. 1 illustrates these steps). The resulting ssVEP averages were then transformed into the frequency domain using Discrete Fourier Transform (DFT) on 80 data points (400 ms). Thus, real and imaginary parts of the 12.5 Hz component were obtained, reflecting stimulus-locked 12.5 Hz ssVEP activity.

2.6. Statistical analysis

Measures of the typical heart rate changes seen during cardiac defense were obtained by averaging heart rate changes for each participant and trial over three time segments of 2–7 s, 8–12 s, and 18–22 s following defense stimulus onset. The presence of an overall tri-phasic pattern (initial acceleration, subsequent deceleration, second acceleration) was then examined using an analysis of variance (ANOVA) with repeated measures of *time* (segment 1–3), *trial* (first, second), and a between-participants factor of order (aversive first, neutral first).

In a second step, effects of picture content on heart rate change were examined. To this end, heart rate changes during the first two picture presentations were averaged across the presentation time of 4800 ms, respectively for each participant, trial, and picture. An ANOVA using a between-participants factor of *order* (aversive first,

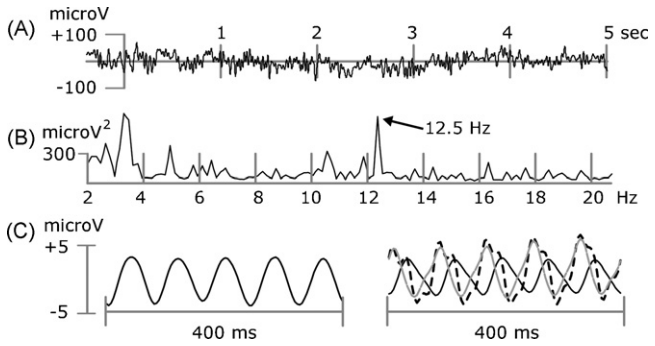

Fig. 1. Illustration of the data reduction process. Panel A shows an example single-trial EEG segment, taken from the first participant in the first experimental trial, at electrode site POz. The frequency spectrum in panel B suggests that 12.5 Hz activity is present in this single trial, where time 0 marks the onset of the flickering stimulus stream. The lower panel (C) on the left shows the result of a 400 ms moving window that is shifted in steps of 80 ms over the signal. This amplifies any response that is time-locked to the oscillatory stimulation, and reduces random oscillations. Panel C, right, shows three more example waveforms obtained from three additional participants, documenting that clear ssVEP signals were extracted from single trials.

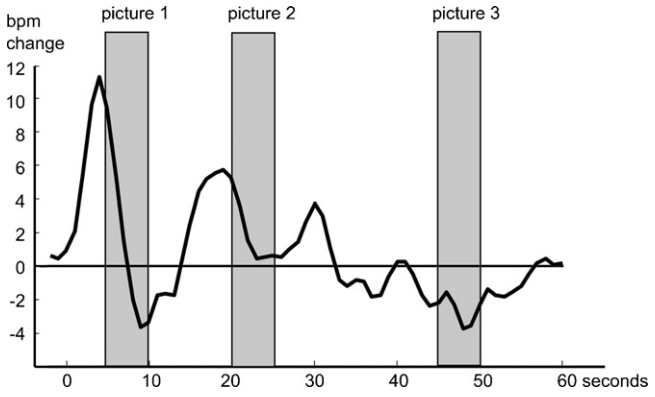

Fig. 2. Grand mean heart rate change (relative to baseline) in response to the auditory defense stimulus, shown for one defense trial. Onset of the defense stimulus is shown at 0 s. Gray bars indicate the temporal position and duration of the flickering pictures. Picture content was counterbalanced across defense trials and participants. It included alternating sequences of version of the same picture (aversive and neutral) for each defense trial.

neutral first) and repeated factors of *picture version* (aversive, neutral) and *temporal position* (5 and 20 s post-noise onset[1]) was then conducted. In this design, effects of trial appear as order × version interactions. Of interest, because pictures were presented during pronounced peaks of the heart rate acceleration in most participants, the picture-related deceleration as measured against a pre-defense baseline may still be in the positive range.

Posterior ssVEP amplitudes were averaged across electrode sites Pz, Poz, and their 9 immediate neighbor electrodes, resulting in one ssVEP amplitude value for each defense trial and picture repetition. In a first step, ssVEP differences between the experimental conditions were evaluated by means of ANOVA with a between-participants factor of *order* (aversive first, neutral first) and within-subject factors of *picture version* (aversive, neutral) and *temporal position* (5 and 20 s after the noise). In this design, effects of trial appear as order × version interactions. A control analysis that compared the different IAPS exemplars did not result in any main effects or interactions involving specific picture (all Fs < 1.6).

The ssVEP and heart rate on the third picture presentation were compared using ANOVAs with a within-participants factor of *trial* (first, second) and a between-participants factor of *order* (aversive first, neutral first). In this design, effects of picture version appear as trial × order interactions. Significant differences in ANOVAs were followed by planned comparisons (contrast analyses), if effects were predicted. Other effects were examined by means of follow-up ANOVAs.

[1] Heart rate change when pictures are repeated are generally reduced (Bradley, 2009) and thus were not significantly different in the latest interval for repeated unpleasant and neutral pictures.

Table 1
Mean heart rate changes in beats per min during picture viewing, relative to a pre-noise baseline. Values are shown for early (5 s) and late (20 s) presentations of pictures with respect to the onset of the defense stimulus, for aversive and neutral pictures. Means reflect 10 participants, and standard deviations are shown in parentheses.

	Aversive	Neutral
Defense trial 1		
Early (5 s)	0.24 (4.33)	4.29 (3.23)
Late (20 s)	3.23 (3.69)	6.73 (3.14)
Defense trial 2		
Early (5 s)	1.92 (4.87)	6.32 (2.61)
Late (20 s)	3.77 (2.30)	5.38 (3.11)

3. Results

3.1. Cardiac defense response

A classic triphasic pattern of initial acceleration, strong deceleration, and subsequent acceleration of the heart rate (see Fig. 2) was evident and supported by a main effect of time, $F_{2,36} = 19.1$, $P < .01$, and a quadratic contrast, $F_{1,18} = 25.9$, $P < .01$. As expected, the initial acceleration was stronger in the first, compared to the second, defense trial (*time* × *trial*, $F_{2,36} = 4.8$, $P < .05$). Post hoc ANOVAs showed that trials differed only for the first acceleration (*trial*, $F_{1,18} = 7.4$, $P < .05$), and not for subsequent temporal regions of the cardiac defense response (Fs < 1.3).

Cardiac deceleration following picture onset (see Table 1) was overall larger when viewing unpleasant, compared to neutral, pictures (main effect of *picture version*, $F_{1,18} = 8.8$, $P < .01$). No other differences reached significance.

3.2. Electrocortical data

As expected, the topography of the grand mean single-trial estimates of the ssVEP amplitude showed an occipital maximum in all conditions, suggesting that the signal is of visual cortical origin (see Fig. 3). As Fig. 3 illustrates, posterior ssVEP amplitude was enhanced when processing external cues that were presented 5 s after noise onset (i.e., in the context of acute fear; main effect of temporal position, $F_{1,18} = 6.1$, $P < .05$). In addition, sVEP amplitude was sensitive to

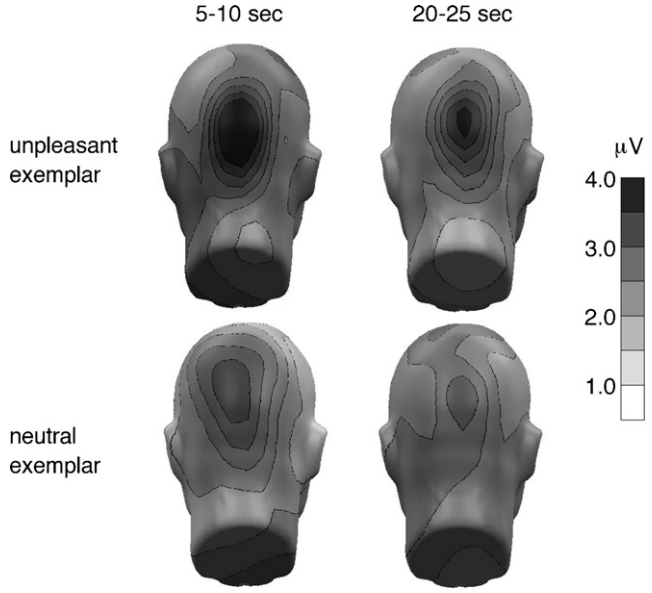

Fig. 3. Grand mean ($N = 20$) topographical distribution of steady-state visual evoked electrocortical activity, extracted from single trials, during the first and second presentation of aversive and neutral pictures.

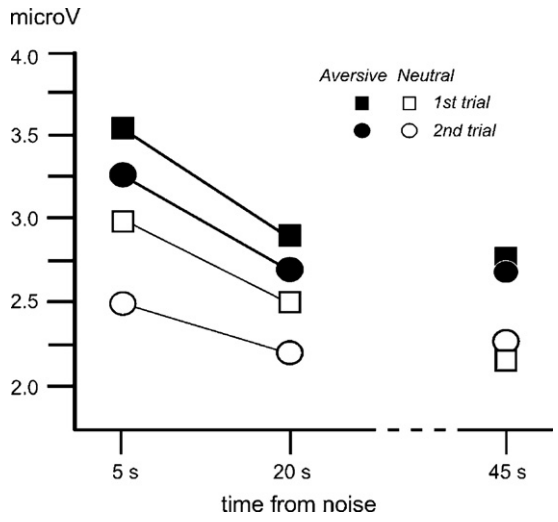

Fig. 4. Mean ssVEP amplitude as a function of temporal distance from the defense stimulus (time from noise), picture version (aversive, neutral), and trial (defense trials 1 and 2). Means reflect averages across 10 participants.

the emotional content of the picture across *temporal positions*, with the aversive versions eliciting greater amplitudes than the neutral versions (main effect of *picture version*, $F_{1,18} = 11.7$, $P < .01$). There was no evidence of an interaction, or any effects involving *order* (all Fs < 1).

For the last (repeated) picture, presented distant (45 s post-noise) from the distressing noise, identical effects of *picture version* were obtained (main effect: $F_{1,18} = 6.9$, $P < .05$) with greater ssVEP amplitude for aversive, compared to neutral, pictures (see Fig. 4, right panel).

4. Discussion

The present study examined whether perceptual processing of external cues is heightened or reduced following acute defense mobilization. Single trials of ssVEP were used to estimate perceptual processing following the presentation of a highly distressing burst of white noise following a lengthy period of quiescence. Three main results were observed: first, cardiac changes were consistent with defensive engagement by the intense noise stimulus. Second, ssVEP amplitudes in response to both aversive and neutral cues were substantially heightened (>200% compared to the late baseline segment) when pictures were shown in close temporal proximity to the auditory defense stimulus. Third, the electrocortical response was consistently enhanced when viewing aversive, compared to neutral, cues. These data are not consistent with a hypothesis of sensory rejection but instead suggest that acute defense as defined by the initial heart rate increase is associated with heightened perceptual processing that continues to accurately discriminate between aversive and neutral cues.

The typical physiological response profile observed during acute defensive engagement suggests massive mobilization for action, including pronounced heart rate increase, locomotion, expressive vocalization, and the report of fear and panic (Roberts et al., 2004). In the present study, the pattern of the cardiac response to the noxious stimulus was consistent with such a pattern: the heart rate change over the 1-min period following the noise stimulus resulted in the prototypical tri-phasic pattern, with two accelerative components, each followed by a subsequent deceleration (Vila et al., 2007). Moreover, the initial cardiac acceleration was substantial, reaching on average a 12-bpm change following exposure to the aversive noise and indicative of strong defensive engagement. Following this initial acceleration, the deceleratory component of the cardiac defense response has been interpreted as reflecting orienting to potential threats (Mata et al., 2009), and consistent with this, heart rate deceleration was most pronounced when viewing aversive, compared to neutral, cues.

Immediately following defense stimulus onset, the amplitude of the ssVEP was heightened for both aversive and neutral cues, relative to pictures presented later in the interval, suggesting that acute defense is associated with heightened perceptual activity, regardless of hedonic content. These data are consistent with the hypothesis that activation of the defense system prompts heightened attention allocation and sensory intake in preparation for action (Bradley, 2009; Lang et al., 1997). These data are also consistent with findings suggesting that an attentional phase characterizes early stages of cardiac defense, based on finding a positive relationship between initial cardiac deceleration and behavioral indices of sensory intake (Vila et al., 2007).

Nonetheless, a difference in the amplitude of the ssVEP between unpleasant and neutral pictures was found throughout the study, including those presented immediately following onset of the aversive noise. The differential ssVEP amplitudes replicate earlier single-trial studies reporting heightened ssVEP when passively viewing unpleasant, compared to neutral, pictures (Keil et al., 2008). Notably, there was no interaction between temporal proximity to the defense stimulus and cue valence, suggesting that electrocortical processing of the visual cue reflects an additive combination of proximity to the defensive event and the emotional content of the external cue. The generators of the ssVEP are localized in extended visual cortex (Müller, Teder, & Hillyard, 1997), with strong contributions from V1 but also higher-order visual cortices (Di Russo et al., 2006). Thus, a perceptual locus of the ssVEP differences is likely, possibly mediated by re-entrant feedback from higher-order cortices or deep cortical regions (Keil et al., 2009).

In terms of methodological considerations, the robustness of the single-trial estimate of the ssVEP amplitude, despite the behavioral and autonomic reactions elicited in acute defense, is critical to the purpose of this study. In the present protocol, robustness of the signal obtained during defensive activation was tested against the ssVEP collected distant from the eliciting defensive event. As illustrated in Fig. 4, the sensitivity of the ssVEP to the emotional content of each picture replicates the typical difference found when viewing aversive and neutral pictures (Keil et al., 2008). These data confirm that single-trial estimation of ssVEP amplitudes is possible in noisy conditions, and furthermore suggest that the heightened perception associated with fear instigation has dissipated by about 20 s, as the ssVEP amplitudes measured at 20 and 45 s post-noise onset are similar in both amplitude and modulation.

Taken together, the present results indicate that substantial enhancement of attention and perception to external cues is part of an acute defensive episode. This enhancement is not specific to the threat cues, but affects all novel cues. With increasing temporal distance from the defensive event, visual cortical facilitation is attenuated, reaching a level that appears to be similar to that measured for affective cues in a calm state. Thus, acute fear facilitates visual perception of external cues while retaining accurate discrimination between threatening and safe cues.

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