

Effects of affective content and motivational context on neural gain functions during naturalistic scene perception

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Abstract

Visual scene processing is modulated by semantic, motivational, and emotional factors, in addition to physical scene statistics. An open question is to what extent those factors affect low-level visual processing. One index of low-level visual processing is the contrast response function (CRF), representing the change in neural or psychophysical gain with increasing stimulus contrast. Here we aimed to (a) establish the use of an electrophysiological technique for assessing CRFs with complex emotional scenes and (b) examine the effects of motivational context and emotional content on CRFs elicited by naturalistic stimuli, including faces and complex scenes (humans, animals). Motivational context varied by expectancy of threat (a noxious noise) versus safety. CRFs were measured in 18 participants by means of sweep steady-state visual evoked potentials. Results showed a facilitation in visuocortical sensitivity (contrast gain) under threat, compared with safe conditions, across all stimulus categories. Facial stimuli prompted heightened neural response gain, compared with scenes. Within the scenes, response gain was smaller for scenes high in emotional arousal, compared with low-arousing scenes, consistent with interference effects of emotional content. These findings support the notion that motivational context alters the *contrast sensitivity* of cortical tissue, differing from changes in *response gain (activation)* when visual cues themselves carry motivational/affective relevance.

KEYWORDS

contrast, facial stimuli, naturalistic scenes, steady-state visually evoked potentials

1 | INTRODUCTION

It is well established that naturalistic vision and scene perception are massively parallel and dynamic processes, which are informed by contextual factors such as action goals, motivational states, and predictions from memory, in addition to reflecting physical scene statistics. Effects of motivational and contextual factors on visual perception have

been extensively studied by manipulating the motivational relevance associated with visual cues, in human observers as well as in experimental animals. For example, visual stimuli associated with threat and danger facilitate perception and visual attention (Alpers et al., 2005; Brosch et al., 2010; Lang et al., 1993; Phelps et al., 2006; Schupp et al., 2006). They are preferentially reported under binocular rivalry (Gerdes & Alpers, 2014); they are more accurately and more rapidly

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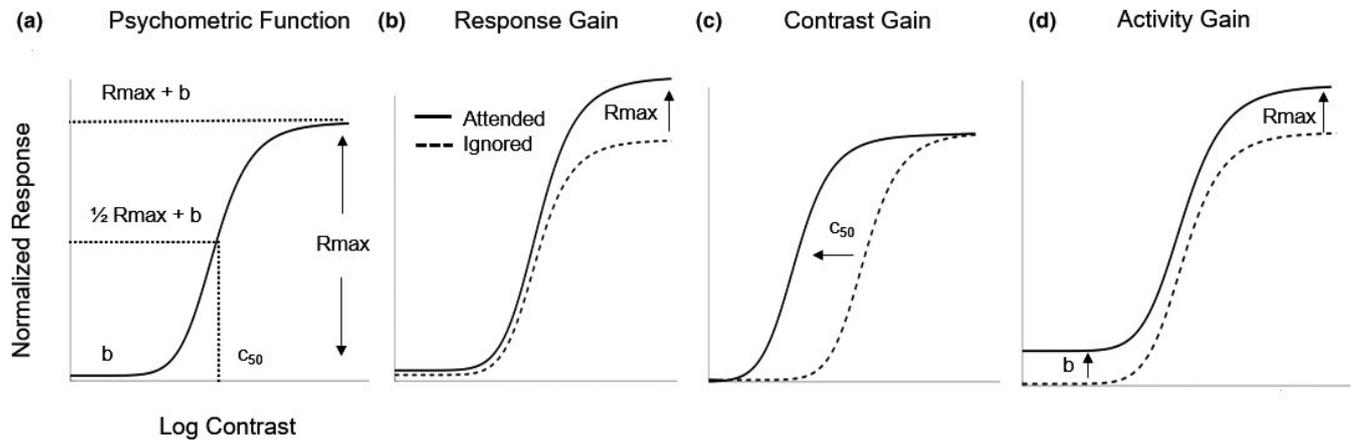


FIGURE 1 The psychometric function (a) and different types of gain control mechanisms: the response, contrast, and activity gain model of visual attention. (b) Evidence for response gain can be seen by upward scaling of the contrast response function in the amplitude (R_{\max}). (c) Contrast gain is best characterized by a leftward shift of the function (c_{50} -parameter). (d) Activity gain postulates an increase in spontaneous baseline activity (b and R_{\max})

detected and discriminated from non-targets during visual search (Öhman & Mineka, 2001); they evoke greater visuo-cortical responses in electrophysiological (Miskovic & Keil, 2012) as well as hemodynamic (Bradley et al., 2003) recordings; and they are rated as perceptually more vivid and salient, compared with neutral cues (Todd et al., 2012). A body of work has also shown that emotional arousal affects processes related to bottom-up attention and short-term memory (Sutherland & Mather, 2012, 2018) prompting the notion that arousal may bias the allocation of limited capacity (Mather & Sutherland, 2011). In line with this notion, viewing motivationally or affectively salient content may interfere with competing cognitive processes that serve other goals (Dolcos et al., 2014). For example, visuo-cortical responses are diminished when varying emotionally salient, compared with neutral, scenes are presented in rapid succession (Bekhtereva et al., 2018), or when a visual event is in the spatial and/or temporal vicinity of an affectively salient stimulus (Deweese et al., 2016). One goal of the present study is to characterize the extent to which emotional scene content and motivational context facilitate versus interfere with robust indices of low-level visuo-cortical processing.

Previous studies have often used highly controlled stimulus material to identify the modulation of visuo-cortical areas when manipulating affective content and motivational context, targeting specific physical dimensions such as color (Keil et al., 2013), luminance (Schettino et al., 2016), orientation (McTeague et al., 2015), or contrast (Song & Keil, 2013, 2014). By contrast, the extant literature has rarely manipulated physical stimulus parameters across different categories of naturalistic stimuli, for example, complex scenes or scene elements, while varying emotional/motivational significance for the observer. Such a manipulation is, however, desirable to provide a neuromechanistic framework for a large body of work on emotion–attention interactions, seen in

healthy observers as well as in clinical populations (Bradley et al., 2012). Specifically, effects of affective and context variables on lower-level visual processing may be quantitatively described using established psychometric response functions, measured in response to systematic changes in low-level stimulus properties (Huang & Dobkins, 2005).

The contrast response function (CRF) is such a metric of lower-level visual processing, suitable for psychometric response function analyses. Specifically, the CRF indexes the change in neural (firing rate; potential magnitude) or psychophysical (detection/discrimination rate) responses as the contrast of a visual stimulus increases. The CRF is known to vary with the spatial frequency of the eliciting stimulus (Albrecht & Hamilton, 1982) and has been examined in studies of higher cognition, for example, to characterize the changes in visual sensitivity and gain during selective attention (e.g., Ling & Carrasco, 2006). CRFs are characterized by a sigmoid function (see Figure 1a), with a non-linearity in the low-contrast range, a steep, monotonic increase at intermediate contrasts, and a saturating non-linearity at high contrasts (Huang & Dobkins, 2005). The shape of the CRF is readily modeled by sigmoid cumulative distribution functions such as the Naka-Rushton, Weibull, or Gumbel (log-Weibull). These sigmoid-shaped psychometric functions are defined by the asymptotic maximum amplitude (R_{\max}), a baseline response level (b), the semi-saturation constant (c_{50} , i.e., the contrast corresponding to the 50% response level of the CRF), and the slope parameter (s) of the sigmoid curve (Naka & Rushton, 1966; see Figure 1a).

The parameters of the psychometric function allow researchers to quantify changes in lower-level sensory sensitivity in response to experimental manipulations. If a specific model parameter is affected by the manipulation, then the nature of the modulation can be readily described in terms of its putative underlying mechanisms. The contrast gain mechanism reflects a selective facilitation of the CRF in

the intermediate contrast range, that is, below the maximum of the CRF (Ling & Carrasco, 2006). It is visible as a horizontal leftward shift of the CRF, reflecting greater sensitivity at lower contrast (i.e., a sensitized threshold, Huang & Dobkins, 2005, see Figure 1c). In comparison, the response gain mechanism (Figure 1b) involves a multiplicative response increase, which affects the CRF increasingly, as the contrast increases (Huang & Dobkins, 2005; Reynolds et al., 2000). Finally, an activity gain mechanism (Figure 1d) has been discussed in which response gain combines with an additionally boosted response at the baseline level (Kim et al., 2007). This gain mechanism postulates heightened sensitivity across the entire range of the CRF (Williford & Maunsell, 2006; Huang & Dobkins, 2005), including increased spontaneous activity and later amplification of high-contrast stimuli.

The few previous studies examining the effect of emotional content on CRFs have largely found evidence supporting a response gain mechanism, that is, they observed higher accuracy/response amplitudes measured as psychophysical or neural data, during high-contrast stimulation, for example, when viewing angry, compared with neutral facial expressions (Phelps et al., 2006), or when viewing grayscale gratings paired with a noxious loud noise (Song & Keil, 2014).

A valuable tool for quantifying CRFs at the neural population level are steady-state visual evoked potentials (ssVEPs; Müller & Hillyard, 2000; Norcia et al., 2015). The ssVEP is elicited by repetitive stimulus presentations, modulated in luminance (i.e., flickered) or contrast (e.g., pattern reversal), with strongest contributions from the primary visual cortex (V1), in addition to higher-order visual cortices (Di Russo et al., 2007; Russo et al., 2003; Müller et al., 1997). The temporal frequency of the ssVEP equals the frequency of the presented stimulus, often including higher harmonics (Müller et al., 1998). Thus, the signal can be reliably separated from noise, analyzed in the time–frequency domain (Wieser et al., 2016), with the ssVEP amplitude interpreted as reflecting the magnitude of neural mass activity in the visual cortex (Norcia et al., 2015; Regan, 1989). Compared with psychophysical methods, CRFs measured at the neural population level allow inferences regarding specific neurocomputations related to emotion–perception interactions. Because the ssVEP, unlike event-related potentials, represents a stationary, sustained, signal from lower-tier visuocortical brain areas, the ssVEP method furthermore opens a window in human sensory cortical processes at a high spatial and temporal precision, difficult to obtain with other neuroimaging methods (see Wieser et al., 2016, for a discussion of these properties).

A type of ssVEP paradigm well suited for the present study is the sweep-ssVEP (Regan, 1973), in which a continuous physical stimulus dimension such as spatial frequency or contrast is gradually changed as the stimulus itself is regularly and rapidly modulated at the driving frequency (Norcia et al., 2015). The envelope of sweep-ssVEPs can, thus, be

used as a continuous measure of the changing visuocortical engagement that is associated with ramping up or down a feature dimension of interest, such as contrast, color, or spatial frequency (Ales et al., 2012). The present study uses this technique to obtain neural CRFs evoked by ramping up the contrast of naturalistic scenes varying in emotional content and viewed in different motivational contexts.

1.1 | The present study

Previous research has demonstrated that population-level (neural mass) CRFs measured by sweep-ssVEPs show heightened response gain when evoked by simple conditioned threat cues, that is, gratings that reliably predict the onset of a noxious event (Song & Keil, 2014). However, the value of a stimulus can also be defined by changing the motivational context through verbal instructions. In the so-called threat-of-shock paradigm, participants are instructed that noxious events such as electric shocks or a loud noise may occur whenever a certain stimulus cue is present (e.g., background color, specific sounds, compound features), while another cue signals safety (Wieser et al., 2016). This paradigm has been used to characterize physiological responses related to anxious anticipation and prediction (Robinson et al., 2013). Defensive responses (autonomic changes and self-reported discomfort) during the instructed threat cue are observed even in the absence of aversive experiences related to the threat cue (Bublitzky et al., 2014), making it a promising tool for studying the effects of a threat context on cognitive processes such as memory (Weymar et al., 2013), decision-making (Bublitzky et al., 2017), and perception, for example, visual processing (Bublitzky & Schupp, 2012).

The present study uses sweep-ssVEPs evoked by naturalistic scenes during safety and threat to examine how motivational (anxious anticipation) and scene content affect the CRF (Song & Keil, 2013; Tsai et al., 2012). This approach allows us to examine the following experimental questions and hypotheses:

First, many theoretical notions predict that motivational states such as anxious apprehension/threat anticipation heighten an observer's sensory sensitivity (Bogels & Mansell, 2004; Weymar et al., 2014), which in the present study would be reflected in heightened contrast gain, with c_{50} shifted to the left. By contrast, alternative views stipulate that apprehension during threat anticipation works as an internal distraction mechanism (e.g., Sari et al., 2017), interfering with sensory processing. Under this notion, we would expect reduced contrast gain (greater c_{50}), reduced response gain (smaller R_{max}), or both, when participants anticipate threat, compared with safety.

Second, the affective content of faces and scenes has been shown to facilitate higher-order visual processing, and in some cases retinotopic visuocortical processes (McTeague

et al., 2015). If the same principles apply to CRFs, then more engaging (arousing) content should prompt heightened response gain. By contrast, recent studies have found evidence for the notion that emotionally arousing content engages high-order processes that interfere with the rapid and periodic cortical activation associated with the steady-state potential technique (Bekhtereva et al., 2018). Following this notion, more engaging content is expected to prompt sweep-ssVEP envelopes that are smaller in R_{\max} , larger in c_{50} , or both.

Alternatively, the CRFs in lower-tier visual areas may not be modulated by these manipulations, supporting theoretical accounts that emphasize the role of non-retinotopic, higher-order cortical and subcortical systems in optimizing perception of motivationally relevant stimuli (Buffalo et al., 2010; Lang & Bradley, 2010; Rolls et al., 1996). Note that it would be challenging to test the three conceptual notions discussed above, regarding the role of the lower-level visual cortex with methods based on psychophysics or event-related potentials, both of which do not afford the ability to specify the neurophysiological locus of a continuous CRF.

Finally, in a set of exploratory analyses, we address potential mechanisms underlying changes in neural population gain by quantifying different aspects of the single-trial ssVEP amplitude. These analyses aim to provide information regarding the extent to which differences in the CRF of the sweep-ssVEP reflect variability in amplitude or phase-locking, within trials (i.e., within-trial phase stability) or across trials (inter-trial phase locking). For example, previous work has reported that the within-trial stability (phase similarity between subsequent cycles) of the ssVEP across the duration of a given flicker train increases for selectively attended as well as for Pavlovian conditioned cues (Wieser et al., 2014). Thus, these exploratory analyses allowed us to examine the large-scale neural mechanisms underlying any effects observed at the level of trial-averaged data, including whether ssVEP-CRF differences reflect changes in neural timing, changes in response magnitude, or both.

2 | MATERIALS AND METHODS

2.1 | Participants

Students of the University of Florida ($N = 18$; 8 female; age $M = 20.22$ years, $SD = 1.44$) participated for psychology course credit. All participants had normal or corrected-to-normal vision and reported a negative personal and family history of photic epilepsy. Procedures were approved by the institutional review board of the University of Florida, and written informed consent was obtained from all participants. Based on poor electroencephalogram (EEG) data quality (more than 50% bad EEG trials), one additional participant was not included in this sample. To determine the

sample size, a power analysis was conducted using G*Power (Version, 3.1.9.2.; Faul et al., 2007). In this analysis, detection of an effect using repeated measures ANOVA and assuming a power of $(1 - \beta) = 0.90$, with a moderate effect size of 0.25 (estimated based on studies reviewed in Wieser et al., 2016) and $\alpha = 0.05$, required a sample size of $N = 19$.

2.2 | Stimuli

Manipulation of emotional content was implemented by selecting pictures depicting scenes and faces that varied systematically in emotional content. A total of 72 pictures were selected based on emotional content (pleasant, neutral, unpleasant, threatening) and normative scores for emotional arousal and hedonic valence. These comprised pictures of scenes ($n = 48$ pictures) and pictures of faces ($n = 12$ pictures). Forty-eight scenes were selected from the International Affective Picture System (IAPS; Lang et al., 2005) and the world wide web, to form eight content categories containing six pictures each (pleasant, happy people/families and cute animals; neutral, daily activities and farm or wild animals; unpleasant, crying/grieving humans and injured/dead animals; and threatening, victimization [aggression, physical altercation, weapons] and animal threat scenes). Erotic and mutilation categories, although effective in driving emotion and attention, are less suitable for studies of low-level vision, as they share highly predictable low-level features (Schupp et al., 2007). They also encourage saccadic exploration of small, peripheral areas of interest to a larger extent than other content (Bradley et al., 2011).

Pictures of faces comprised 24 gray-scaled facial expressions corresponding to 12 actors (6 females, 6 males) of the Karolinska Directed Emotional Faces database (KDEF; Lundqvist et al., 1998). Neutral and angry facial expressions by the same actor were selected (i.e., 12 neutral and 12 angry facial expressions; for identification numbers, see Appendix A). All pictures were previously used in a series of studies (Deweese et al., 2014, 2016; Liu et al., 2012) in which evaluative ratings were collected along with autonomic indices of emotional engagement. These previous studies drew samples from the same University of Florida population. Thus, given the duration of the experimental paradigm and the large number of pictures, we did not collect evaluative ratings in the present study.

All stimuli were pre-processed and controlled for physical characteristics, using functions implemented in the MATLAB Image Processing Toolbox (R2007b; Mathworks, Inc.). First, pictures were cropped with the emotionally relevant scene element (the person(s), animal, or face) positioned at the center of the 562×768 pixel grid, while keeping the scene background symmetrically around the central scene element (see Figure 2 for an example). Subsequently, grayscale pictures

were matched for luminance and contrast, by adjusting the grayscale values to reach a peak luminance of 157 CD/m² (Gossen Mavospot luminance meter), a mean pixel luminance (grayscale values) of 100, and a mean pixel contrast (standard deviation of the grayscale values) of 50. Subsequently, we computed each picture's entropy and compared entropy values pairwise across picture types (all *t*s < 0.602, all *p*s > .55). We interpreted this as evidence that luminance, contrast, and entropy were similar across picture types. To facilitate fixating of the central aspects of each stimulus and to minimize effects of contrast in the stimulus periphery, pictures were then submitted to a 2D Laplacian Gaussian filter kernel (size 562 × 768 pixels, *SD* = 120 in width, *SD* = 200 in height), resulting in a visible high-contrast central oval and decreasing contrast to the sides (see Figure 2d).

In a given trial, one individual picture was presented in a periodic fashion, with picture off and on cycles alternating at a rate of 12 Hz, while the contrast of the “on” state was gradually increased. Each contrast level was shown for 41.7 ms followed by 41.7 ms of gray screen, repeated 40 times during each trial, resulting in a periodic (12 Hz) stimulation (3,333 ms), evoking sweep-ssVEPs (Ales et al., 2012; Norcia et al., 2015). Thus, over the course of one trial, luminance contrast of the pictures gradually increased over time, implemented by enhancing each stimulus' Michelson contrast in 40 logarithmic steps from 0.2% to a maximum of 90%, resulting in a rising pattern of stimulus contrast, while evoking ssVEPs. Figure 2e illustrates this sequence.

The auditory threat stimulus was a 90-dB SPL (duration, 1,000 ms) white noise played once during an inter-trial interval in the last block (after the 50th trial in that block) through

speakers placed behind the participant. This is routinely done in threat-of-shock type studies to avoid changes/differences in the defensive stance of the observer from before and after the shock or noise (Bradley et al., 2005). In brief, the literature in this field shows that participants tend to maintain a level of anxious anticipation throughout long periods of time and several blocks, when not experiencing the noxious event (Bublitzky et al., 2014). On experiencing the event, however, the defensive disposition decreases as participants on average report that the actual stimulus was not as aversive as expected (Bublitzky et al., 2017). All stimuli were generated using MATLAB (R2007b; Mathworks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Visual stimuli were displayed centrally with a fixation point (a small black circle), shown only during the inter-stimulus-interval, on a gray background on a 23-inch LED screen (Samsung LS23A950, refresh rate of 120 Hz). The fixation point disappeared on flicker onset (*t* = 0 in Figures 3a and 4b) and returned immediately after stimulus offset. For Karolinska faces, the fixation point appeared at the location corresponding to the face's nasion, that is, above the nose, slightly below the horizontal line connecting the eyes. For scenes, we attempted to place the central scene element as close to the location of the fixation point as possible. See the discussion for limitations of this approach.

2.3 | Design and procedure

The purpose of the experimental design was to manipulate the motivational context (viewing under threat vs. under safety), in addition to manipulating picture type and

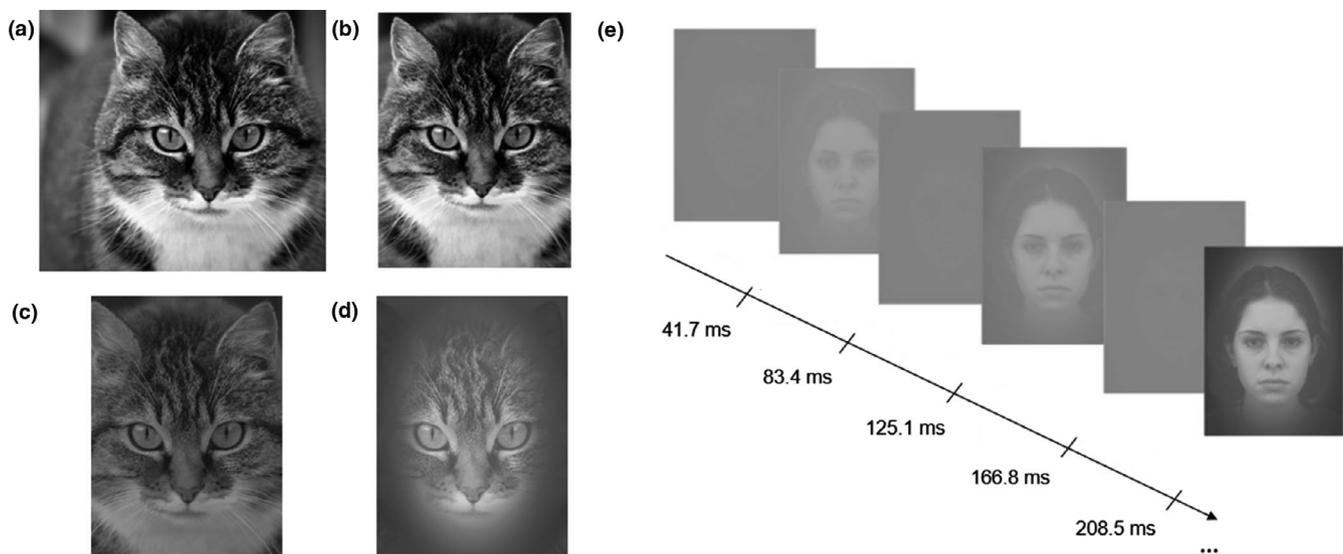


FIGURE 2 Illustration of the image normalization steps applied to original color pictures. An example scene picture is shown in Panel a in its grayscale version. Each picture was cropped (b), controlled for stimulus size, entropy, mean luminance, and mean contrast (c), and finally filtered with a Gaussian kernel filter, shown in Panel d. (e) Schematic illustration of one example trial (3,333 ms), with inter-trial intervals randomly varying between 1,500 and 3,000 ms

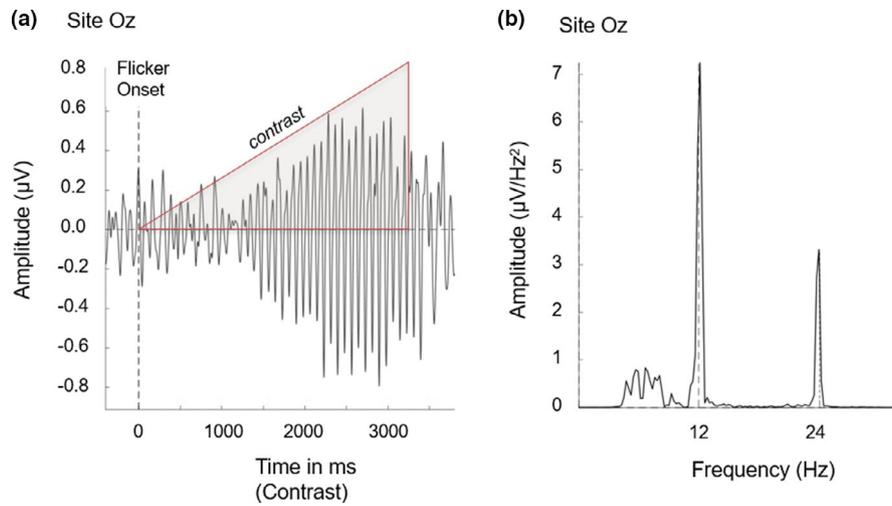


FIGURE 3 (a) Example time-course of 12-Hz ssVEP with increasing stimulus contrast for a representative occipital sensor (Oz), averaged for KDEF stimuli in safety blocks. (b) Frequency power spectra as derived by FFT for Oz. Pronounced peaks at the driving frequency (12 Hz) and harmonics (24 Hz) are visible. Residual ongoing activity in lower bands, but distal from the 12 Hz response, is visible in the lower theta and alpha range (5–9 Hz). Note that activity in this range has relatively high power, following the $1/f$ shape of the EEG spectrum

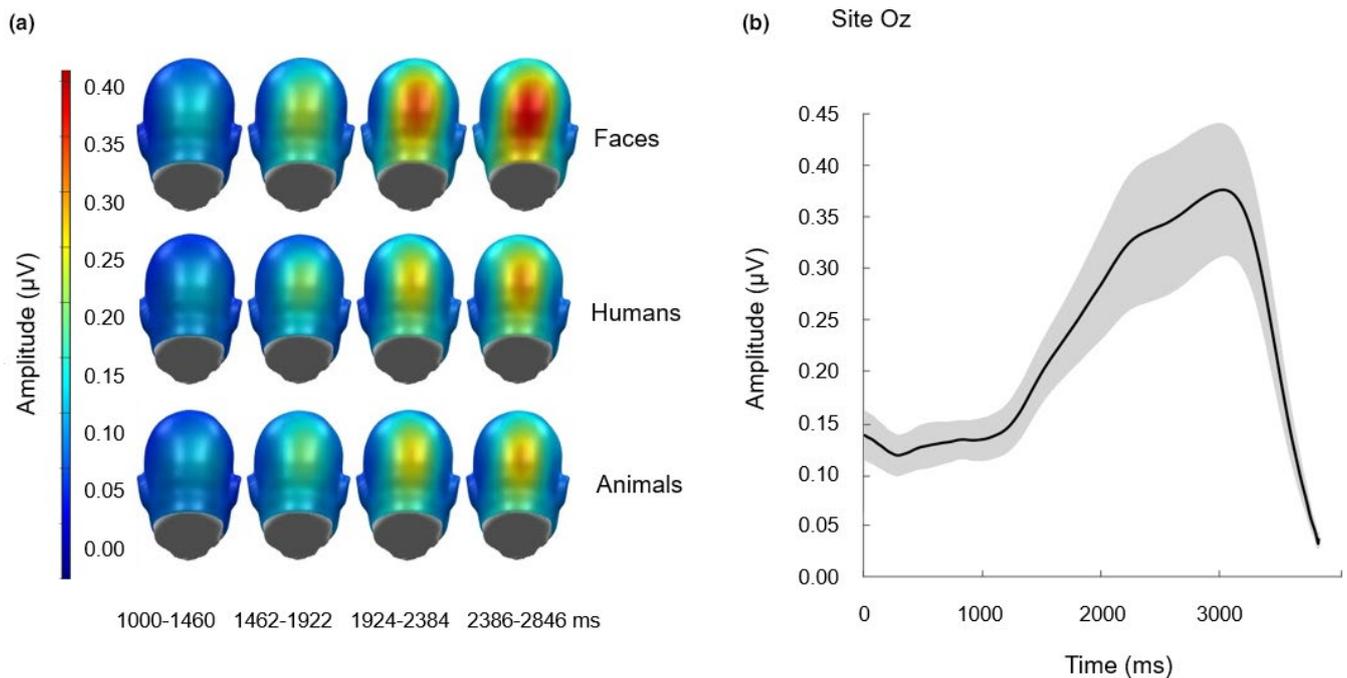


FIGURE 4 (a) Grand mean ($n = 18$) topographical distribution of steady-state visual evoked potential (ssVEP) amplitude with increasing contrast over occipital sites as a function of picture type. (b). Grand mean time course of the Hilbert envelope of the ssVEP with increasing stimulus contrast, across picture types for a representative occipital sensor (Oz). Shading indicates the standard deviation across participants

affective content. To manipulate motivational context, we induced anticipatory anxiety in a blocked design, following standard instructed threat/safety paradigms (e.g., Bradley et al., 2005). A total of 288 trials were organized into four blocks, two threat and two safety blocks, respectively. Each of the 72 pictures was shown once in each block. Threat or safety blocks were indicated by colored bars (1 degree of

visual angle in width) on both sides of the screen, which remained on-screen throughout the block, including during picture presentation. Block conditions were pseudorandomized and applied consistently throughout the experiment. The meaning of a threat (red) or safety (green) block was indicated by the experimenter and explained by instructions on the screen prior to the experiment. Participants

were instructed that they may hear a loud burst during threat blocks, that is, only when the red color was visible at the edges of the screen. Having given informed consent, participants were seated in a sound-attenuated, dimly lit electrically shielded testing room in which the electrode net was applied. Oral and written instructions were provided. Participants viewed the display at a distance of 106 cm and were instructed to view the pictures attentively, to maintain gaze at the center of the screen, and to avoid eye movements and blinks during picture presentations. Inter-trial intervals varied randomly between 1,500–3,000 ms. Participants were asked to give ratings of anxious apprehension before the first block and ratings of unpleasantness of the noise after the last block (0 = *not anxious [unpleasant] at all*, 100 = *as anxious [unpleasant] as possible*).

After the sweep-ssVEP session, participants performed a recognition task in which they viewed all old pictures as well as the same number of new pictures (foils), matched picture-wise for semantic content. Data from this task were used for cross-validation, as described below. All 144 pictures were viewed in random order and remained on-screen until participants gave an old/new response using a standard computer mouse.

2.4 | EEG recordings and data analysis

The EEG was continuously recorded from 129 electrodes using a HydroCel Electrical Geodesics (EGI) system. Data were digitalized at 500 Hz, using the vertex sensor (Cz) as the recording reference. All electrode impedances were below 40 k Ω . Offline EEG data were pre-processed using the EMEGS (ElectroMagnetoEncephalograph) toolbox for Matlab (Peyk et al., 2011). An 18th-order low-pass Butterworth filter of 30 Hz (3 dB point) and a 7th-order high-pass Butterworth filter of 6 Hz (1 dB point) were applied, and epochs of 400 ms pre- and 3,800 ms post-onset of the flickering stimuli were extracted. Trials with artifacts were identified based on distributions of statistical parameters of the EEG epochs (absolute value, standard deviation, maximum of the differences) across time points for each channel using the procedure of artifact rejection as described by Junghöfer et al. (2000). Eye movement was assessed using electrooculogram sensors located above and below each eye, as well as at the outer canthi, and trials showing detectable gaze changes during picture presentation were discarded, to avoid confounds of condition differences in CRFs by differential saccadic scanning patterns. If contaminated with artifacts, cranial sensors were interpolated with statistically weighted, spherical spline values. The average number ($\pm SD$) of retained trials across individuals was 218.9 ± 31.9 of 288 trials in total and did not vary between experimental conditions.

The number of channels excluded ranged from 1 to 9 ($M = 3.17$, $SD = 1.95$).

2.5 | Steady-state visual evoked potential analysis

The present study used sweep-ssVEPs to assess neural CRFs evoked in the visual cortex. To enable computation of the dependent variables described in more detail below, artifact-free epochs were first averaged separately for the three picture types (KDEF, IAPS with humans, IAPS with animals), Block (threat vs. safety), and Emotion (KDEF, neutral vs. angry; IAPS, pleasant, neutral, threatening, unpleasant). The time-varying amplitude of the sweep-ssVEP signal was then extracted by means of the Hilbert transformation. To this end, data were first bandpass-filtered with a 12th-order Butterworth filter having a width of 0.5 Hz around the target frequency of 12 Hz. Then, the Hilbert transform was applied using the *hilbert.m* function in the Matlab environment, and the time-varying amplitude at 12 Hz extracted as the modulus of the real and imaginary part of the transform. The resulting time-varying measure reflects the envelope of the trial-averaged ssVEP, thus varying as a function of (a) the magnitude and (b) the inter-trial phase similarity of driven oscillatory activity in the visual cortex. To eliminate any offset related to the flicker onset, the mean of a 100-ms segment preceding picture onset was subtracted as baseline.

2.6 | Gumbel function parameter fit

To quantify the neural CRF with few, conceptually meaningful, parameters (baseline, c_{50} , slope, response level, see Introduction), we fit the time-varying Hilbert envelope of the ssVEP in each condition to a psychometric function. Specifically, we selected the mathematical implementation of the Gumbel (log Weibull) function, designed for logarithmic contrast steps as used in this study. To allow fitting of the ssVEP to the Gumbel function, two additional data reduction steps were completed. First, the electrode space data were reduced to a single time-varying signal, by means of averaging across a region of interest that included mid-occipital site Oz and its two closest neighbors. Second, the resulting time series (the sweep-ssVEP Hilbert envelope) was down-sampled into 13 steps reflecting the range from zero to maximum contrast.

The resulting 13 data points were then fitted to the Gumbel function using functions of the Palamedes toolbox (Prins & Kingdom, 2018), implemented in Matlab software. All four parameters of the psychometric function were set to vary freely, and their maximum likelihood estimation was performed using Nelder-Mead simplex search (Nelder

& Mead, 1965). Only the c_{50} and R_{\max} parameter were considered for hypothesis testing, but the baseline and slope parameters were examined to ensure specificity of findings and satisfactory model fit. Problems with fitting the function to the data would, for example, be indicated by extreme slope values, which were, therefore, stored and examined as a manipulation check. In addition, the goodness of fit was quantified by the root mean square error (RMSE, the SD of the residuals; Schubert et al., 2017). A maximum of 800 iterations were run for each parameter, and a log search grid was pre-defined for the slope parameter. The Gumbel psychometric function defining the response for each contrast level C is given as follows:

$$R(C) = \text{baseline} + (R_{\max} - \text{baseline}) \times \left(1 - e^{-10^{s(C - c_{50})}}\right),$$

where R is the response to contrast C , R_{\max} the maximum response amplitude, c_{50} is the semisaturation constant, and s is the slope of the curve.

2.7 | Steady-state visual evoked potential single-trial analysis

The envelope of the trial-averaged ssVEP is affected not only by the magnitude of the neural activity at the driving frequency but also by the similarity of the phase at that frequency, across the trials entering the time domain average. In addition, trials vary in terms of the regularity in which the flickering stimulus drives neural oscillations, representing another source of variability in the Hilbert envelope. To assess the contribution of such trial-by-trial variability to the trial-averaged sweep-ssVEP envelopes, a moving-average window analysis with a window of four cycles for the 12-Hz stimulus frequency was conducted on each single trial as described in Thigpen et al. (2018). First, a time window of 200 ms before flicker onset was subtracted as baseline. To perform the analysis on integer numbers at the frequency of interest (12 Hz), the original time window was then resampled to 600 Hz with a piecewise cubic spline interpolation. Subsequently, 4-cycle windows were shifted by one cycle, and the window content was averaged, moving the averaging window through the steady-state stimulation period while leaving out low-contrast segments (600–3,300 ms after flicker onset). The procedure yields estimates of the power and phase stability (by window averaging normalized complex phase at the driving frequency) using Fourier transformation (see Wieser et al., 2016). The resulting values were quantified by averaging first across trials and then across electrodes according to the weights of the first principal component for each sensor, using trial topographies as observation, for each participant separately (see Thigpen et al., 2018 for more details).

2.8 | Statistical analyses

Fitting the parameters of a psychometric function requires minimal noise, which may be present in single-participant data. We, therefore, followed recent methodological work on model fitting and statistical analysis in within-subject designs (Prins & Kingdom, 2018; Schwarzkopf, 2015; Yarrow, 2018). Specifically, we implemented a parametric bootstrap analysis (Wasserman & Bockenholt, 1989) for estimating Bayes factors of the effects of interest. To this end, we generated 2000 grand mean CRFs for each condition of interest, randomly drawing from the 18 participants with replacement, and fitted the Gumbel distribution to the resulting bootstrap CRFs, resulting in distributions of 2000 estimates for each parameter, for the conditions in PICTURE TYPE (faces, IAPS with humans, IAPS with animals), BLOCK (threat, safety), EXPRESSION (angry, neutral), and SCENE CONTENT (pleasant, neutral, threat, unpleasant). Note that EXPRESSION was only available for face stimuli, and SCENE CONTENT only for IAPS pictures. The present study was not designed to detect interactions between those factors, as evinced by bootstrap distributions for interaction effects, which suffered from low signal-to-noise of the underlying sweep-ssVEP being based on fewer trials than main effects. Interaction effects were, therefore, not examined.

Pairwise Bayes factors were calculated between all conditions comprised in one experimental factor, that is, PICTURE TYPE (3 conditions); BLOCK (2 conditions); EXPRESSION (2 conditions), and SCENE content (4 conditions). To this end, we based our approach on the bootstrap-based procedure proposed by Schwarzkopf (2015). First, the difference between two conditions of interest for a given parameter was calculated for each bootstrapping step, resulting in a difference distribution. Odds for an effect to be present in the data were then calculated from this distribution as $L(\text{effect})/(1-L(\text{effect}))$, where $L(\text{effect})$ is the likelihood of a value in the bootstrapped difference distribution to be above zero. The Bayes factor is given as the ratio of posterior odds over prior odds, with the prior odds of conditions differing expected to be 1 (corresponding to a likelihood of 0.5). Following Schwarzkopf (2015), we compared the empirical posterior odds not to these theoretical priors but to empirical priors obtained by repeating the same bootstrapping with randomly assigned condition labels, to account for potential biases, including skews of the distributions. These permutation-based bootstrapped distributions were transformed into odds as described above, and the BF_{10} was calculated as the ratio of posterior odds over permutation (prior) odds from a distribution representing the null effect. For the interpretation of Bayes factors, we used the categories first proposed by Jeffreys (1961), and similar to Lee and Wagenmakers (2014), where BF s between 3 and 10 represent moderate evidence, 10 to 30 strong evidence, and BF s > 30 represent very strong or extreme ($BF > 100$) evidence for the hypothesis.

2.9 | Cross-validation against evoked potentials

Fitting CRF parameters to neural data is a relatively new practice. We, therefore, sought convergent validity between the estimated CRF parameters and established metrics of neural response to contrast. Specifically, to cross-validate the CRF parameters against established electrophysiological indices of visuocortical reactivity, we measured event-related potentials evoked by the onset of the same 72 stimuli in addition to 72 new pictures. All pictures were manipulated following the procedure described above and shown in full contrast, in a separate session, after completion of the sweep-ssVEP session. A low-pass filter of 40 Hz and a high-pass filter of 0.1 Hz was applied, and epochs of 400 ms pre- and 1,000 ms post-onset extracted. The average number ($\pm SD$) of retained trials across individuals was 100.22 ± 23.96 of 144 trials in total. The number of channels excluded overall ranged from 1 to 11 ($M = 4.56$, $SD = 3.32$). For the P1, a time window from 120 to 160 ms for KDEF stimuli and a time window from 130 to 170 ms for IAPS pictures was extracted. For the N1, a time window was selected from 170 to 210 ms. for both stimulus sets. Components were scored as the mean amplitude within time windows. Instead of using electrode clusters, a PCA was run on the specified time windows for the KDEF and the IAPS picture set individually. Following the procedure described above, the first component was extracted as a weight vector for each sensor to obtain a single value for the P1 and the N1 for each picture set (KDEF, IAPS), respectively.

2.10 | Exploratory analyses

As described above, we conducted exploratory analyses to characterize factors that contributed to condition differences in CRF parameters, particularly in terms of R_{\max} . To this end, several correlational analyses were conducted. The relationship between the R_{\max} parameter of sweep-ssVEPs, and phase stability within and between trials, was assessed by correlation of the parameter estimates of the sweep CRF and phase stability. These analyses were contingent on effects in the primary analyses and are detailed below.

3 | RESULTS

3.1 | VAS ratings

As expected, self-reported nervousness/unpleasantness increased from pre-session levels ($M = 27.06$, $SD = 22.18$) to post-session levels, $M = 55.8$, $SD = 23.02$, $t_{16} = -5.31$, $p < .001$, supporting the effectiveness of the threat of noise manipulation.

3.2 | Electrophysiological data (steady-state visual evoked potentials)

The 12-Hz on-off picture stream evoked pronounced 12-Hz oscillations. A representative time course of the ssVEP signal for an electrode corresponding to site OZ of the international 10–20 system (Figure 3a) and its Discrete Fourier Transformation (Figure 3b) are illustrated in Figure 3. The maximum of the ssVEP signal was seen over the occipital cortex (see Figure 4a). As expected, ssVEP amplitude varied with the time-varying stimulus contrast, that is, the amplitude envelope measured with the Hilbert transform gradually increased over time, tracking the increasing contrast (Figure 4b). Note that the ssVEP signal shows a relative delay with respect to the contrast increase, that is, it starts ramping up only after a certain minimum contrast is reached. This property is well captured by the sigmoid psychometric function. Its parameters also capture differences in “baseline” contrast levels (i.e., time periods where the contrast is too low to be reflected in the ssVEP amplitude) as well as any differences in latency between conditions that may occur in this initial sensitivity to low contrast. We have observed this same phenomenon across several previous sweep ssVEP studies (e.g., Friedl & Keil, 2020).

3.3 | Effects of threat versus safety across picture types

The fit of the sweep ssVEP data to the Gumbel function was very good ($RMSE = 0.06$). Comparing the parameters of the sweep-ssVEP CRF under threat versus safety across all picture types supported the hypothesis that anxious anticipation of threat heightens sensory sensitivity, over the null hypothesis. Specifically, the c_{50} -parameter was lower under threat compared with safety ($BF_{10} = 5.7$), consistent with heightened contrast gain when viewing the stimuli under threat of noise (see Figure 5). No difference between threat and safety blocks emerged for the response level parameter, R_{\max} ($BF_{10} = 1.8$).

3.4 | Effects of picture type

Paralleling analyses of BLOCK, above, data were fit well by the Gumbel function when separated by PICTURE TYPE ($RMSEs = 0.03$, 0.04 , and 0.03 for faces, scenes with humans, and scenes with animals, respectively). There was moderate evidence to support differences in the c_{50} -parameter as a function of picture type, where both scenes with animals and scenes with humans had lower contrast gain (c_{50}) compared with faces ($BF_{10} = 10.2$ for faces compared with scenes with humans, and $BF_{10} = 6.8$

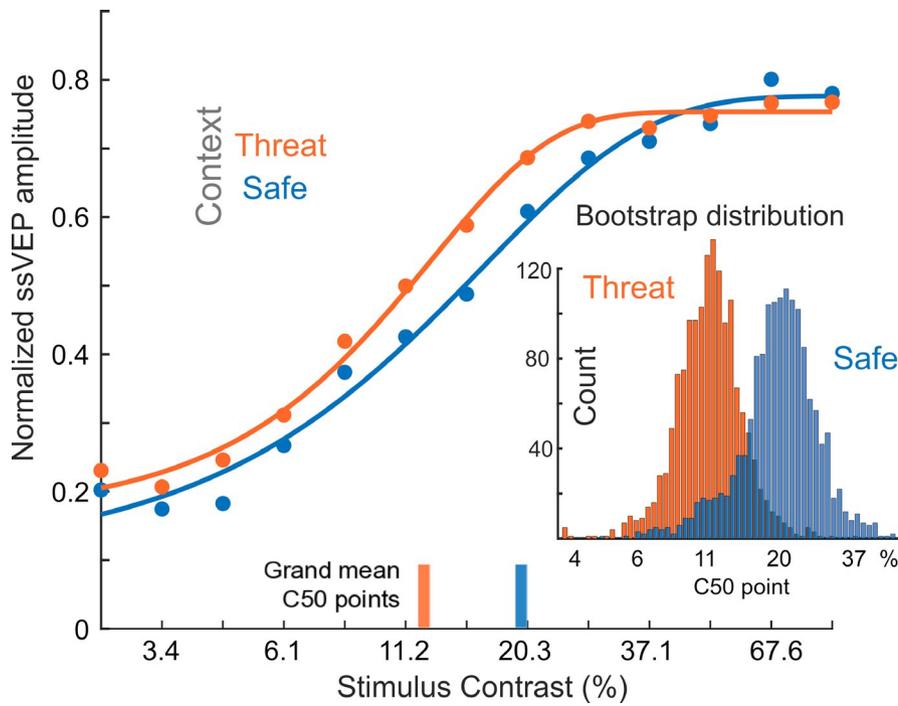


FIGURE 5 Grand mean ($n = 18$) of estimated contrast-response functions under threat and safety, across all stimulus types. Dots indicate the observed data, and the line indicates the best fit. A leftward shift of the function is evident when participants viewed stimuli under threat, compared with safety. The inset shows bootstrap distributions of the c_{50} -parameter under threat and safety, which illustrate the strength of the evidence supporting the notion that threat anticipation heightens contrast sensitivity, reflected in a $BF_{10} = 5.7$. Vertical bars on the contrast axis indicate the c_{50} points for each grand mean psychometric function

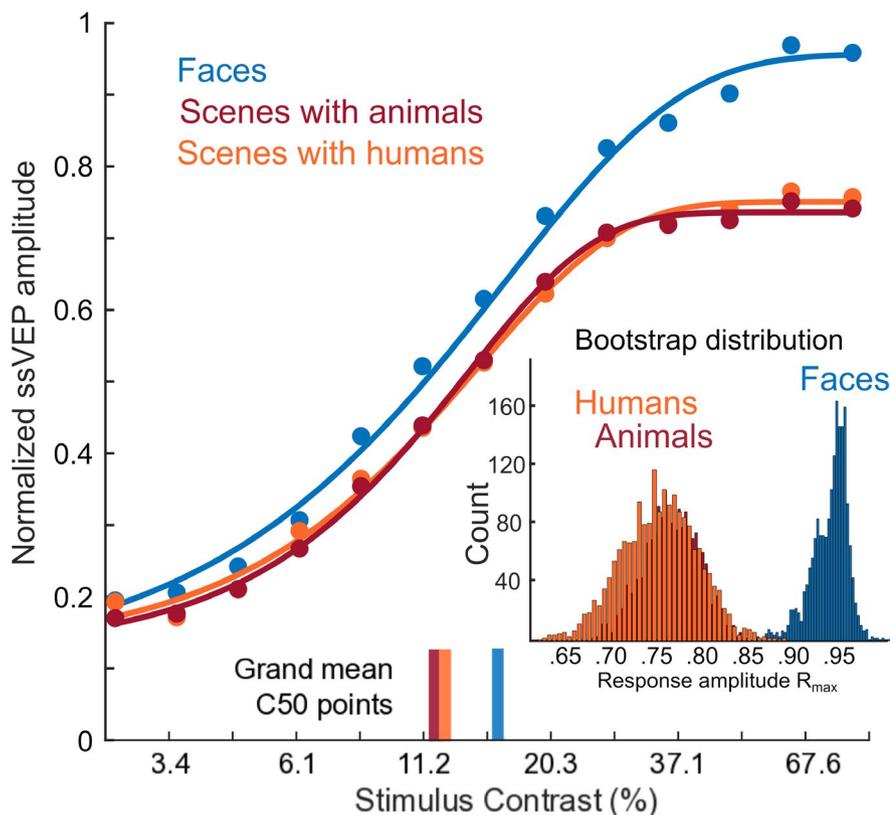


FIGURE 6 Grand mean ($n = 18$) of estimated contrast-response functions when viewing different stimulus types. Dots indicate the observed data, the line indicates the best fit. The response level parameter R_{max} was greater when viewing faces, compared with scenes depicting animals or humans. Bootstrap distributions of the response level parameter R_{max} are shown in the inset and illustrate the strength of the evidence supporting the notion that faces prompted greater response gain, compared with scenes. Vertical bars on the contrast axis indicate the c_{50} points for each grand mean psychometric function, which were lower for both types of scenes, compared with faces, as well

for faces compared with scenes with animals). Extreme evidence was found for a difference in terms of the response level parameter R_{max} , which was greater when viewing faces, compared with viewing scenes with animals ($BF_{10} = 1999$), or scenes with humans ($BF_{10} = 1997$; see Figure 6).

3.5 | Effects of facial expression

The Gumbel function fit the empirical CRFs for angry and neutral faces well (RMSEs = 0.04 and 0.02, respectively). There was, however, no evidence for the modulation of any of the parameters of the CRF by facial expression (all $BF_{10} < 3$).

3.6 | Effects of emotional scene content

Again, the empirical CRFs were well fit by the Gumbel function, when broken down by emotional content (RMSEs = 0.04, 0.03, 0.04, 0.04 for pleasant, neutral, threatening, and unpleasant content). In terms of parameter differences, the data provided strong support for the hypothesis that scene content interferes with, rather than facilitates response gain. The R_{\max} parameter was smaller when viewing pleasant, threatening, and unpleasant, compared with neutral scenes ($BF_{10} = 1999, 498, \text{ and } 3.0$, respectively). Consistent with interference exerted by scene content that was high in emotional arousal, the c_{50} -parameter was greatest when viewing unpleasant, compared with neutral and pleasant pictures ($BF_{10} = 13.6 \text{ and } 13.8$, respectively), but there was no evidence to support a difference between c_{50} -parameter estimates when viewing unpleasant and threatening pictures ($BF_{10} = 1.8$, see Figure 7).

3.7 | Single-trial amplitude and phase stability

To explore potential factors contributing to heightened response amplitude for faces observed in the main analysis, the metrics obtained from single trials were averaged across sensors using PCA weights of the first component (with trials as

observations) for each participant. The resulting subject-level averages entered 2×3 (Block \times Picture Type) repeated-measure ANOVAs, one ANOVA for each of three dependent variables: mean and variance (across trials) of the mean single-trial ssVEP power, and mean phase stability across the trial measured as the average of within-trial phase locking values of an occipital electrode cluster, see Figure S1a.

There was a main effect for within-trial phase stability, arising as a function of Picture Type, $F_{2,34} = 7.62$, $p = .002$, $\eta_p^2 = 0.31$, with higher mean phase stability for trials with KDEF stimuli compared with trials with humans ($p_{\text{adj}} = .013$) or animals ($p_{\text{adj}} = .031$), and no difference between IAPS subsets ($p_{\text{adj}} = .990$), see Figure S1b. Strong support for this effect is also provided by the Bayesian ANOVA, $BF_{10} = 326.97$, estimation error = 0.9%. No other significant main effects or interaction emerged ($F_s < 0.67$, $p_s > .520$, $BF_{01} > 4.60$, estimation error < 2.7%).

No main effects or interactions were observed for mean single-trial power, $F_s < 1.10$, $p_s > .326$, $BF_{01} > 3.88$, estimation error < 1.9%. In contrast, single-trial power was more variable across trials in safety blocks, as indicated by a main effect of Block ($F_{1,17} = 5.10$, $p = .037$, $\eta_p^2 = 0.23$, $BF_{10} = 1.32$, estimation error = 2.1%) on single-trial power variability, see Figure S1c. No further effects emerged, $F_s < 0.34$, $p_s > .712$, $BF_{01} > 7.46$, estimation error < 2.0% for the null model including the main effect of Block.

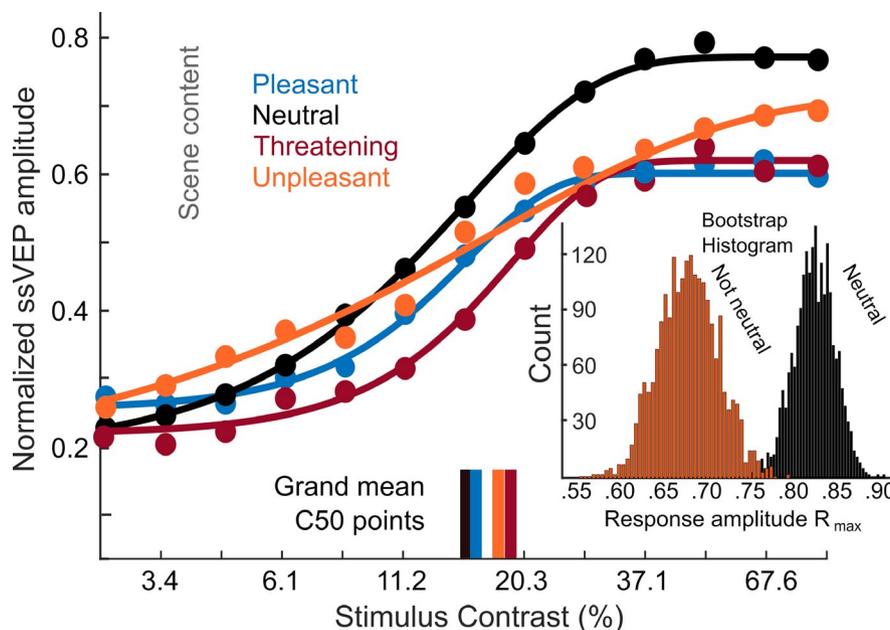


FIGURE 7 Grand mean ($n = 18$) of estimated contrast-response functions when viewing scenes differing in content. Dots indicate the observed data; the line indicates the best fit. The inset shows bootstrap distributions of the response level parameter R_{\max} for neutral scenes, compared with all other scene contents. These histograms illustrate the strength of the evidence supporting the notion that neutral content (black bars) prompted greater response gain compared with the other contents (brown bars). Vertical bars on the contrast axis indicate the c_{50} points for each grand mean psychometric function, showing heightened c_{50} for unpleasant and threatening content, compared with pleasant and neutral

3.8 | Cross-validation of fitted parameters against P1 and N1

The total (baseline plus response) amplitude parameter estimated for the sweep-ssVEP response to facial stimuli was positively correlated with the face-evoked P1 amplitude evoked during recognition, $r_{18} = .504$, $p = .033$, but not with the N1 amplitude, $r_{18} = -.018$, $p = .942$. Similarly, the total amplitude to complex scenes was related to the corresponding P1 response, $r_{18} = .516$, $p = .028$, but not to the N1 response, $r_{18} = .402$, $p = .098$. Thus, participants with greater total response amplitude as determined from fitted CRF parameters also showed greater early visual responses (i.e., P1 amplitudes). This provides converging evidence that the response parameters of the CRF model are neurophysiologically meaningful.

4 | DISCUSSION

The present study demonstrated that stimulus content and motivational context (anxious apprehension of a loud noise) impact low-level visual processing, here quantified as the neural CRF, evoked by contrast-changing naturalistic scenes and faces. Across analyses, results showed small to moderate effects of content and context, and large effects of picture type (faces vs. naturalistic scenes) on the CRF. In line with previous sweep-ssVEP work (Friedl & Keil, 2020; Hamer & Norcia, 2009; Song & Keil, 2014), neural activity over occipital cortex increased with increasing stimulus contrast, plateauing just before the maximum contrast (90% Michelson) was reached. Stimuli with faces showed overall greater response amplitude than naturalistic scenes depicting people or animals. This effect was accompanied by greater phase stability of the ssVEP signal within face trials, that is, a more stable alignment of the EEG phase to the stimulus rate when viewing faces, compared with scenes. Individual trial amplitude did not show this modulation, suggesting that amplitude facilitation when viewing faces was at least partly mediated by phase consistency and temporal stability of the driven brain oscillation, rather than by differences in neural population size alone.

Moderate evidence was found for the notion that motivational context (implemented here as anxious anticipation of a noxious stimulus) heightens the sensitivity but not the activity level of sensory systems. Across all stimulus types, the c_{50} -parameter was substantially reduced when under threat, compared with safety. By contrast, the response level was unaffected by the threat manipulation, suggesting that contrast sensitivity, but not the strength of the neural population responses is affected by the motivational context of anxious apprehension. The mapping of gain mechanisms to cognitive concepts has been challenging because manipulations

traditionally associated with “top-down modulation” and “bottom-up saliency” have been shown to alter both contrast and response gain mechanisms (Herrmann et al., 2010; Katzner et al., 2011). Recent work in monkeys (Sani et al., 2017) has demonstrated that anticipatory attention (consistent with hypervigilance) prompts contrast-gain mechanisms, early in stimulus processing, whereas multiplicative (response-gain) mechanisms become more prominent over the duration of a trial, as recurrent processing and heightened inter-trial synchrony act to enhance the ssVEP envelope to behaviorally relevant stimuli (Kim et al., 2007). As such, the present data add mechanistic information to theories in fear and anxiety research, many of which broadly postulate that states of anxious apprehension are accompanied by attentional hypervigilance (Lipp & Derakshan, 2005; Öhman & Mineka, 2001; Wieser, Reicherts, et al., 2016). In a similar vein, excessive hypervigilance represents a frequently observed symptom in mental health problems along the fear, trauma, and anxiety spectrum (Amir et al., 2009; Bogels & Mansell, 2004; Mahan & Ressler, 2012). Characterizing the nature of anxiety-related changes in sensation and attention is, therefore, relevant for translational and clinical studies, which have increasingly sought in neurophysiologically meaningful disease markers (Kotov et al., 2017; Lang et al., 2016).

In the present study, participants viewed the same stimuli under threat and safety instructions, with the order of blocks counterbalanced. All participants reported an increase in anxious apprehension during the threat block, compared with the safety block. Thus, whereas differences in the CRF for different picture categories may suffer from confounds with physical stimulus properties, the heightened contrast gain during threat occurred independently of physical stimulus features. These observations extend previous studies which found lowered contrast thresholds after priming with emotional cues (Phelps et al., 2006) and broadened contrast sensitivity functions after viewing arousing conditioned stimuli (Lee et al., 2014) to situations in which anxiety is induced by instruction. Neurophysiologically, heightened contrast sensitivity has been linked to pre-stimulus top-down modulation originating in anterior cortical structures (Sani et al., 2017), thought to involve GABAergic mechanisms (Ferguson & Cardin, 2020), and evident in the animal model during states of arousal (Vinck et al., 2015).

In terms of scene content, pleasant, unpleasant, and threatening content prompted lower response gain in the sweep-ssVEP CRF, compared with neutral scenes. Furthermore, scenes overall prompted lower response gain than simple facial portraits. This pattern of findings is consistent with the notion that pleasant, unpleasant, and threatening complex scene content interferes with the lower-level processing that underlies the CRF as defined by the envelope of the ssVEP (Keil & Heim, 2009). Response gain changes in the visual cortex have been linked to heightened output of neural

populations, perhaps mediated by the release of GABAergic interneurons (Katzner et al., 2011). Such modulation may act to increase the population gain without affecting the selectivity, or the input gain of visuocortical neurons, and as such may be mediated by arousal (Lee et al., 2014). This interpretation is contrary to the present findings, where affectively neutral, low-arousing stimuli prompted the highest response gain. Findings in which pleasant, unpleasant, and threatening scene content interferes with rapid visual processing in retinotopic areas have been increasingly reported over the past decade (Riels et al., 2020). Computational models and systematic analyses across different driving frequencies have suggested that such interference may be specific to scalp recorded population signals in which individually heightened responses interfere with each other when elicited in rapid succession (i.e., destructive interference; Bekhtereva et al., 2018). Future work may use multimodal imaging in conjunction with CRF modeling to examine the network interactions mediating the stimulus-specific response gain modulation observed here for faces and neutral scenes. Such work may shed light on the question whether emotional content interferes with low-level visual contrast processing, or whether the interference effects observed here arise as an artifact of the ssVEP method. Such work may also take into account a growing body of work examining determinants of visuocortical gain mechanisms such as stimulus size, stimulus duration, and varying indices of behavioral and brain state. For example, in a recent review of the literature, Ferguson and Cardin (2020) report evidence for gain-modulating factors such as instructed attention, learning, locomotion, arousal, and neuromodulatory (e.g., cholinergic, adrenergic) activity. In rodents, many of these factors, all of which are readily linked to emotional processes, affect visuocortical gain through different mechanisms, not only at the cellular but also at large-scale level (Vinck et al., 2015). Thus, future studies in human observers may build on the animal model to develop specific experimental designs and testable hypotheses regarding different manipulations of behavioral states linked to affective experience.

The present study avoided using the most salient scene categories, known to drive extreme ERP responses (i.e., erotic and mutilation content), given its goal to identify gain changes related to graded manipulations in content and context. A sizable body of studies suggests that brain responses to emotional content depend on the experienced arousal of the observer (e.g., Olofsson et al., 2008; Schupp et al., 2004). Threat content (i.e., pointed guns, angry people) is often rated as less engaging and in these cases has been found to elicit smaller responses than other aversive picture content (Frank & Sabatinelli, 2019; Weinberg & Hajcak, 2010). Interestingly, sweeping along the dimension of contrast, modulation of emotional content was reflected in heightened neural response only, but not in sensitivity, that is, there was no evidence that contrast gain changes as a function of

picture content. However, this may result from the categories used in this study (low-arousing pictures) and may differ in clinical populations, for example, in those with specific phobias (McTeague et al., 2018). Paralleling the contrast gain effect of threat, stimulus material that is phobia related might also prompt a sensitized threshold, rather than gaining from an amplification overall, as fear-relevant stimuli are detected faster than irrelevant stimuli (Öhman, Flykt, & Esteves, 2001).

The heightened response gain for facial stimuli compared with scenes may reflect entropy differences as well as smaller variation between face exemplars compared with scene exemplars in terms of overall composition. Obviously, faces are inherently more homogeneous (constant composition, orientation, and visual angle; Sabatinelli et al., 2011), and trial-by-trial changes are minimized compared with pictures that show a variety of contexts and scenes. This is consistent with findings from Britton et al. (2006), who argued that faces are processed in a facilitated fashion relative to complex scenes, with the latter requiring additional cognitive resources, thus evoking different brain response patterns. Feature differences (e.g., shape, eyes, nose, mouth) between exemplars are less pronounced for faces than for complex scenes (see Alpers et al., 2011; Berdica et al., 2018). Furthermore, faces are known to effectively drive activity in lateral visual areas, including the fusiform and lateral occipital cortex (Schweinberger et al., 2007). If such prioritized processing in face-sensitive brain regions were to underlie the present findings, the topography of the sweep-ssVEP would be expected to differ from a mid-occipital maximum, as seen in studies targeting face processing (Rossion, 2014). The present topography (see Figure 4a) is at odds with the notion that heightened response gain for faces merely reflects the involvement of additional brain regions. Finally, decades of work into face processing have suggested that faces are processed holistically. Holistic processing emphasizes the overall gestalt of the face over a decomposition of visual input into scene aspects as has been observed when processing non-face objects (Farah et al., 1998). Such holistic, efficient processing of an overall facial gestalt may well prompt more consistent, phase-similar oscillatory responses within and across trials, in line with the present findings. Although picture complexity, as indexed by entropy values, was not different between the three picture sets, phase stability analyses suggested higher and more robust alignment of visuocortical engagement for faces, consistent with greater response amplitude after trial averaging and with higher phase stability for faces.

The current study has strong methodological implications because it modeled sweep-ssVEP envelopes by means of the psychometric function — a rarely used approach in electrophysiological studies of visual cognition. Overall, the present study supports the notion that the sweep-ssVEP method with controlled stimulus material enables testing of hypotheses

regarding the lower-tier visuocortical processing of naturalistic stimuli. Pleasant, unpleasant, and threatening scene content prompts differences in response gain, but interpreting these effects requires comparing responses with stimuli that belong to the same broad category. Examining phase-locking metrics along with metrics of amplitude aids in the interpretation of the results. Comparisons across different types of stimuli (e.g., faces vs. scenes) should be avoided or interpreted with caution, as differences in stimulus composition affected the sweep-ssVEP, despite attempts to equate factors such as contrast, luminance, entropy, and spatial frequency. The sweep-ssVEP technique yields meaningful and robust estimates of the neural CRF, allowing researchers to examine the effects of variations along continuous feature dimensions on visual processing within manageable session durations. The technique is not limited to the dimension of contrast, opening up avenues for adapting it to higher-order cognitive dimensions of interest such as sweeping across semantic or affective categories. A model-based approach to human electrophysiology is desirable because it provides a means for reducing the envelope waveform to few, conceptually meaningful variables, avoiding widely acknowledged problems such as arbitrary peak picking, or averaging across large, non-stationary time windows (Keil et al., 2014; Luck, 2005). The total amplitude extracted from this procedure was correlated with the amplitude of the P1 ERP response, measured during a separate session. This cross-validation analysis suggests that the response parameter is a valid estimate of neural mass activity, while also providing important information on the CRF. The sweep-ssVEP method varies the dimension of interest *within* each trial (Hamer & Norcia, 2009; Norcia et al., 2015). Compared with the classical approach (e.g., used in ERP studies) in which each step of the dimension (e.g., contrast, spatial frequency, luminance) is presented statically in a given trial, the sweep-ssVEP method dramatically reduces the number of trials needed for a robust signal. This highlights the usefulness of the sweep-ssVEP technique for studying systematic variations along a feature dimension of interest, with short session durations, particularly important for clinical research.

Several limitations should be noted when interpreting the present results. Despite its value for quantifying competition in visual processing (i.e., simultaneous presentation of spatially overlapping stimuli, see Andersen & Müller, 2010; Pei et al., 2002) the sweep-ssVEP makes it difficult to evaluate neural activity other than activity at the target frequency. The present study also did not analyze effects at anterior sensor locations, limiting results to the visuocortical domain. Gross eye movements were monitored through electrooculograms but not through a high-precision eye tracker. Thus, it is conceivable that some of the ssVEP findings partially reflect systematic differences in small exploratory eye movements, known to particularly affect free viewing of emotional scenes

(Bradley et al., 2011). Finally, the driving frequency of the stimulus might influence or even favor specific stimulus categories (e.g., faces; Gruss et al., 2012) or interfere with specific frequency bands, which, therefore, should be selected based on prior work (Kaspar et al., 2010), or counterbalanced carefully.

5 | CONCLUSIONS

The current study provides support for the broad notion that lower-level visual perception is shaped by contextual factors and affective content. Adding to extant frameworks on emotion–perception interactions (Miskovic & Anderson, 2018; Todd et al., 2020), we identify different gain mechanisms for contextual factors such as anticipatory state (prompting contrast gain changes) compared with emotion scene content (prompting response gain changes). As such, the present findings add mechanistic information to broad notions of heightened attention or facilitated processing of emotionally arousing stimuli. Future work may use the sweep-ssVEP technique to examine altered response gain with other naturalistic stimuli, such as video, virtual reality, or individually selected scenes, often used in clinical/translational studies (e.g., Mühlberger et al., 2009), or even in clinical intervention (Pallavicini et al., 2013).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

AK designed the study; AK, AT, MF analyzed the data; AK, AT, MF, GWA drafted the paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at <https://osf.io/egm5t/>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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