

Electrocortical and electrodermal responses covary as a function of emotional arousal: A single-trial analysis

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Abstract

Electrophysiological studies of human visual perception typically involve averaging across trials distributed over time during an experimental session. Using an oscillatory presentation, in which affective or neutral pictures were presented for 6 s, flickering on and off at a rate of 10 Hz, the present study examined single trials of steady-state visual evoked potentials. Moving window averaging and subsequent Fourier analysis at the stimulation frequency yielded spectral amplitude measures of electrocortical activity. Cronbach's alpha reached values $>.79$, across electrodes. Single-trial electrocortical activation was significantly related to the size of the skin conductance response recorded during affective picture viewing. These results suggest that individual trials of steady-state potentials may yield reliable indices of electrocortical activity in visual cortex and that amplitude modulation of these indices varies with emotional engagement.

Descriptors: Dense-array EEG, Emotion, Motivation, Arousal, Picture perception, Skin conductance response

Hemodynamic imaging and electrophysiological studies have converged to show that activity in visual cortex is facilitated when viewing affective pictures, with the amplitude of neural signals increasing as a function of the emotional intensity rated by participants (e.g., Bradley et al., 2003). Adding to an increasing body of hemodynamic neuroimaging studies, work capitalizing on event-related potentials (ERPs) has focused on the time course of this modulation. These studies have converged to show late (>300 ms) ERP enhancements for affectively arousing stimuli, which correlate significantly with hemodynamic parameters (Sabatinelli, Lang, Keil, & Bradley, 2007). There has also been evidence that the steady-state visual evoked potential (ssVEP), which is an oscillatory brain response to rapidly flashing stimuli, shows a similar sensitivity to emotional content (Keil et al., 2003).

To achieve sufficient signal-to-noise ratios, the electrophysiological studies discussed above relied on averaging signals across experimental trials in which different exemplars with similar emotional content were presented (e.g., erotica, landscapes, mutilation, etc.). Category-based averaging to obtain ERP time series has been a fruitful approach to examining the spatial and temporal electrocortical dynamics associated with emotional

picture perception. In addition, covarying cross-category ERPs with averaged data reflecting peripheral physiology has yielded substantial evidence for content-related changes in visual perception and physiological reactivity (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). For some experimental questions, however, it would be desirable to measure electrocortical activation associated with a specific picture in a brief time interval. This might help, for instance, to better understand trial-by-trial changes related to repeated exposure to the same stimulus. Alternatively, research in clinical populations may benefit from studying visual responses to single scenes, for example, one representing a high-fear situation. In addition, changes of such specific responses over the course of treatment could be examined using single-trial approaches.

The ssVEP is a measure that can produce reliable estimates of electrocortical processes with short epochs of data. It is a continuous brain response elicited by a repetitive visual stimulus that is periodically modulated in intensity at a fixed rate of 6–8 Hz or greater. Phenomenologically, a visual stimulus appears to flicker when using steady-state presentation. Using electroencephalography, these signals can be recorded at the scalp as an oscillatory waveform that has the same fundamental frequency as the flickering stimulus (Regan, 1989). Frequency-domain analyses can then be used to extract the response of interest at the known stimulation frequency, resulting in high signal-to-noise ratios even when the number of trials is limited. The amplitudes of ssVEPs have been shown to be sensitive to cognitive and affective features of experimental tasks, including spatial selective attention (Müller, Malinowski, Gruber, & Hillyard, 2003),

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executive control (Silberstein, Ciorciari, & Pipingas, 1995), and emotional stimulus content (Keil et al., 2003; Kemp, Gray, Eide, Silberstein, & Nathan, 2002). Recent work using magnetoencephalography has suggested that amplitude enhancement of the ssVEP in response to affectively arousing pictures is mediated by fronto-parietal regions (Moratti, Keil, & Stolarova, 2004). Furthermore, coregistration of measures reflecting autonomic nervous system activity (i.e., heart rate and skin conductance) suggested that amplitude enhancement in visual cortex was related to engagement of affective-motivational physiology (Moratti & Keil, 2005). Thus, participants showing greater heart rate acceleration when observing aversive conditioned visual stimuli also showed greater electrocortical facilitation (Moratti, Keil, & Miller, 2006).

In the present study, affective pictures flickered at a rate of 10 Hz, for a duration of 6 s per trial. A high-density electrode array (257 sensors) was employed together with a distributed source analysis procedure (minimum norm estimate, MNE) to investigate the topography and estimated source distribution of the ssVEP extracted from single trials. For single-trial analyses, assessing the reliability and internal consistency of the obtained estimates is a critical first step. Based on classical test theory, our approach focused on the homogeneity of the test items (here: amplitude estimates) themselves. As Simons and Miles (1990) pointed out in their comprehensive review, test homogeneity for an event-related brain potential measure refers to the consistency of component amplitude from trial to trial. Amplitude measures are considered homogeneous (internally consistent) if the rank ordering of subjects remains stable across trials (e.g., participants with larger amplitudes on one trial have larger amplitudes on subsequent trials, compared to other participants), which can easily be assessed using Cronbach's coefficient alpha. Thus, Cronbach's alpha was calculated for each sensor and dipole site, resulting in maps that reflected the reliability of the single trial estimates for both voltage and source strength estimates.

Single-trial estimates of source strength were determined using a minimum norm (MNE) model. Although not providing precise neuro-anatomical localization, the MNE as implemented here allows one to infer the gross location of the origin of the surface-recorded signal. In addition, dipolar generators that are tangential with respect to the scalp tend to be represented as one active area, as opposed to two areas, which is the case with voltage or Laplacian maps (Hauk, Keil, Elbert, & Muller, 2002). Extending previous work with ssVEPs in affective perception, this study aimed to exploit the excellent signal-to-noise ratio available with this technique in order to obtain single-trial estimates of the cortical response. The skin conductance response was also recorded throughout the experiment, as a measure of emotional engagement.

Based on previous ssVEP studies, we expected that emotional picture presentation would be associated with greater stimulus-locked spectral amplitude in the 10-Hz band, compared to neutral pictures (Keil et al., 2003). Furthermore, the sources of the signal contributing to differences in this late positive potential were predicted to lie within posterior cortical areas, reflecting alterations of visual processing by emotional content. It was hypothesized that the amplitude of the skin conductance response—a measure of emotional engagement on each trial—would be systematically related to the ssVEP amplitude obtained from single trials in each participant. In a similar manner, we assessed how affective ratings of arousal for each picture predicted ssVEP amplitude. To ascertain that emotional, rather

than perceptual, processes were related to ssVEP amplitude, it was also assessed whether physical stimulus parameters (e.g., brightness, contrast) and complexity ratings significantly influence ssVEP measures for individual International Affective Picture System (IAPS) pictures.

Methods

Participants

Twelve right-handed students (6 female) with normal or corrected-to-normal vision whose age ranged from 18 to 21 years (mean age 18.5 years) gave informed consent to participate in the study. They were given class credit for participation.

Stimuli and Design

Fifty colored pictures were selected from the IAPS (Lang, Bradley, & Cuthbert, 2005) based on normative pleasure and arousal ratings, forming five categories. The pleasant pictures consisted of 10 erotic couples and 10 cute animals, the neutral pictures consisted of 10 persons, and the unpleasant pictures consisted of 10 mutilated bodies and 10 animal threat scenes. The IAPS picture numbers are given in Figure 5, below. Normative ratings of hedonic valence for pictures in these categories differed (pleasant: 7.37, neutral: 5.08, unpleasant: 2.69), as did normative ratings of emotional arousal (pleasant: 5.38, neutral: 3.40, unpleasant: 6.24). Because the present study focused on single-trial (i.e., single picture) data, rather than on category averages, the goal of picture selection was not to match emotional arousal in the pleasant and unpleasant categories, but to create a picture set with high variability in both dimensions of the affective space. The pictures were presented on a 19-in. screen from a LCD projector with a vertical refresh rate of 70 Hz, subtending a visual angle of 10° horizontally and of 7° vertically. A fixation point was marked in the center of the screen and was present throughout the experiment. Each picture was presented for 6000 ms in a flickering mode at a rate of 10 Hz (thus containing 60 on/off cycles), with the picture shown for 43 ms, followed by 57 ms black screen during each cycle. Each intertrial interval lasted 12,000 ms, to ensure that the skin conductance response reached baseline levels between trials and to provide participants resting time between the 6000-ms picture trials.

Electrophysiological Recordings

Electroencephalogram (EEG) was recorded continuously from 257 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 k Ω , 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 online by means of 0.1-Hz high-pass and 100 Hz low-pass filtering.

Procedure

Participants were greeted and informed about the experimental procedures. Subsequently, the sensor net was applied and participants viewed two blocks of pictures, each consisting of the same 50 pictures. During the first block, the EEG and skin conductance responses were recorded; during the second block, affective ratings of valence and arousal were obtained using the

Self Assessment Manikin (SAM; Lang, 1980). The order of the stimuli within each block was pseudorandomized, with the restriction that no more than three pictures in the same affective category could occur in a row. A central fixation point was present throughout the study to aid participants in maintaining their gaze in the center of each picture. Accordingly, they were instructed to avoid eye movements and eyeblinks and to view the pictures while they were on the screen.

The skin conductance response was simultaneously recorded using electrodes placed adjacently on the hypothenar eminence of the left palmar surface using standard 8-mm silver–silver chloride electrodes filled with 0.05 M NaCl paste. The signal was recorded with a Coulbourn S71-22 skin conductance coupler calibrated prior to each session to detect activity in the range of 0–40 mS. The amplitude of the skin conductance response was calculated in half-second bins and was scored as the peak change value during the 6-s picture presentation with respect to a 1-s prestimulus baseline.

Data Reduction and Artifact Control

Epochs of 6800 ms (800 ms pre-onset to 6000 ms post-onset of the flickering pictures) were obtained from the continuously recorded EEG. In a first step, data were low-pass filtered at a frequency of 40 Hz (24 dB/octave) and then submitted to the procedure proposed by Junghöfer, Elbert, Tucker, and Rockstroh (2000) for artifact correction. This procedure uses distributions of amplitudes, standard deviations, and change values to identify channels and trials that contain artifacts. Recording artifacts are first detected using the recording reference (i.e., Cz), and subsequently global artifacts are detected using the average reference. In a next interactive step, distinct sensors from particular trials are removed based on the distribution. Data at eliminated electrodes are replaced with a statistically weighted spherical spline interpolation from the full channel set (Junghöfer, Elbert, Leiderer, Berg, & Rockstroh, 1997).

The mean number of approximated channels across conditions and subjects was 29. With respect to the spatial arrangement of the approximated sensors, it was ensured that the rejected sensors were not located within one region of the scalp, as this would make interpolation for this area invalid. Spherical spline interpolation was used throughout both for approximation of sensors and illustration of voltage maps (Junghöfer et al., 1997). Single trials with excessive eye movements and blinks or more with than 40 channels containing artifacts were discarded. The validity of this procedure was further tested by visually inspecting the vertical and horizontal EOG as computed from a subset of the electrodes that were part of the electrode net. Trials that showed remaining ocular artifacts were dismissed at this step of the analysis. Subsequently, data were arithmetically transformed to the average reference, which was used for all analyses. After artifact correction, an average of 82% of the 50 trials was retained in the analyses. Each missing trial in the present study resulted in a missing value for the subsequent correlation analyses. Thus, it was tested whether specific pictures were more frequently rejected. This was not the case. Single-trial data for any given picture were available from at least 8 individuals.

Extraction of ssVEPs

The 10-Hz Fourier components representing stimulus-locked oscillations for each single trial were extracted by means of a moving average at the stimulation frequency (Keil et al., 2003). To avoid contamination with the initial ERP, an 800–6000-ms

poststimulus part of each epoch was used for these analyses. For each single trial, the data segment was treated as follows: A 500-ms window (containing five cycles of ssVEP) was shifted across the epoch in steps of 100 ms, and the potential within the shifting windows in the time domain was averaged, resulting in a 500-ms segment containing five cycles of the 10-Hz ssVEP and reflecting an average across 47 sliding windows. Examples for these time series are shown in Figure 1. The resulting ssVEP averages were then transformed into the frequency domain using discrete Fourier transform (DFT) on 125 data points. DFT after averaging increased the sensitivity to phase-locked (evoked) oscillatory activity (i.e., the ssVEP) at the frequency of interest, as opposed to non-phase-locked (induced) 10-Hz oscillations (i.e., alpha activity) that might be abundant during the viewing epoch, but are not to be confused with the 10-Hz ssVEP. Thus, real and imaginary parts of the 10-Hz component were obtained, reflecting stimulus-locked 10-Hz ssVEP activity. These single-trial derived measures were examined as described below.

Source Estimation

Cortical sources were estimated using the L2 (minimum) norm estimate (MNE), following the approach suggested by Hauk et al. (2002). The MNE is an inverse method for reconstructing the primary current that underlies a scalp-recorded brain potential. In our implementation, this approach does not aim to provide precise neuroanatomical localization, but to enhance spatial accuracy of the two-dimensional representation (e.g., Hauk, 2004). In the present case, the MNE was determined for the real and imaginary part of the 10-Hz Fourier component obtained after the moving average procedure. These values were then used for further processing as described below, paralleling the procedure for the voltages. Because MNE projection results in three orientations of the model dipoles located on multiple spherical shells, dependent variables for these three orientations at each model source location were combined by means of Fisher *z*-transform, averaging, and retransformation. As opposed to taking the norm of the three-dimensional complex vector directly, this approach allowed us to examine source solutions for the different orientations before integrating them, as an added method check. As the focus of this research was on cortical sources, the outermost shell of the source model was selected for all analyses (see Hauk et al., 2002). This shell is located at 80% of the distance from the scalp to the center of the spherical head model. Amplitude was computed for voltages and MNE (source space) data as the vector length of the real and imaginary part of the DFT, resulting in one value for each location (electrode and model source of the MNE, respectively).

Statistical Analysis

Cronbach's alpha. Cronbach's alpha was calculated for each sensor and dipole site, using all available single-trial amplitude estimates as the variables. This resulted in maps for voltage and source strength that reflected the reliability of the single trial estimates for each sensor and/or dipole site.

Correlation analyses. For participant-level analyses, Spearman rank correlation analyses were conducted across pictures, relating skin conductance change or ratings of arousal to the ssVEP amplitude at each electrode and model dipole. Rank-based statistics seemed more appropriate than regression analyses for these experimental questions, given (a) the ordinal nature of the self-report ratings and (b) the fact that the skin

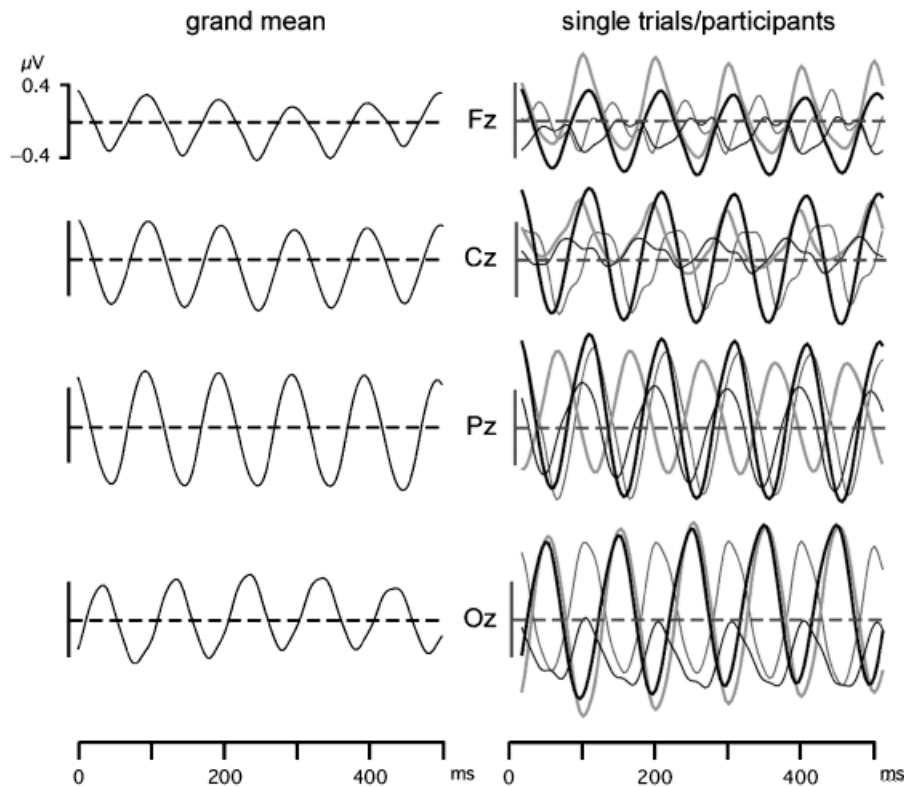


Figure 1. Grand mean (left column, $n = 12$) and examples of single-trial, single-participant oscillatory waveforms (right column) as extracted by means of sliding windows over the 6000-ms ssVEP epoch. Right-hand waveforms represent the first trials in the series for 2 different participants (black lines) and the last trials of 2 other participants (gray lines). Time series are shown for electrode sites Fz, Cz, Pz, and Oz. Note: positive is up.

conductance response typically habituates over time, resulting in variance across trials. This procedure yielded correlation maps highlighting brain regions or electrode sites that were related to changes in skin conductance or to self-reported emotional arousal, across pictures.

For group analyses, ssVEP measures were averaged across the 12 participants and grand mean correlation maps between the same variables were generated following the same approach used for single participants. Given the number of comparisons, the threshold of statistical significance for the topographical correlation maps was determined using a permutation approach; for each participant and electrode/source location, 8000 random permutations of the picture orders were created, thus assigning the single-trial estimates of ssVEP randomly to skin conductance values and ratings of emotional arousal. Spearman correlations were calculated for each permutation and were entered into a distribution of permutation correlations. The upper and lower half-percentiles of this distribution were defined as the significance thresholds for rank correlations, resulting in critical values of $\pm .318$. Thus, Spearman correlation coefficients beyond $\pm .318$ were considered significant at the .01 level.

Regression analyses. As an added control, regression analyses were conducted, predicting the ssVEP amplitude across participants using physical and structural parameters of the pictures. This procedure assessed the potential influence of (1) average brightness, (2) average contrast, (3) brightness at 1° of visual angle at the center, (4) size of the jpeg file, and (5) median spatial frequency (based on Fourier decomposition). Stepwise regression analyses were calculated, predicting posterior ssVEP am-

plitude in voltage space and in source space on the basis of these structural criteria. A predictor inclusion criteria of .05 was used throughout.

Analyses of variance. The SAM pleasure and arousal ratings as well as skin conductance scores were evaluated by means of one-way ANOVAs with a factor of picture content (pleasant, neutral, and unpleasant). Where appropriate, degrees of freedom were adjusted using the Greenhouse–Geisser method (Greenhouse & Geisser, 1959). Uncorrected F values are reported together with corrected p values, where appropriate.

Results

Internal Consistency

Internal consistency of the single-trial amplitude estimates was moderate to high at all electrode sites and model dipoles. In voltage space, Cronbach's alpha varied between .79 at temporal electrodes to .98 at central sites (see Figure 2, top). A similar pattern was observed in minimum norm space, in which the highest alphas (.99) were observed at parieto-central, bilateral source locations, and minimum alphas (.84) were seen at anterior temporal and frontal locations (see Figure 2, bottom). Thus, these data suggest that single-trial estimates of ssVEP electrocortical activity can be assessed reliably in voltage and source space, yielding internally consistent indices across the entire scalp and source volume, respectively.

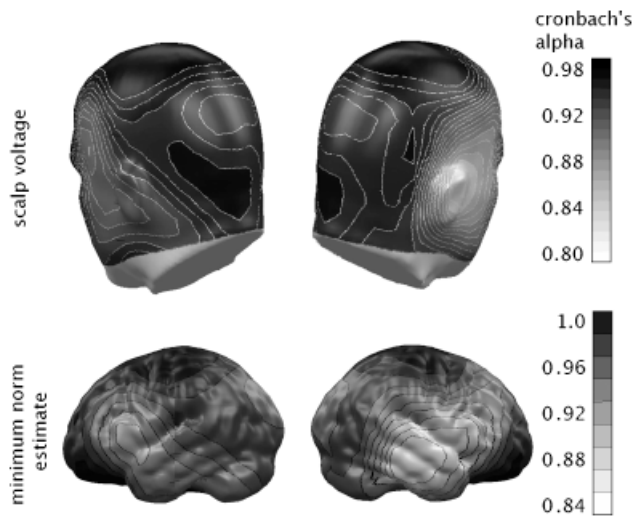


Figure 2. Topographical distribution of internal consistency of single-trial measures of 10-Hz ssVEP amplitude as measured by Cronbach's alpha at each electrode (top row) and dipole location (bottom row). Note that the overall range of alphas was satisfying for both variables, values being greater than .80 for voltage data and greater than .84 for minimum norm data.

Correspondence among Psychophysiological Variables: Participant Level

Skin conductance response. The skin conductance response during picture viewing showed the expected pattern of enhanced amplitude when viewing pleasant or unpleasant, compared to neutral, pictures, $F(2,22) = 6.4, p < .01$, partial eta squared = .37. The quadratic pattern of this effect (pleasant > unpleasant > neutral content) was reflected in a quadratic contrast pattern, $F(1,11) = 28.2, p < .001$, partial eta squared = .96. Ratings of arousal showed the same pattern, with pleasant and unpleasant pictures rated as more arousing than neutral pictures, $F(2,22) = 110.8, p < .001$, partial eta squared = .91, quadratic trend, $F(1,11) = 102.0, p < .001$, partial eta squared = .90. Ratings of hedonic valence also showed the expected pattern, with a linear increase from unpleasant to pleasant categories, $F(2,22) = 299.5, p < .001$, partial eta squared = .92. This pattern was related to a linear trend, $F(1,11) = 89.4, p < .001$.

Voltage data. Relating the ssVEP amplitude (see Figure 3, left column) at each electrode to ratings of emotional arousal across trials (i.e., pictures) for each participant separately resulted in significant correlations at parieto-occipital recording sites for most participants (see Figure 3, middle column). A similar pattern was observed when relating skin conductance response to ssVEP amplitude (see Figure 3, right column). Overall, ssVEP amplitude showed a stronger relationship with skin conductance than with ratings of emotional arousal. Coefficients did not reach significance in only 1 of the 12 individuals, (see Figure 3, bottom row).

Minimum norm estimate. As suggested by the internal consistency values, the single-trial estimates in source space were of good signal quality. Again, a pronounced parieto-occipital maximum of source strength in most participants indicated that the ssVEP originated mostly from visual cortical areas. Correlations between arousal ratings and ssVEP amplitude reached significance in each participant, varying between .23 and .56 at central

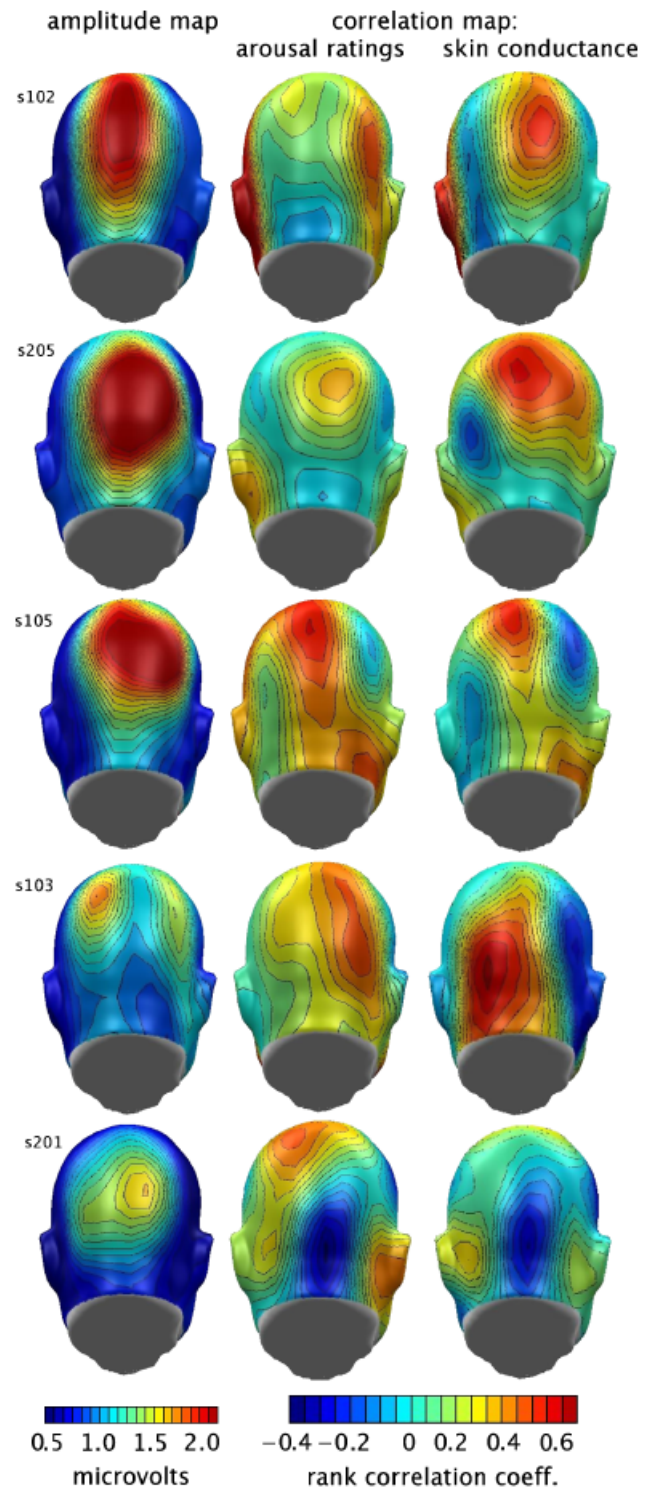


Figure 3. Single-participant topographies of parameters used in the present study. Left column: average amplitude across picture trials in voltage space. Middle column: rank correlation maps showing the relationship between single-trial ssVEP amplitude estimates and individual arousal ratings for each picture/trial. Right column: rank correlation maps showing the relationship between single-trial ssVEP amplitude estimates and the skin conductance response for each trial. Data are shown for 4 randomly selected participants and for subject s201 (bottom row), who was the only participant not showing significant correlations between skin conductance and ssVEP amplitude.

parieto-occipital source locations, with a mean (across participants) correlation of .30 over all sites posterior to the Cz electrode. Moreover, coefficients among skin conductance and ssVEP amplitude reached significance for all but 1 participant (the same participant noted above). Again, Spearman correlations were generally higher when relating ssVEP amplitude to skin conductance activity, ranging between .26 and .55, with a mean of .36 across all dipole locations posterior to the center of the source space, than to arousal ratings.

Correspondence among Psychophysiological Variables: Group Level

Group analyses for the grand mean of the psychophysiological variables *across pictures* confirmed the single-participant results. As shown in the correlation maps in Figure 4, averaged parieto-occipital ssVEP amplitude in voltage space was predicted by both the mean emotional arousal rating and the mean skin conductance response. The relationship with the skin conductance response reached a peak correlation at site Pz of .49 and was slightly larger than coefficients for arousal ratings, $r_s = .42$. Figure 5 shows the relationship between skin conductance and pooled ssVEP amplitude in a region of interest including the 24 electrode sites nearest to Pz. Similar correlation patterns were seen for the source space analyses, with peak correlations for the relationship between the skin conductance response and the ssVEP amplitude at central parieto-occipital, $r_s = .47$, as well as right parietal, $r_s = .43$, and left temporal, $r_s = .40$, locations.

Regression Analyses for Physical and Structural Parameters

Two stepwise regression analyses were conducted predicting the regional mean at parieto-occipital electrodes and source locations, respectively, using five variables characterizing the structural properties of the pictures such as contrast, brightness, and a number of different measures of picture complexity (see Methods). None of these variables reached the .05 significance levels in any analysis, suggesting that ssVEP amplitude was not linearly related to physical picture parameters.

Discussion

One goal of the current study was to examine whether single trials of ssVEP using a 6-s presentation duration can be used to reliably estimate electrocortical activity related to viewing a specific picture. To this end, we used a simple moving average approach, followed by Fourier analysis and linear source space projection. Similar procedures have been suggested for multi-epoch data (Mast & Victor, 1991) and can be extended to include analysis of phase relationships within and across the epoch of interest (Lachaux, Rodriguez, Martinerie, & Varela, 1999). The present study focused on amplitude measures and showed that over all electrodes and source areas, internal consistency, assessed using Cronbach's alpha, was high (greater than .79), suggesting that single trials of ssVEP can be employed to derive reliable indices of electrocortical processing. An important advantage of this approach is that these estimates reflect neural activity during a single experimental trial (and specific stimulus). It should be noted that information about temporal changes across the viewing epoch is not available as a consequence of the sliding averaging procedure, with time information about average evoked oscillations at the stimulation frequency retained. Future research could use this information to calculate measures of phase-locking

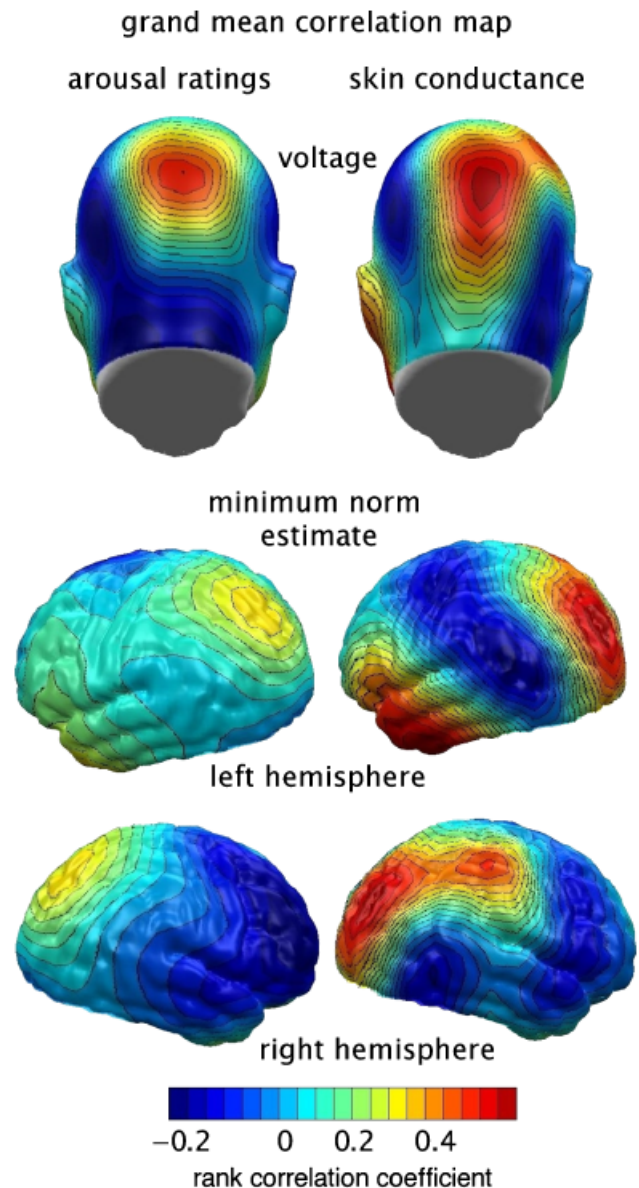


Figure 4. Grand mean rank correlation topographies. Left column: rank correlation maps showing the relationship between single-trial ssVEP amplitude estimates and individual arousal ratings for each picture/trial after averaging across participants. Right column: rank correlation maps showing the relationship between single-trial ssVEP amplitude estimates and the skin conductance response for each trial after averaging across participants.

across sliding windows (Tallon, Bertrand, Bouchet, & Pernier, 1995) or intersite phase relationships (Lachaux et al., 1999).

As a second important question, the relationship between single-trial ssVEP amplitude and emotional arousal was examined by comparing the amplitude of the skin conductance response for each picture to the single-trial estimates of ssVEP within and across participants. Correlation maps showed that the electrocortical response at parietal-occipital and temporal sites was systematically related to the amount of autonomic change as measured by skin conductance. To a similar degree, ssVEP activity was related to the ratings of emotional arousal given for each picture. Importantly, most of these results could be seen at the level of the individual participant. Source-space analyses,

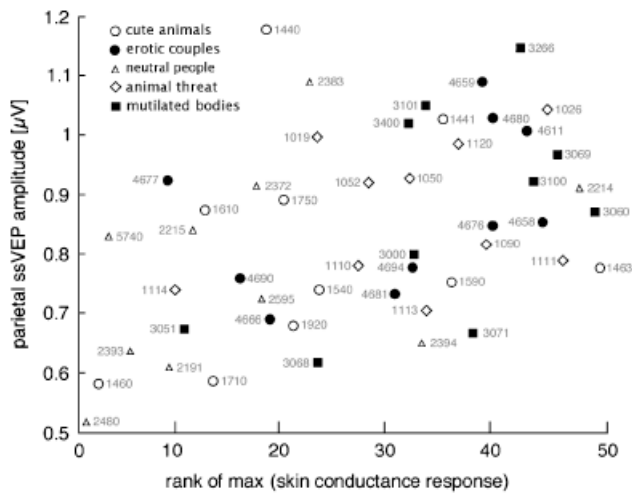


Figure 5. Scatter plot illustrating the relationship between the grand mean (across $n = 12$ participants) skin conductance responses and ssVEP amplitude estimates for each picture in the study. Amplitude values reflect a region of interest including the 24 electrode sites nearest to Pz.

using a simple inverse model of brain electric activity, suggested that oscillatory activity in extended visual cortex, but also in the right parietal lobe and left temporal lobe, was related to sympathetic nervous system arousal as indexed by the skin conductance response. These findings are in line with hemodynamic imaging work relating skin conductance reactivity to cerebral blood flow. For instance, Critchley Elliott, Mathias, and Dolan (2000) reported covariation between skin conductance and blood oxygen level dependent responses to stimuli in a decision-making task in visual cortices (Brodmann areas 18 and 19) and in the right inferior parietal lobule (Brodmann area 40). These areas are consistent with the present correlation maps that reflect electrocortical processes.

We did not find evidence for specific medial frontal cortex covariation with skin conductance (Cheng, Richards, & Helmstetter, 2007). In terms of the neural mechanism mediating enhancement of extended visual cortex when perceiving an affective stimulus, one hypothesis suggests that afferent modulation of occipital and temporal cortex by more anterior cortical and subcortical structures plays a crucial role in this process (Lang, Bradley, & Cuthbert, 1997). In particular, the amygdaloid complex and parieto-frontal cortex have been suggested as potential origins of re-entrant modulation (Baizer, Desimone, & Ungerleider, 1993; Iwai & Yukie, 1987). Consistent with concepts of selective attention research (Martinez et al., 1999), re-entrant signals entering visual areas may thus tune visual cortical neurons, altering thresholds and/or enhancing gain in the networks representing the relevant features (Vuilleumier & Driver, 2007). The steady-state signal is particularly suited to examine such re-entrant processes because it represents repeated activation of

visual cortex by the same stimulus over time, thus enabling re-entrant modulation to act over a series of visual responses to the same stimulus. This has led to investigations of ssVEP functional connectivity, which have pointed to increased re-entrant coupling between visual cortex and anterior areas when participants view emotionally arousing stimuli (Keil et al., in press).

It should be emphasized that the present source projection procedure was not expected to provide precise neuroanatomical localization and the pronounced correlations between skin conductance and ssVEP amplitude in the temporal pole/lateral frontal cortex regions may be related to involvement of widespread regions in frontal cortex. In addition, the strong focus on cortical sources and the selection of the outermost shell in our source space (see Methods) may have led to an overestimation of radial sources (i.e., oriented perpendicular to the scalp surface). Thus, other source estimation procedures such as regional source projection (Weisz et al., 2007) or depth-weighted distributed source models (Supp, Schlögl, Trujillo-Barreto, Muller, & Gruber, 2007) could also be used to address questions regarding neural generators involved in the modulation of ssVEPs. An additional constraint is that a core structure hypothesized to mediate sympathetic nervous system activity is the amygdaloid complex (Knight, Nguyen, & Bandettini, 2005), which cannot be adequately measured using the present method.

The relationship between structural parameters of each picture and ssVEP amplitude was examined using regression analysis. There was no evidence for a linear relationship between these variables, although the distribution of picture stimuli in the skin conductance–amplitude space (see Figure 5) suggests at least some influence of brightness: Pictures with dominant white and bright areas (e.g., picture 1440, baby seal) tended to also be high in ssVEP amplitude. This may suggest that, although no *linear* relationship exists between physical parameters and ssVEP amplitude, very bright (or dark) pictures can add error variance to single-trial analyses. Despite this, the relationship of ssVEP to emotional engagement, measured using either skin conductance response or ratings of emotional arousal, was high and significant, and control of physical parameters within a single study is clearly easy to implement.

The ssVEP technology, with single trial analysis, is relatively inexpensive and can be used to supplement routine interview assessment in clinical studies. It will be informative to utilize this methodology in cases where the experimental question requires analysis of single trials with specific visual content, as in studies of specific phobia or other disorders associated with abnormally heightened/reduced response to specific visual stimuli. Relatedly, studying changes of functional and dysfunctional responses of the visual system over time may also benefit from single-trial information. Taken together, the present approach suggests that the relationship between central and peripheral indices of emotional processing can be reliably examined for specific stimulus content and at high temporal resolution.

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