Emotional Perception: Divergence of Early and Late Event-related Potential Modulation

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Abstract

■ The early posterior negativity (EPN) is a mid-latency ERP component that is reliably enhanced by emotional cues, with a deflection beginning between 150 and 200 msec after stimulus onset. The brief, bilateral occipital EPN is followed by the centroparietal late positive potential (LPP), a long duration slow-wave that is strongly associated with emotional arousal ratings of scenes. A recent study suggests that the EPN is particularly sensitive to human bodies in scenes, independent of emotional intensity. Here, we directly investigate the influence of human body features on EPN modulation, using emotional and neutral scenes depicting people across a range of body exposures and orientations, in addition to scenes of pleasant, neutral, and unpleasant animals. The results demonstrate that the EPN is quite sensitive to human body features and weakly related to arousal ratings, whereas the LPP is strongly modulated by scenes that receive high arousal ratings. Based on these results and relevant work on body-specific visual perception, we speculate that modulation of the EPN may strongly reflect the early detection of human bodies, which serves as a predictor of emotional significance, whereas LPP modulation is more closely associated with the extended elaborative processing of scenes that are explicitly judged to be emotionally arousing. ■

INTRODUCTION

The collection and interpretation of scene-evoked cortical potentials is a powerful paradigm in the effort to understand the mental processes supporting the perception of emotional cues. Two of the most well-studied ERPs associated with emotional processing are the early posterior negativity (EPN) and the late positive potential (LPP). The amplitudes of these potentials have been shown to be enhanced by emotionally arousing, relative to neutral content (Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp, Stockburger, et al., 2006; Pastor et al., 2008). This arousal effect can be reliably found during naturalistic scene perception, and it is also evident (although to a reduced extent) during the perception of emotional faces (Langeslag, Gootjes, & van Strien, 2018; Yoon, Shim, Kim, & Lee, 2016; Herbert, Sfärlea, & Blumenthal, 2013; Jaworska et al., 2012; Schupp, Öhman, et al., 2004), hand gestures (Flaisch, Schupp, Renner, & Junghöfer, 2009), and words (Schindler & Kissler, 2016; Kissler & Herbert, 2013; Herbert, Junghöfer, & Kissler, 2008; Kissler, Herbert, Peyk, & Junghöfer, 2007).

Despite similarities in the pattern of modulation, the EPN and LPP represent different but related aspects of emotional perception. The EPN and LPP are temporally and spatially distinct, with the EPN appearing as a negative voltage deflection over left and right lateral occipital sensors from 150 to 300 msec after scene onset (Schupp, Junghöfer, Weike, & Hamm, 2004; Junghöfer, Bradley, Elbert, & Lang, 2001) whereas the LPP is a slow-wave positivity over central-parietal electrodes with a peak approximately 400–900 msec after scene onset (Schupp et al., 2007; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). Studies that have attempted to localize the neural sources of these ERPs find that the EPN is likely driven by lateral occipital extrastriate activity (Junghöfer et al., 2006; Schupp, Stockburger, et al., 2006) whereas the LPP may represent a combination of activity from multiple dorsal and ventral visual cortical regions, as well as anterior cortical sources (Sabatinelli, Keil, Frank, & Lang, 2013; Liu, Hairston, Schrier, & Fan, 2011; Moratti, Saugar, & Strange, 2011). Taken together, these ERPs likely represent different stages involved in the discrimination and perception of emotional cues, with the EPN possibly reflecting the initial effects of emotional content in the secondary visual cortex, whereas the LPP indexes the activity of widespread networks of activity associated with the conscious experience of emotional arousal.

Some studies have identified scene factors that differentially modulate the EPN and LPP. Bradley, Hamby, Löw, and Lang (2007) used principal components analysis to identify clusters of electrodes that distinguished simple (figure-ground) from complex emotional scenes, locating a posterior occipital region that overlaps with the scalp location and latency (150–250 msec) of the EPN. This cluster showed enhanced voltage negativity during simple scene perception, and no sensitivity to emotional content.

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A centroparietal cluster of sensors showed strong emotional modulation from 400 to 700 msec, equivalent with the LPP, and showed no sensitivity to scene complexity. This important article obligated all future study of the EPN to employ scenes that are balanced for complexity across emotional and neutral content. Particularly relevant for the current research question, Löw, Bradley, and Lang (2013) manipulated emotional scene complexity and the inclusion of humans in scenes and assessed the impact of these factors on the EPN, as recorded using rapid serial visual presentation of scenes at 3 Hz. This study identified the largest EPN modulation for emotional people depicted in simple, figure-ground scenes, followed by the EPN in response to neutral people in figure-ground scenes, followed by the EPN in response to emotional people in complex scenes. Thus, the presence of clearly identifiable people in scenes was more meaningful to EPN modulation than whether those people were engaged in an emotional act. Further evidence for the impact of clearly identifiable people on EPN modulation, a recent study (Farkas, Oliver, & Sabatinelli, 2020) found that scenes of upright, unclothed people (nudists) evoke a larger EPN than do scenes of erotic couples, despite garnering weak arousal ratings. Despite enhancing the EPN, nudist scenes led to reduced LPP amplitudes relative to that evoked by erotic scenes. This unexpected finding necessitated an experiment that more explicitly tests the effects of human body exposure and orientation on EPN modulation.

In the current experiment, we aimed to replicate the sensitivity of the EPN to nudist, compared with erotic scenes (Farkas et al., 2020), while adding new scene categories, additional measures of scene features (SFs), and targeted analyses to parcel the potential relationships between these factors and modulation of the EPN and LPP. We consider body exposure to be a comparatively subordinate SF relative to emotional scene content categories. We employed the nudist and erotic scenes from our previous experiment, and added seven additional scene categories with varied levels of body exposure across emotional and neutral contents. We included scenes depicting pleasant, neutral, and unpleasant animals to provide a nonbody comparison. Our intention is to begin to disentangle the specific effects of body exposure from higher-level emotional features of scene perception (pleasantness, arousal) and subordinate features (animal/human, clothed/unclothed, upright/supine).

We quantified characteristics of the scenes using self-report and objective image values. These SFs included self-reported valence, arousal, body exposure, and body orientation, as well as digitally derived aspects of each scene, including the number of pixels containing unclothed body parts, energy in low and high spatial frequency bands, and Shannon's entropy. The study employed two parallel analyses to understand how these SFs are associated with the modulation of the EPN and LPP. The first was a traditional analysis in which each participant's average ERP across the 15 exemplars of each scene category was compared. To evaluate the contribution of SFs more precisely, a by-scene analysis assessed which SFs were associated with EPN and LPP amplitudes, irrespective of scene category. In the by-scene analyses, we used multiple regression and four variable-selection or regularization (VSR) methods. Our research question concerned the relative impact of multiple scenes features, many of which have been shown to independently influence ERP magnitude in prior studies. To simplify data interpretation, a multi-analysis approach was chosen to define which variables had the strongest association with ERP modulation and which variables and models would be the most stable and predictive in a new data set. We hypothesized that scenes containing people would evoke the largest EPN (Löw et al., 2013), and that erotic (Weinberg & Hajcak, 2010; Schupp et al., 2007) and nudist scenes (Farkas et al., 2020) will elicit the greatest EPN amplitudes. We also expect that scenes receiving elevated ratings of arousal will be associated with enhanced EPN modulation (Frank & Sabatinelli, 2019; Junghöfer et al., 2001). When analyzed by scene exemplar, we hypothesize that scenes containing upright, exposed bodies would better predict the EPN than the LPP, which should have a stronger association with average self-reported arousal for each scene (Thigpen, Keil, & Freund, 2018; Cuthbert et al., 2000).

METHODS

Participants

Fifty-seven participants were recruited from the University of Georgia student body and compensated with course credit. All participants gave informed consent after receiving a description of the study approved by the University of Georgia human subjects institutional review board. Seven participants were excluded from the final analysis after ERP preprocessing revealed excessive artifact leading to the loss of more than 50% of the trials from any one scene category. The remaining 50 participants were between the ages of 18 and 26 years (M = 19.7 years, SD = 1.40 years), with 28 self-reporting as female (self-reported ethnicity: Asian 7.1%, Black 7.1%, White 85.7%) and 22 as male (Asian 9.1%, Black 13.6%, Hispanic 4.6%, Hispanic & White 4.6%, Multiracial 4.6%, White 63.6%). Participants identified as right-handed and reported no history of mental illness. The sample size was predetermined based on previous work using most of the same scenes (Farkas et al., 2020).

A second online sample was recruited through Amazon's Mechanical Turk (Mturk) to rate the extent of body exposure and body orientation of the scene stimuli. Participants were compensated $1.50 to provide these ratings. Participants were presented with an informed consent approved by the University of Georgia institutional review board. Mturk participants (n = 79) had to live in the United States and be between the ages of 18 and 26 years. Seven online participants consistently used the same number for every scene rating and were excluded from the final analysis. Two participants appeared to give random ratings and were also excluded. After exclusions, there were 70 participants in the final online ratings sample.

Naturalistic Scenes

Nine categories of 135 naturalistic scenes were selected, based on valence and arousal ratings from previous studies in our laboratory. A minority of scenes were taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1997) whereas the remainder were gathered through uncopyrighted sources and are consistent in nature and composition with the IAPS. Scenes were presented at an 800 × 600 pixel resolution at 90% JPEG quality (https://JPEG.org). Luminance and complexity were selected to be equivalent between categories, as measured by independent t tests with p values greater than .20. Scenes that were outliers in luminance and complexity were mildly edited with GNU Image Manipulation Program (https://www.gimp.org/). Complexity was measured by the file size of the JPEG images at 90% quality, which has been reported as a suitable measure of complexity in human perception (Donderi, 2006). If a scene file was too large at 90% quality, a 1 × 1 pixel Gaussian blur was used, which has a negligible effect on perceived sharpness of the content.

The nine scene categories included erotica, pleasant animals, victorious athletes, nudists, neutral animals, neutral people (fully clothed), threatening animals, threatening people, and mutilations. An example scene for each category can be seen in Figure 1. Erotic scenes depicted an attractive male–female couple engaged in consensual intercourse. The pleasant animal category contained scenes of baby ducks, puppies, and kittens. Victorious scenes depicted athletes in expressive moments of success. Nudist scenes contained unclothed couples of various ages walking on beaches or parks, not engaged in sexual activity. The neutral animal category depicted adult animals such as cows, squirrels, and chickens. The neutral people category depicted clothed people engaged in normal activities like riding in buses or talking to each other. The threatening people category featured one or more persons with aggressive body positions and facial expressions, often brandishing weapons. Threatening animal scenes contained predators such as wolves, jaguars, and sharks aggressively posturing or attacking. Mutilation scenes displayed graphic injuries of open wounds or disfigured body parts. The scenes were chosen to roughly equate the amount of body exposure within each valence subset. Erotica, nudists, and mutilations scenes often have uncovered skin making up a large portion of the scene as compared with the victorious athletes, neutral people, and threatening people categories that contain clothed individuals. Finally, the three animal categories allowed for tests of emotional ERP modulation effects independent of any human bodies being present in the scene.

Procedure

After providing informed consent, participants were brought into an electrically shielded chamber for EEG cap fitting, which lasted about 10 min. The 135 scenes were then presented to each participant for 2 sec each, with an intertrial interval between 3.5 and 5.5 sec. Participants were asked to keep their eyes fixated on a small red dot in the middle of the scene. The complete set of 135 scenes were organized into two pseudorandom sets. Half of the participants passively viewed the first set, whereas the other half viewed the second set. To keep the nine categories of content evenly spread throughout the set, every 18 scenes had to feature two scenes from

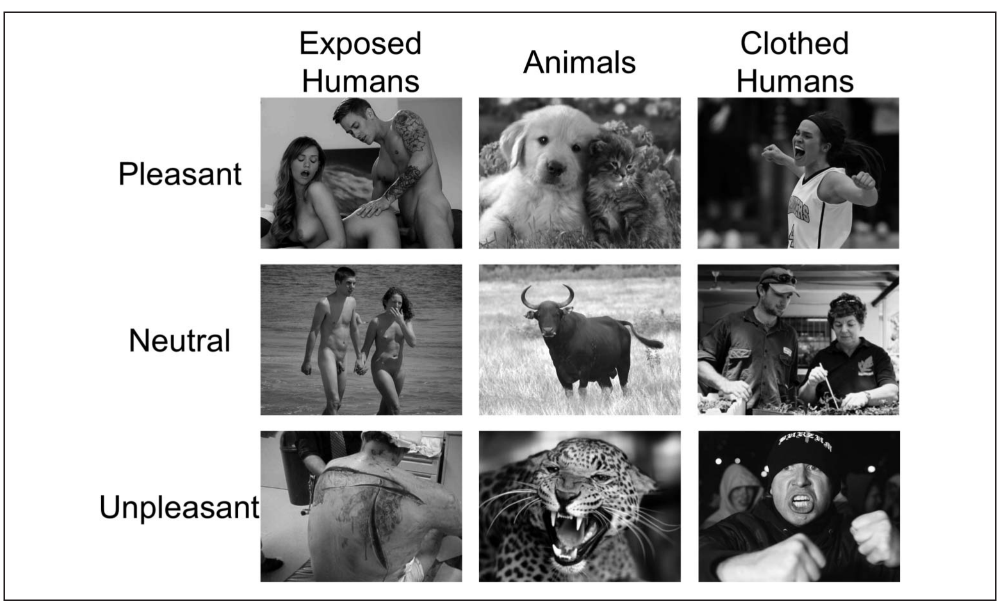

Figure 1. Example scenes from each category. Starting from the top and moving from left to right, displayed here are example scenes from the categories of erotica, pleasant animals, victorious athletes, nudists, neutral animals, neutral people, mutilations, threatening animals, and threatening people.

each category. There were no statistically significant category differences between participants that saw Set 1 versus Set 2. Scenes were presented on a 32-in. LCD monitor that occupied 31° of the horizontal visual field of view.

Scene Self-reports

After data collection, the EEG cap was removed and participants were seated outside of the chamber in a quiet room. The University of Georgia, Athens (UGA) participants reported how pleasant and aroused each scene made them feel on a 9-point scale (with half-increments) using the Self-Assessment Manikin (Bradley & Lang, 1994). Participants were seated and read a script describing the rating procedure. Participants then viewed a printed version of each scene in a binder and recorded their responses on a worksheet. The worksheet had the Self-Assessment Manikin figures and scales with emotion nouns at the top of the page for participants to reference.

To quantify the additional SFs of body exposure and orientation, an online sample was recruited to rate the 90 scenes depicting humans on each dimension. Participants were instructed that the study could last an hour, but most participants finished within 30 min. Participants accessed the study through a Qualtrics link, which presented the consent form and required their approval. If participants agreed to take part in the study, they began rating each scene in a pseudorandom order by using a click and drag scale that ranged from 1 to 9. Each scale was displayed one at a time underneath the scene the participant was viewing. The marker started in the middle of the scale on the number 5, and participants were required to move the marker before they could move on to the next scene and scale. The scale allowed for precision to the tenth decimal place (e.g., 1.1, 1.2). For the body exposure scale, a written question stated, "How much exposed or unclothed body parts are depicted in the scene?" The scale presented below the question ranged from 1 being *all exposed body parts* to 9 being *no exposed body parts*. The body orientation scale stated, "How upright, or normally oriented are the people in the scene?" with the scale ranging from 1 indicating *completely upright* to 9 indicating *very unusually oriented*.

Quantifying Scene Features

To further quantify the extent to which exposed body parts were present in scenes, the sum of pixels containing exposed body parts was counted for each scene. Using GNU Image Manipulation Program, a transparent layer was made over each JPEG scene. On this layer, the LASSO tool was used to manually trace the exposed body parts in each scene. Body parts that were covered by clothes or accessories such as arm bands and sunglasses were excluded. After tracing, the paint bucket tool was used to fill in the shapes with a solid color. The histogram tool was then used to record how many pixels had been filled by the paint bucket tool. The sum of pixels containing exposed body parts for each scene could then be compared with the total scene size.

As described above, scenes were chosen to be comparable in perceptual complexity, placed in natural environments, and balanced across categories to be equivalent in JPEG file size. The process of fully quantifying scene complexity is quite complicated and beyond the scope of this study (Donderi, 2006); however, to expand our assessment of SFs, Shannon information-entropy (from this point simply entropy) was also calculated for each scene using MATLAB (Mathworks.com). The entropy measure is found by using the first order histogram frequencies of gray values as probabilities. If every gray value is equally likely to occur, entropy is maximized, whereas if the scene contains only one value, then entropy is minimized. We also assessed any remaining effects of JPEG file size.

Spatial frequency was assessed using the SHINE MATLAB-based toolbox (Willenbockel et al., 2010). For each scene, the relative energy was found for all possible integers of cycles per image from the lowest frequency of 1 to the maximum of 300 (the highest frequency complete cycle for an image with a height of 600 pixels). Low spatial frequencies have exponentially higher relative energies than high spatial frequencies, so energy was transformed logarithmically with a base of 10 for analyses. Low spatial frequency was defined as the average transformed energy from 1 to 40 cycles, and high spatial frequency was the average from 41 to 300 cycles. This is consistent with prior definitions of scene spatial frequency (De Cesarei & Codispoti, 2013). Analyses that involved spatial frequency were also computed with thresholds at 50, 60, 70, and 80 cycles for separation between low and high spatial frequencies, and the results did not meaningfully change.

EEG Data Acquisition and Reduction

Continuous EEG data were recorded using a 64-channel BioSemi ActiveTwo system (BioSemi), which has preamplified electrodes positioned according to the 10/20 system. The electrode voltage was referenced to two additional common mode electrodes (Common Mode Sense and Driven Right Leg). The sampling rate was 512 Hz. ActiView acquisition software (actiview.org) was used to ensure offsets between 50 and −50 millivolts during EEG set up, and to monitor online data acquisition.

Offline, EEG data were segmented and preprocessed using the Electro Magnetic Encephalography Software analysis package for MATLAB (EMEGS; emegs.org; Peyk, De Cesarei, & Junghöfer, 2011). Data were processed in close accordance with the guidelines of Junghöfer, Elbert, Tucker, and Rockstroh (2000) through a method known as statistical correction of artifacts in dense array studies (SCADS). The data were adjusted using a low-pass Butterworth filter with a stopband of 40 Hz and a passband of 30 Hz to control for high-frequency noise. A high-pass Butterworth filter was also implemented with a passband of 0.1 Hz and stopband of 0.05 Hz. Data were segmented from 100 msec before to 2000 msec after scene onset. The 100 msec of data before scene onset was used to baseline-adjust the ERPs. Sensors and trials were screened for high voltage artifacts identified through an automated analysis of each electrode per trial in EMEGS in which the median values of maximum amplitude, standard deviation, and the maximum first derivative were used to find unusable trials and unreliable electrodes. Data were then transformed to an average reference (Peyk et al., 2011) and was again screened for artifact contaminated trials and sensors in the same automated process. Contaminated sensors were removed and replaced with values calculated through a spherical spline interpolation allowing the least noisy and closest electrodes to contribute the most to the new replacement amplitude. The data were kept in an average-reference that allows for simple visualization of the EPN, which can be difficult to identify with other reference positions such as the mastoid (Junghöfer et al., 2006).

After the data were preprocessed, the ERPs for each participant were extracted for each scene and an average was calculated for each scene category. Electrodes and latency windows representing the EPN and LPP were derived by a previous study that used the same scene presentation procedure (Farkas et al., 2020). The EPN was measured by extracting voltage from the lateral-posterior electrodes P7, PO7, O1, P8, PO8, and O2 from 150 to 300 msec after scene onset (shown in Figure 4). The LPP was recorded over midline parietal electrodes Cz, CPz, Pz, CP1, and CP2 from 400 to 900 msec after scene onset (shown in Figure 5).

Statistical Analyses

Omnibus repeated-measures ANOVAs were used to assess the overall effect of scene content on the ERP measures, with paired *t* tests used to break down specific category differences. This was done for the variables of valence, arousal, rated body exposure, rated body orientation, and EPN and LPP amplitude as μvolt change from baseline. All statistical tests were done with R software (r-project.org). To address our hypotheses, we planned to use paired *t* tests as a tool to make clear to the reader which scene categories had a differential impact on ERP amplitudes. Thus, these are not post hoc comparisons in need of a correction for multiple comparisons. However, we have included in the figure descriptions which comparisons would not survive Bonferroni correction (.001).

Our study question required the comparative assessment of multiple SFs, which cannot be assumed to be independent. To assess the impact of our many variables by-scene conservatively, we used multiple regression and four VSR regression methods to discern if and how SFs are related to EPN and LPP modulation. Multiple regression allowed us to use all SFs as predictors for each ERP within the same model, where each variable acts as a covariate. This can help to identify which variables account for common or unique variance. The VSR methods were used to identify which SFs have the most meaningful relationships with ERP modulation, and to minimize potential impact of collinearity of our many variables. Whereas multiple regression maximizes the amount of variance explained, VSR methods use additional information to find the simplest and most predictive multiple regression models for a hypothetical future data set. In other words, the VSR models allow us to identify which variables are most meaningful by assessing whether these variables warranted inclusion in the found models. By using four VSR methods, we can assess the consistency of variable relationships that were meaningful across models. Altogether, this multistep approach should yield a more reliable estimate of the ways in which our SFs are associated with EPN and LPP modulation. These analyses were only used for the scenes that depicted human content, where body-related SFs are relevant to our hypotheses. The SFs used for the 90 human scenes were valence, arousal, rated body exposure, rated body orientation, body exposure pixels, low spatial frequency, high spatial frequency, JPEG file size, and entropy.

Standard multiple regression and VSR models are shown together in Table 2. The values for each variable were transformed into standardized beta coefficients to simplify interpretation of the strength of the relationship. Statistical significance for each coefficient is presented only for the standard multiple regression results. For VSR models, only those variables that warranted inclusion in the final model list a coefficient. The four VSR regression methods used include (1) best-subset ranked by Bayesian information criteria (BIC), (2) best-subset ranked by cross validation, (3) LASSO regression, and (4) sparse LASSO regression. Best-subset regression involves computing a multiple regression for every combination of the predictor variables. The best multiple regression model can then be found based on an information criterion or cross validation prediction accuracy. Our first best-subset model was found based on BIC, which balances the variance explained by the model with a penalty for model complexity. This process was implemented with the *regsubsets* function contained in the leaps package (Lumley, 2017). The next best-subset model was found with a fivefold cross validation procedure repeated 1000 times. In this procedure, each scene was randomly assigned to one of five groups. All possible multiple regression models were then fit to four of the groups. Prediction accuracy was then found based on how well the models predicted ERP amplitude for the fifth test group of scenes as measured by the root-mean-square error (RMSE), which is the absolute prediction error. The process was repeated with each of the groups acting as the test data. The fivefold procedure was repeated 1000 times to increase the reliability of the results. The model with the lowest average RMSE from all folds through 1000 iterations is presented here as the best model. For both best-subset regression models, we

Table 1. The Mean Values for Valence, Arousal, EPN, LPP, Body Exposure Rating, and Body Orientation Rating

	Erotica	*Sports Victory*	*Neutral Nudists*	*Neutral People*	*Threatening People*	*Mutilations*	*Pleasant Animals*	*Neutral Animals*	*Threatening Animals*	*Repeated-measures ANOVA Result*
UGA sample N = 50										
Valence (1–9)	5.64 (0.24)$_{C}$	7.02 (0.18)$_{B}$	4.80 (0.15)$_{D}$	5.03 (0.48)$_{D}$	2.90 (0.14)$_{F}$	2.40 (0.18)$_{G}$	8.09 (0.16)$_{A}$	5.86 (0.10)$_{C}$	4.27 (0.15)$_{E}$	$F(8, 392)$, = 137.81, p = .001; η_p^2 = .738
Arousal (1–9)	6.52 (0.20)$_{A}$	5.86 (0.24)$_{B}$	4.76 (0.15)$_{C}$	3.80 (0.17)$_{E}$	5.97 (0.20)$_{B}$	6.15 (0.30)$_{AB}$	4.97 (0.33)$_{C}$	4.07 (0.18)$_{D}$	6.03 (0.18)$_{D}$	$F(8, 392)$ = 25.02, p = .001; η_p^2 = .338
EPN (μV)	3.93 (0.68)$_{B}$	6.89 (0.58)$_{C}$	2.54 (0.64)$_{A}$	9.08 (0.58)$_{E}$	7.11 (0.60)$_{CD}$	7.97 (0.63)$_{D}$	7.82 (0.57)$_{D}$	8.87 (0.62)$_{E}$	6.91 (0.64)$_{C}$	$F(8, 392)$ = 55.66, p = .001; η_p^2 = .532
LPP (μV)	4.96 (0.43)$_{A}$	0.40 (0.30)$_{F}$	3.06 (0.44)$_{B}$	−1.54 (0.26)$_{G}$	1.07 (0.34)$_{DE}$	1.93 (0.44)$_{C}$	1.03 (0.24)$_{DE}$	0.47 (0.34)$_{EF}$	1.56 (0.36)$_{CD}$	$F(8, 392)$ = 46.75, p = .001; η_p^2 = .488
Mturk sample N = 70										
Body exposure (1–9)	8.48 (0.05)$_{B}$	3.85 (0.13)$_{D}$	8.75 (0.04)$_{A}$	1.88 (0.10)$_{F}$	2.17 (0.09)$_{E}$	6.30 (0.21)$_{C}$	N/A	N/A	N/A	$F(5, 345)$ = 857.16, p = .001; η_p^2 = .925
Body orientation (1–9)	3.63 (0.20)$_{D}$	7.51 (0.15)$_{AB}$	7.79 (0.21)$_{A}$	7.30 (0.13)$_{B}$	5.99 (0.25)$_{C}$	3.21 (0.14)$_{E}$	N/A	N/A	N/A	$F(5, 345)$ = 167.66, p = .001; η_p^2 = .708

Standard error for each is within the parentheses. Results of pairwise comparisons are depicted with the subscript letters. If two categories in the same row share the same letter, the categories were found to not be statistically different at a critical p value of .05. The repeated-measures ANOVA results are presented in the final column.

report how the model fits on the overall set of scenes. This is because best-subset regression is a variable selection algorithm and does not return a model with coefficients tuned for future use. The third VSR method used was LASSO regression, which is a regularization method that shrinks slope coefficients by a L1 penalty scaled by a tuning parameter. The optimum tuning parameter was found based on a fivefold × 1000 iteration cross validation procedure. Similar to best-subset regression, this method can remove variables from the model that do not improve prediction accuracy. However, it is computationally less expensive and returns a model that should be more predictive in a new data set. Sparse LASSO regression is the model with the largest L1 penalty, which was still within 1 *SE* of the RMSE of the best LASSO regression. The sparse model is nearly equivalent in accuracy, but yields fewer, more essential predictor variables. A simpler model is generally preferred because it is easier to interpret and is less susceptible to overfitting.

RESULTS

Scene Category Analyses - Self Report

Valence was significantly different across scene categories as found by a repeated-measures ANOVA, $F(8, 392) = 137.81$, $p < .001$; $\eta_p^2 = .738$. Overall category results can be seen in Table 1. Results of pairwise comparisons are depicted with the subscript letters, such that if two categories were statistically equivalent, they share the same letter. Figure 2 shows individual participant valence and arousal self-reports as well as the overall sample mean for each category. Pleasant animal scenes elicited the highest valence ratings, which differed from the second-most pleasant category of victory scenes, $t(49) = 7.28$, $p < .001$, $d = 1.03$. Victory scenes elicited more rated pleasantness than the neutral animal category, $t(49) = 6.48$, $p < .001$, $d = 0.92$, as well as erotica scenes, $t(49) = 4.70$, $p < .001$, $d = 0.67$. Erotic scenes where not different than neutral animals valence ratings, but received higher pleasantness ratings than scenes of neutral people, $t(49) = 2.43$, $p = .019$, $d = 0.34$. Valence ratings did not differ between neutral people and nudist scenes. Nudist scenes elicited higher valence ratings than threatening animal scenes, $t(49) = 2.77$, $p = .007$, $d = 0.39$. However, the threatening animals evoked less valence ratings than threatening people scenes. Finally, mutilation scenes elicited the lowest valence ratings as compared with the second most unpleasant scene category of threatening people, $t(49) = 2.98$, $p = .004$, $d = 0.42$ (Table 2).

A repeated-measures ANOVA was significant for the self-reports of emotional arousal across the nine scene categories, $F(8, 392) = 25.02$, $p < .001$; $\eta_p^2 = .338$. Erotic and mutilation scenes elicited the highest ratings of arousal and were not statistically different. Erotica scenes evoked more rated arousal than threatening animal scenes, $t(49) = 2.51$, $p = .016$, $d = 0.35$; threatening people scenes, $t(49) = 2.23$, $p = .030$, $d = 0.32$; and victorious

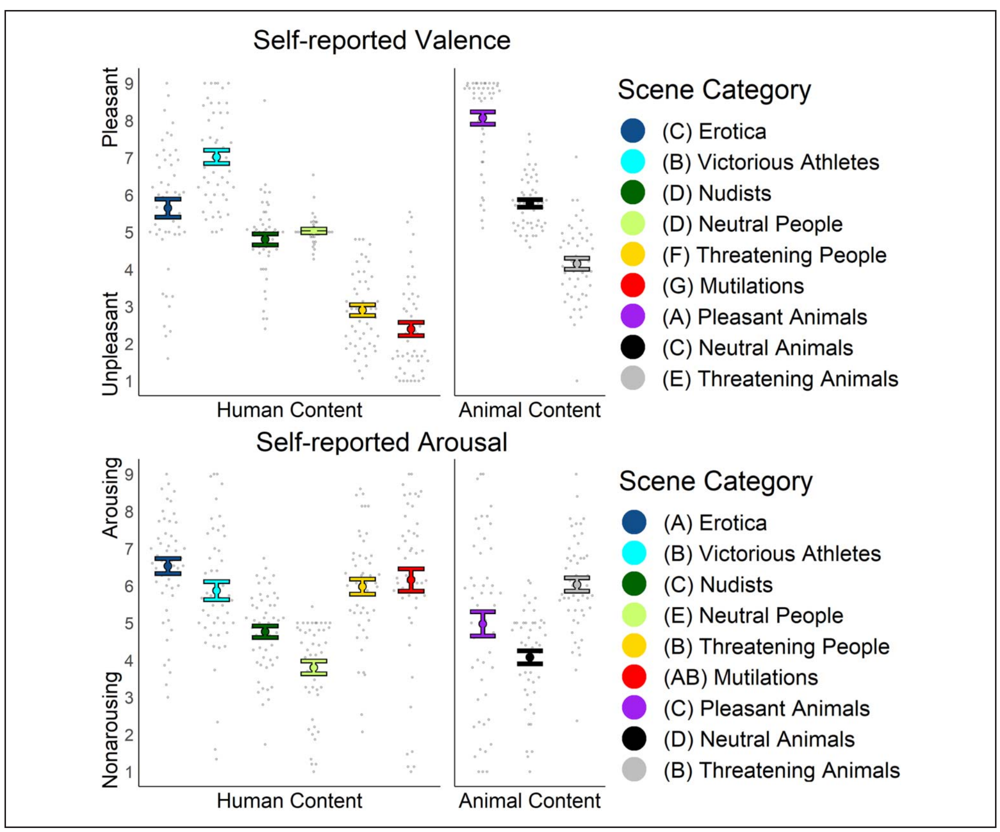

Figure 2. Self-reported valence and arousal for each category. Each gray dot is the category average for a participant (n = 50). Colored dots and error bars are the overall category average and standard error for all participants. Letters on the key indicate which categories were statistically different by paired *t* tests. If two categories share the same letter, there was not a significant difference between the categories at critical *p* value of .05. If corrected for multiple comparisons to a critical *p* value of .001, valence ratings would not be different between the pairs of erotica versus neutral people, nudists versus threatening animals, and mutilation versus threatening people. Using the same threshold, arousal ratings would not have differed for erotica versus threatening animals, erotica versus threatening people, erotica versus victorious athletes, victorious athletes versus pleasant animals, and neutral people versus neutral animals.

Table 2. Multiple Regression and VSR Models Result for the 90 Human Scenes

	Multiple Regression Standardize Beta Coefficients									*Model Statistics*				
	Valence	*Arousal*	*JPEG File Size*	*Entropy*	*Body Exposure Rating*	*Body Orientation Rating*	*Body Exposure Pixels*	*Low-spatial Frequency*	*High-spatial Frequency*	*F*	*p*	R^2_{adj}	*BIC*	*RMSE*
EPN														
Standard multiple regression	−.17	−.14	.01	.10	−.48**	−.28*	−.14	−.23	−.13	11.90	< .001	.52	410	
Best-subset regression (BIC)					−.74	−.27							392	
Best-subset regression (CV)		−.17			−.64	−.37		.22	−.12				396	1.93
LASSO regression	−.15	−.10		.10	−.49	−.22	−.10	.19	−.10					2.08
Sparse LASSO regression				.08	−.46			−.01						2.16
LPP														
Standard multiple regression	−.00	.33**	−.04	.11	.78**	−.07	−.20*	−.18	.06	29.58	< .001	.74	317	
Best-subset regression (BIC)		.36			.69								297	
Best-subset regression (CV)		.38			.79		−.15						297	1.14
LASSO regression		.32			.66	−.04	−.04	−.05	.01					1.21
Sparse LASSO regression		.23			.57									1.25

Model and variable statistical significance is only applicable for the standard multiple regression. For Models 2 through 5, variables can be deemed important if they warranted inclusion in the final reported model.

* $p < .05$.

** $p < .001$.

athlete scenes, $t(49) = 2.49$, $p = .016$, $d = 0.35$. Mutilation, threatening animals, threatening people, and victorious athletes scenes were not different in self-reported arousal. Pleasant animal scenes evoked less arousal than victorious athlete scenes, $t(49) = 2.32$, $p = .024$, $d = 0.33$, but were not different in rated arousal from nudist scenes. Nudist scenes elicited more arousal than neutral animal scenes, $t(49) = 3.39$, $p = .001$, $d = 0.48$. Lastly, participants reported that neutral animal scenes were more arousing than the neutral people scenes, $t(49) = 2.45$, $p = .018$, $d = 0.35$.

The Mturk sample reported the six human scene categories had a different amount of exposed body parts as found through a repeated-measures ANOVA, $F(5, 345) = 857.16$, $p < .001$; $\eta_p^2 = .925$. Mturk ratings of body exposure and body orientation can be seen in Table 1 and Figure 3. The nudist category was perceived as having the most exposed body parts and were significantly different than erotic scenes, $t(69) = 6.30$, $p < .001$, $d = 0.75$. Erotic scenes were perceived as having more exposed body parts than mutilation scenes, $t(69) = 10.93$, $p < .001$, $d = 1.31$. Participants felt mutilation scenes had more body part exposure than victorious athlete scenes, $t(69) = 12.25$, $p < .001$, $d = 1.46$. In turn, victorious athlete scenes were rated as including less exposed body than threatening people scenes, $t(69) = 19.30$, $p < .001$, $d = 2.31$. Threatening people scenes were reported as more clothed than the final scene category of neutral people, $t(69) = 6.51$, $p < .001$, $d = 0.78$.

Mturk reports of body orientation were different between scene categories, $F(5, 345) = 167.66$, $p < .001$, $\eta_p^2 = .708$. Participants rated the nudist category as having the most normally oriented depicted people, but the nudists scenes were not statistically different to the second highest rated category of victorious athletes. Nudist scenes were more normally oriented than neutral people scenes, $t(69) = 2.16$, $p = .034$, $d = 0.26$, but victorious athlete scenes were rated as not different than the neutral people category. The neutral people were more normally oriented than the threatening people scenes, $t(69) = 5.26$, $p < .001$, $d = 0.63$. The threatening people category was rated higher than the erotic scenes, $t(69) = 7.77$, $p < .001$, $d = 0.93$. Finally, the erotic scenes were reported as more normally oriented as the people in the mutilation scenes, $t(69) = 2.18$, $p = .033$, $d = 0.26$.

Scene Category Analyses

EPN. A repeated-measures ANOVA found significant modulation of the EPN across the nine scene categories, $F(8, 392) = 55.66$, $p < .001$; $\eta_p^2 = .532$. The EPN waveforms can be seen in Figure 4, whereas the amplitudes are shown in Table 1, including significant contrast effects, indicated by different subscript letters. Nudist scenes modulated the EPN the most and were significantly different than modulation evoked by erotic scenes, $t(49) = 4.41$, $p < .001$, $d = 0.62$. EPN modulation from erotic scenes were greater than modulation elicited by victorious athletes,

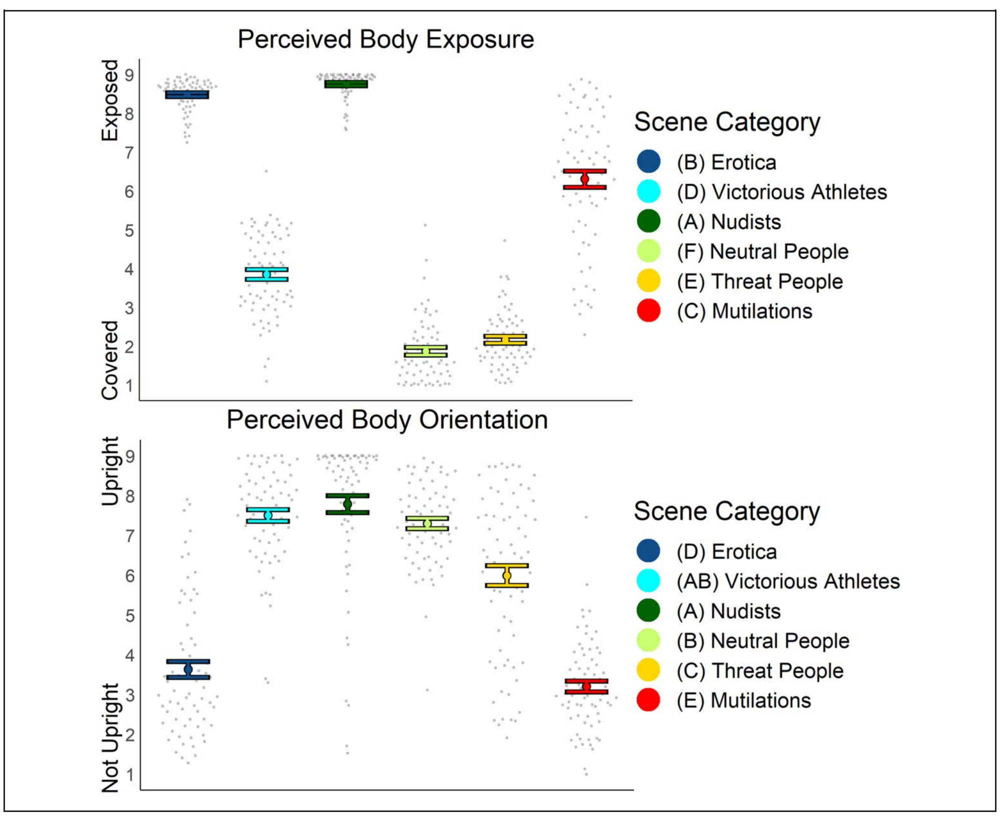

Figure 3. Perceived body exposure and body orientation per each category from the Mturk sample ($n = 70$). Each gray dot represents the average rating for each participant, whereas the colored dots and error bars represent the overall average and standard error, respectively. In the legend, if categories do not share a letter, they were statistically different at a critical p value of .05. If corrected for multiple comparisons to a critical p value of .001, all category differences in body exposure ratings would still be statistically significant. Using the same threshold, body orientation ratings would not have statistically differed for nudists versus neutral people and erotica versus mutilation scenes.

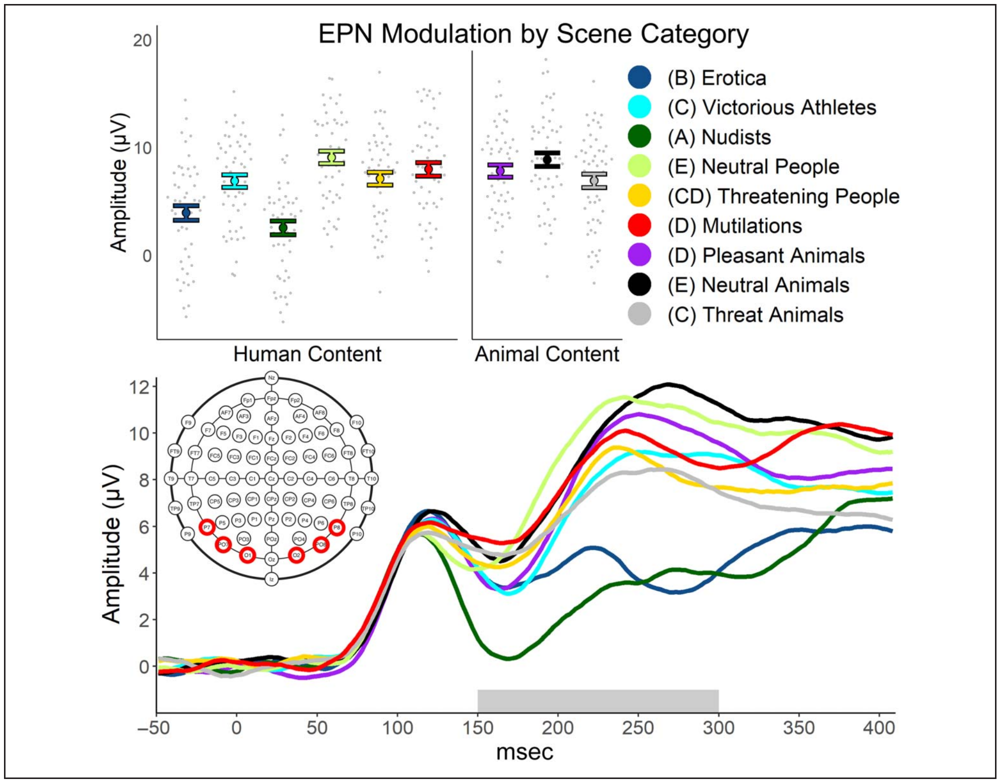

Figure 4. The top depicts the average participant and category EPN amplitude by category. The bottom displays the EPN waveform by category. In the legend, if categories do not share a letter, they were statistically different at a critical *p* value of .05. If corrected for multiple comparisons to a critical *p* value of .001, the EPN would not have statistically differed for pleasant animals versus victorious athletes, pleasant animals versus threatening animals, pleasant animals versus neutral animals, mutilation versus neutral animals, and mutilation versus neutral people.

$t(49) = 8.00$, $p < .001$, $d = 1.13$; threatening animals, $t(49) = -7.50$, $p < .001$, $d = 1.06$; and threatening people scenes, $t(49) = 8.59$, $p < .001$, $d = 1.21$. However, the three categories of victorious athletes, threatening animals, and threatening people did not differ significantly in EPN modulation. Pleasant animal scenes modulated the EPN less than victorious athlete scenes, $t(49) = 2.61$, $p = .012$, $d = 0.37$, and the threatening animal scenes,

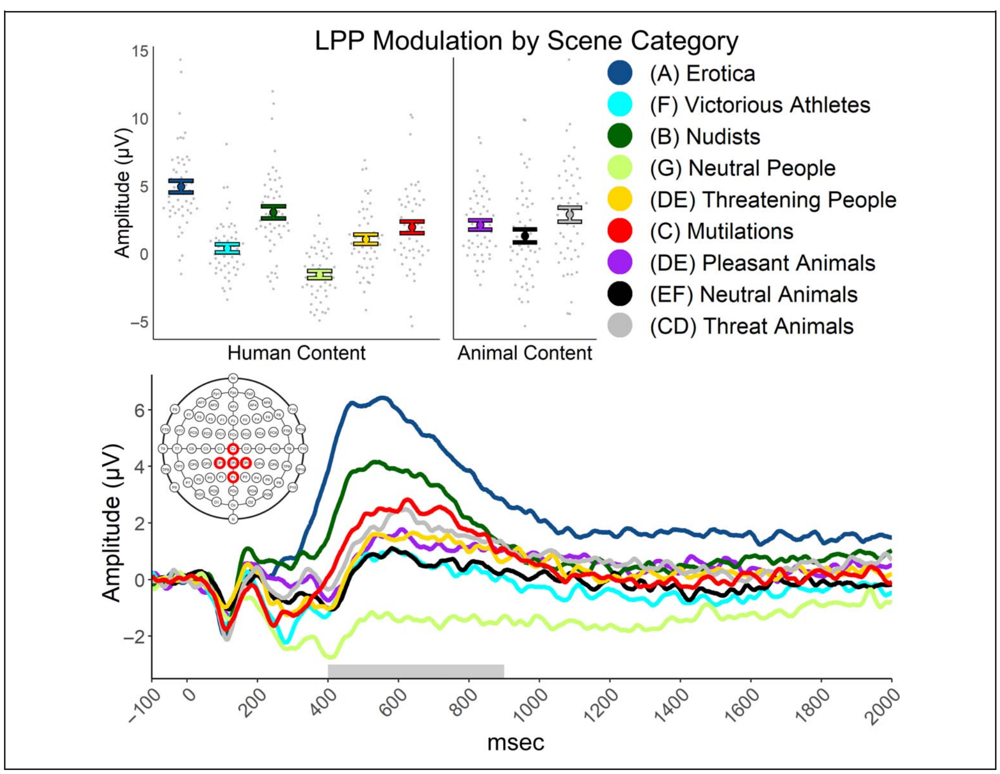

Figure 5. The top depicts the average participant and category LPP amplitude by category. The bottom displays the LPP waveform by category. In the legend, if categories do not share a letter, they were statistically different at a critical *p* value of .05. If corrected for multiple comparisons to a critical *p* value of .001, the LPP would not have statistically differed for nudists versus mutilation, nudists versus threatening animals, mutilation versus threatening people, mutilation versus pleasant animals, threatening animals versus neutral animals, threatening animals versus victorious athletes, and threatening people versus victorious athletes.

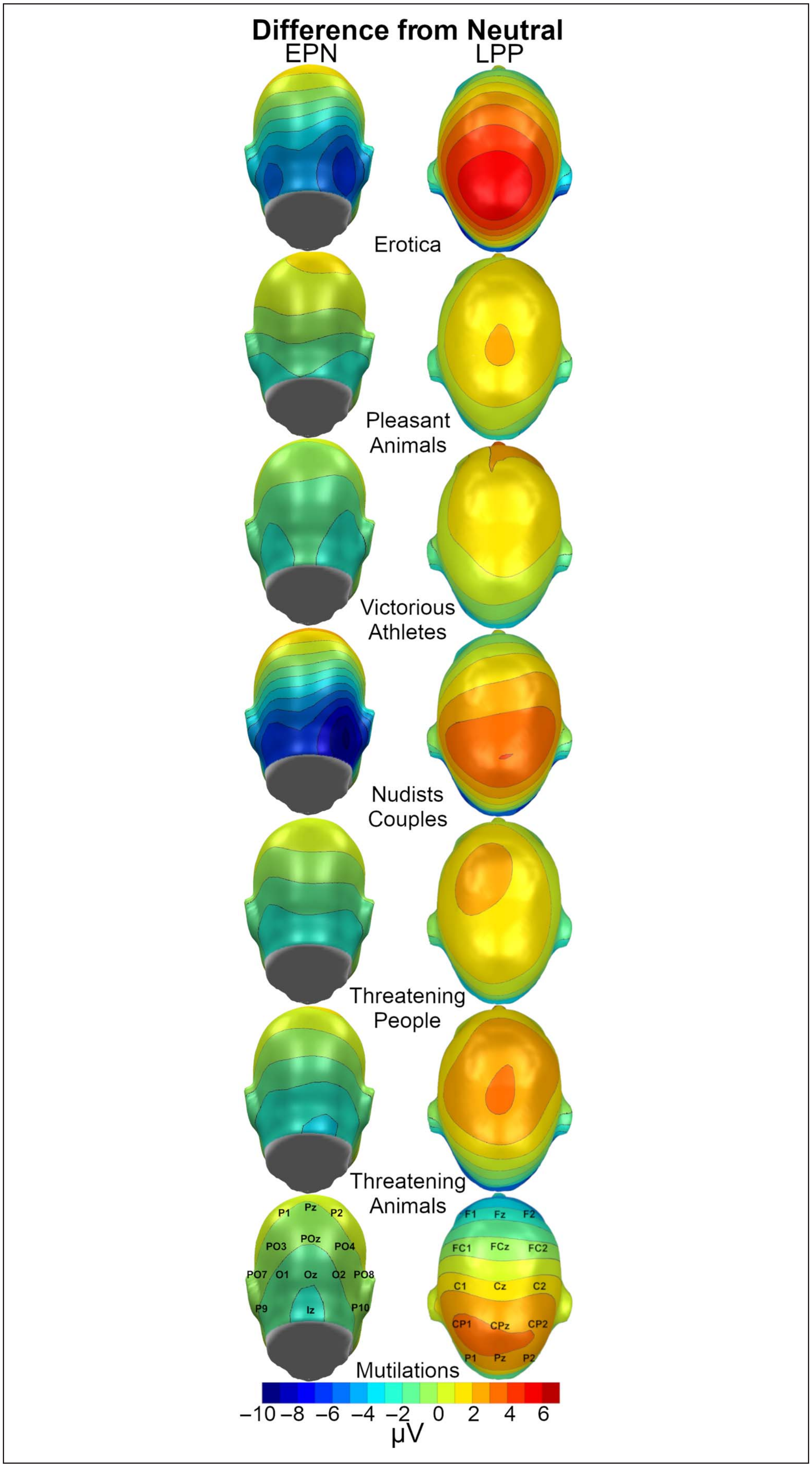

Figure 6. Scene category topographies for the EPN (150–300 msec) and LPP (400–900 msec) visualized as the difference in microvolts from the neutral people and animal categories. Each color represents a range of 1 microvolt, such that the darkest blue represents a microvoltage difference between −10 and −9.

$t(49) = 2.54$, $p = .014$, $d = 0.36$. However, the pleasant animal, threatening people, and mutilation scenes did not differ in EPN amplitude significantly. Mutilation scenes modulated the EPN more than neutral animals, $t(49) = 2.34$, $p = .023$, $d = 0.33$, and neutral people scenes, $t(49) = 2.45$, $p = .018$, $d = 0.35$. Neutral animal and neutral people scenes did not differ in EPN modulation.

LPP. A repeated-measures ANOVA found a difference in LPP modulation across the nine scene categories, $F(8, 392) = 46.75$, $p < .001$; $\eta_p^2 = .488$. The LPP waveforms can be seen in Figure 5, whereas the amplitudes are shown in Table 1, including contrast effects. Erotic scenes modulated the LPP the most and was statistically different than the next most potent scene category of nudists, $t(49) = 6.11$, $p < .001$, $d = 0.86$. Nudist scenes modulated the LPP more than mutilation, $t(49) = 2.94$, $p = .005$, $d = 0.42$, and threatening animal scenes, $t(49) = 3.21$, $p = .002$, $d = 0.45$. However, mutilation and threatening animal scenes statistically did not differ in LPP amplitude. Mutilation scenes evoked more LPP modulation than threatening people scenes, $t(49) = 2.85$, $p = .006$, $d = 0.40$, and pleasant animals scenes, $t(49) = 2.14$, $p = .037$, $d = 0.30$. Threatening animal modulation was not different to the modulation of threatening people and pleasant animal categories. Neutral animal scenes elicited less LPP modulation than the threatening animal scenes, $t(49) = 2.82$, $p = .007$, $d = 0.40$, but the neutral animals were not different than threatening people and happy animal scenes. Victorious athlete scenes modulated the LPP less than threatening people, $t(49) = 2.15$, $p = .037$, $d = 0.30$, and threatening animal scenes, $t(49) = 3.29$, $p = .002$, $d = 0.46$, whereas the victorious athlete scenes were not different to modulation by neutral animal scenes. Neutral people scenes modulated the LPP less than all other categories including the next closest category of victorious athletes, $t(49) = 7.30$, $p < .001$, $d = 1.03$ (Figure 6).

By Scene Analyses

EPN. The EPN standard multiple regression was significant, $F(9, 80) = 11.90$, $p < .001$, $R^2_{\text{adj}} = .52$. Notably, rated arousal was not significantly associated with EPN modulation ($\beta = -.17$, $p = .164$). Scenes, which were rated with high body exposure ($\beta = -.48$, $p < .001$) and upright orientation ($\beta = -.28$, $p = .024$) were associated with greater EPN modulation. The best-subset regression based on BIC included only rated body exposure ($\beta = -.74$) and body orientation ($\beta = -.27$) as meaningful. The best-subset regression based on prediction accuracy (RMSE =1.93) included arousal ($\beta = -.17$), rated body exposure ($\beta = -.64$), rated body orientation ($\beta = -.37$), low-spatial frequency ($\beta = .22$), and high-spatial frequency ($\beta = -.12$) as meaningful. The most predictive LASSO regression (RMSE = 2.08) included all predictor variables except JPEG file size. The sparse LASSO regression (RMSE = 2.16) included body exposure ratings ($\beta = -.46$), entropy ($\beta = .08$), body orientation ratings ($\beta = -.01$), and low-spatial frequency ($\beta = .01$) as meaningful.

LPP. A standard multiple regression of LPP modulation across the 90 human scene set was significant, $F(9, 80) = 29.58$, $p < .001$, $R^2_{\text{adj}} = .74$. Higher rated arousal ($\beta = .33$, $p < .001$) and rated body exposure ($\beta = .78$, $p < .001$) was associated with a larger LPP amplitude, whereas the sum of body exposure pixels ($\beta = -.20$, $p = .024$) had a negative relationship with the LPP. The best-subset model based on BIC included rated body exposure ($\beta = .69$) and rated arousal ($\beta = .36$). The best-subset model based on prediction accuracy (RMSE = 1.14) included arousal ($\beta = .38$), rated body exposure ($\beta = .79$), and body exposure pixels ($\beta = -.15$). The most predictive LASSO regression (RMSE = 1.21) included rated arousal ($\beta = .32$), body exposure ratings ($\beta = .66$), body orientation ratings ($\beta = -.04$), body exposure pixels ($\beta = -.04$), low-spatial frequency ($\beta = -.05$), and high-spatial frequency ($\beta = .01$). The sparse LASSO regression (RMSE = 1.25) included body exposure ratings ($\beta = .57$) and arousal ratings ($\beta = .23$).

DISCUSSION

In this study, we directly assessed the extent to which the emotion-modulated EPN may be sensitive to the presence of exposed body parts in scenes, independent from rated arousal. Across the wide range of scenes selected, the results replicated our initial study (Farkas et al., 2020) and supported the hypothesis that highly exposed bodies and upright body orientation together are strong predictors of EPN amplitude, whereas the rated arousal of scenes was weakly predictive. This pattern contrasts with modulation of the LPP, which consistently reflected scene arousal ratings.

The scene category effect size differences of the EPN and LPP suggest a different hierarchy of sensitivity. Nudist scenes clearly elicited the largest EPN, showing a medium/large 0.62 effect size over erotica, the second-most effective category. This difference is equivalent to the 0.61 effect size between the remaining emotional scene categories and neutral scenes. Averaged together, the nudist and erotica scenes showed a very large 1.38 effect size compared with all other emotional categories. Conversely, erotic scenes elicited the largest LPP, showing a 0.86 effect size over nudists, the second-most effective category. This difference is similar in size to the 1.00 effect between the remaining emotional scene categories and neutral scenes. Averaged together, LPP modulation to the nudist and erotica scenes showed a 1.26 effect size difference as compared with all other emotional categories.

The regression models fit to the 90 individual scenes showed that body exposure ratings were a reliable predictor of EPN and LPP amplitude, whereas standardized beta-coefficients indicate that body exposure ratings had the strongest relationship with the EPN. Notably, rated arousal was not significantly related to EPN modulation in the standard multiple regression, and was selected in just two of the four VSR models. For LPP modulation, rated arousal and body exposure ratings were consistently strong predictors.

These data suggest that the EPN may reflect the early activation of brain networks that function to enhance the perceptual processing of classes of stimuli that reliably predict relevant outcomes (Frank & Sabatinelli, 2017; Bradley, 2009; Lang, Bradley, & Cuthbert, 1998). Specifically, scenes clearly featuring people may enhance EPN modulation because people are associated with aversive and appetitive experience, and it may be that the more clearly a person is depicted in a scene (e.g., upright, unclothed), the larger the EPN, possibly reflecting reentrant feedback from downstream ventral visual structures (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). After this potentially meaningful cue is further processed across the brain, LPP modulation strongly reflects the rated emotional intensity of the scene, while being less sensitive to clearly visible people. This might explain the pronounced sensitivity of the EPN to nudist, relative to erotic scenes, whereas the LPP shows the reverse pattern.

Despite the apparent bias toward bodies, the EPN remains sensitive to nonbody emotional cues as well. This is evident in the EPN modulation by pleasant ($D = 0.39$) and unpleasant ($D = 0.63$) animals scenes relative to neutral animal scenes in the current study, and in published work using emotional faces (Schupp, Öhman, et al., 2004), hand gestures (Flaisch et al., 2009), and even words (Kissler et al., 2007).

Body-specific Activity in the Visual System

There is considerable evidence that body percepts have a privileged status in the human visual system. Studies with newborns have found that upright bodies draw attention more than inverted bodies or other stimuli (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013). fMRI studies have identified a region of lateral occipital cortex that is particularly sensitive to line-drawings of bodies relative to tools (Peelen & Downing, 2007). In the ERP literature, the perception of a headless body on a blank background can elicit a potential similar to the N170 elicited by faces. Although this body-evoked N170 appears at a more anterior scalp location to the EPN and dissipates by 210 msec (Thierry et al., 2006), it has been shown that a greater proportion of skin exposure increases the amplitude of this potential (Alho, Salminen, Sams, Hietanen, & Nummenmaa, 2015; Hietanen, Kirjavainen, & Nummenmaa, 2014; Hietanen & Nummenmaa, 2011). These findings suggest that the human visual system is especially sensitive to body cues.

If bodies elicit a pronounced EPN amplitude because the visual system is tuned to identify these cues, then the EPN could be a useful metric of other features for which the visual system shows a similar processing bias. In other words, the EPN may be less an index of emotional perception, and more a measure of the degree of early recognition of features that predict emotional percepts. Consistent with this distinction, snakes also appear to show particularly efficient processing in the visual system (Soares, Lindstrom, Esteves, & Öhman, 2014; Öhman & Mineka, 2001), and also elicit larger EPN amplitudes than would be expected as compared with arousal ratings and LPP modulation (Van Strien, Eijlers, Franken, & Huijding, 2014; Van Strien, Franken, & Huijding, 2014). Naturally, those cues that predict emotional percepts will most often be emotional, and thus elicit similar EPN and LPP modulation, in keeping with rated arousal. Because of its early latency and broad reactivity to naturalistic scenes, the EPN may enable research to identify the nature and extent of these visual features, and thus help to define the subtle mechanisms of emotional perception in large human samples.

Limitations and Future Directions

Although this work expanded the variety of scene stimuli and feature quantification from earlier efforts, it could still benefit from more heterogeneity of scenes, additional measures of experienced arousal, and more precise calculations of exposed body parts. To understand how specific scene content and features affected EPN modulation, we curated scenes that were quite similar in the content within each category. Although this was useful and intentional for the main objectives of this study, it is possible that discrete content categories affect our by-scene analyses. Potentially, this could lead to what is referred to as a Simpson's paradox, in which the overall relationship does not reflect associations within each category. This concern could be addressed in future studies by evaluating the relationship between perceived body exposure and EPN amplitude for a larger, more diverse scene set. Separately, the LPP results suggest that nudist scenes may have been more arousing than the participants self-reported. This is a difficult issue, but future studies could include physiological measures of arousal such as skin conductance or pupil diameter. Lastly, although the sum of pixels that contained exposed body parts was associated with EPN modulation, it did not capture the effect as well as self-reported body exposure. Although we aimed to keep the action of a scene consistently placed in the middle, and within a standard depth of field, the distance of body parts from the camera lens does vary across scenes, and may have an impact on the utility of this index. Future studies could also investigate if there are intermediate-level visual features of a body that are especially potent modulators of the EPN. A computer simulation study suggests that small fragments of images, such as a part of a face, can provide useful information for accurate classification (Ullman, Vidal-Naquet, & Sali, 2002). Using a similar approach with fragmented pictures of bodies may reveal which features are most influential in body classification, and if the EPN is modulated by specific body features, or the recognition of a full body.

Consistent with prior work that manipulated scene complexity (Nordström & Wiens, 2012; Löw et al., 2013; Bradley et al., 2007), a subset of our analyses suggest that spatial frequency of scenes modulated EPN amplitude, despite the fact that the scene set was composed to be equivalent in JPEG file size across categories. The use of additional indices of scene complexity will be needed to resolve this issue more fully, but we are encouraged by the relationship between body exposure ratings and ERP modulation, which strongly surpassed the modest relationship between low spatial frequency and the ERPs. Considering that the original EPN study (Junghöfer et al., 2001) employed nearly the entire IAPS set (1000+ scenes) and did not identify any reliable relationships with scene color, luminance, or spatial frequency, we are reasonably confident that the nudist-erotica EPN effect is not a result of low-level perceptual differences.

Conclusion

These data suggest a refinement in a common interpretation of what the EPN component represents in visual perception. Researchers have generally concluded that the EPN is modulated primarily by arousing content, much like the LPP (Frank & Sabatinelli, 2019; Sabatinelli et al., 2013; Olofsson et al., 2008; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). The current findings suggest that scenes depicting unclothed bodies in upright postures elicit a greater EPN independent of arousal ratings and LPP amplitude. Thus, in addition to reflecting motivational relevance in general, this EPN sensitivity might be a result of a learned or phylogenetic tendency to attend to human bodies. This ability to distinguish the impact of SFs on early and late stage emotion-modulated ERPs could enable future studies to identify other visual features that show this distinction, thus providing a means to differentiate the mechanisms of emotional perception with noninvasive measures.

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Data Availability Statement

Data and experimental materials from this study will be made available upon request to the authors.

Author Contributions

Andrew H. Farkas: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Supervision; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Dean Sabatinelli: Conceptualization; Formal analysis; Funding acquisition; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing—Review & editing.

Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .521; W/M = .271; M/W = .125; W/W = .083.

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