EMOTIONAL AND FEATURE-BASED MODULATION OF THE EPN IN SCENE PERCEPTION

By

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(Under the Direction of Dean Sabatinelli)

Abstract

The early posterior negativity (EPN) is an event-related potential that can be modulated by the perception of emotionally arousing scenes relative to neutral scenes. In a recent study, we found nudist scenes that elicit low levels of pleasantness and arousal modulated the EPN greatly. Here we attempted to replicate and extend our recent findings by using nine scene categories and collecting additional measures of body exposure. Overall, we found body exposure predicts EPN modulation. Nudist scenes elicited the largest EPN amplitude and they were rated as having the most exposed body parts. Correlations of individual scenes found metrics of body exposure predicted the EPN amplitude of a scene better than the scene's pleasantness or arousal self-report. An auxiliary finding was the late positive potential is also predicted by depicted body exposure. This work indicates the perception of bodies may have a privilege status in the human perceptual system.

Index words: Emotion, Early posterior negativity, Late positive potential, Body parts

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Chapter 1

Introduction

Research combining the use of naturalistic scenes and electroencephalography (EEG) have discovered event related potentials (ERPs) that have furthered understanding of emotion and how it interacts with the visual system. One such discovery is the association between emotionally arousing content and the amplitude of an ERP known as the late positive potential (LPP). The LPP is characterized as a voltage positivity over midline parietal areas (Cuthbert et al., 2000; Schupp et al., 2007). The LPP appears around 300ms and persists until scene offset with a peak amplitude between 400 and 900ms. Highly pleasant and unpleasant scenes that elicit self-reports of heightened arousal, predict a greater LPP amplitude (Bradley, 2009). Functional magnetic resonance imaging (fMRI) research found the probable sources of the LPP to be visual cortices and emotion related areas of the orbital frontal cortex and amygdala (Sabatinelli et al., 2013). The LPP has expanded our understanding of emotion and the brain while also offering researchers a robust method to quantify experienced emotional arousal. Furthermore, the LPP has been foundational to the theory of motivated attention which posits that the human brain preferentially attends and processes emotional content.

A relatively new ERP component known as the early posterior negativity (EPN) may also be part of this motivated attention process because this component also exhibits arousal modulation. Visual perception of emotionally arousing content will increase the modulation of the EPN in a similar manner as the LPP (Junghöfer et al., 2001). However, the EPN's topography over posterior occipital areas and earlier latency of 150 to 300ms, suggests the EPN reflects activity more localized to visual areas that is different than the LPP. If the EPN reflects earlier activity from different cortical areas than the LPP, it could provide unique information about the brain and emotion. The extensive study of the LPP has given researchers confidence to use this component to study mental disorders with emotional symptoms (Michalowski et al., 2015; Weinberg & Hajcak, 2011a) and even as a diagnostic tool for smoking (Robinson et al., 2016) and food addictions (Versace et al., 2016). A better understanding of the EPN could elevate the usefulness of this component as well. Research on the EPN could also expand the understanding of emotion, attention, emotional disorders, and possibly even implicit bias.

While research of the EPN has focused on the general arousal effect, multiple studies have reported some scene content seem to modulate the EPN more than the LPP. Several studies have found that the EPN shows a bias for pleasant scenes relative to unpleasant scenes (De Cesarei & Codispoti, 2006; Flaisch et al., 2008; Frank & Sabatinelli, 2019; Schupp et al., 2004a; Weinberg & Hajcak, 2010). These results suggest the EPN could be a neural measure of experienced pleasure, in addition to arousal. However, other studies have found erotic scenes also modulate the EPN more than equivalently arousing mutilation scenes (Schupp et al., 2006; Schupp et al., 2007). This EPN erotica bias is not as often seen for the LPP which is usually modulated equivalently between erotica and mutilation scenes. Also, an EPN erotica bias could cause study results to look like the EPN has a pleasure bias because researchers often use erotic scenes in pleasant categories. The erotica over mutilation EPN bias may be another manifestation of a pleasure bias, but there is reason to believe mere perception of exposed body parts are having an additive effect with arousal on the EPN. Erotica may stimulate a specific part of extrastriate cortex that fMRI research has shown to be sensitive to the perception of body parts (Downing et al., 2001; Peelen & Downing, 2007). Taken together, it is possible reported pleasure and erotica EPN biases are caused by these categories featuring scenes with exposed body parts.

In two recent studies, our lab assessed whether pleasantness or unclothed body part features modulate the EPN (Farkas, Oliver, & Sabatinelli, in revision). Figure 1 is provided to summarize these results. In the first study, we chose two scene categories that made participants feel pleasant (erotica and victorious athlete scenes), two that made participants feel unpleasant (threatening people and mutilation scenes), and one neutral category (neutral people scenes). Importantly, the four emotional categories allowed for testing of pleasantness effects because they elicited equivalent levels of self-reported arousal. In the second study, we used nudist and erotic scenes to understand if the nudists scenes that featured exposed body parts while eliciting lower self-reported arousal and pleasantness could also modulate the EPN. We found for study one the highly pleasant and equivalently arousing victorious sports scenes did not modulate the EPN as much as erotica. However, the nudists scenes in study two modulated the EPN more than the same erotica scenes. Furthermore, while the EPN was higher for nudist scenes relative to erotica, the LPP showed the opposite pattern with erotica modulating the amplitude to a greater degree than nudist scenes. These findings indicate the EPN may be influenced by body parts while the LPP is more specifically tuned to emotional arousal.

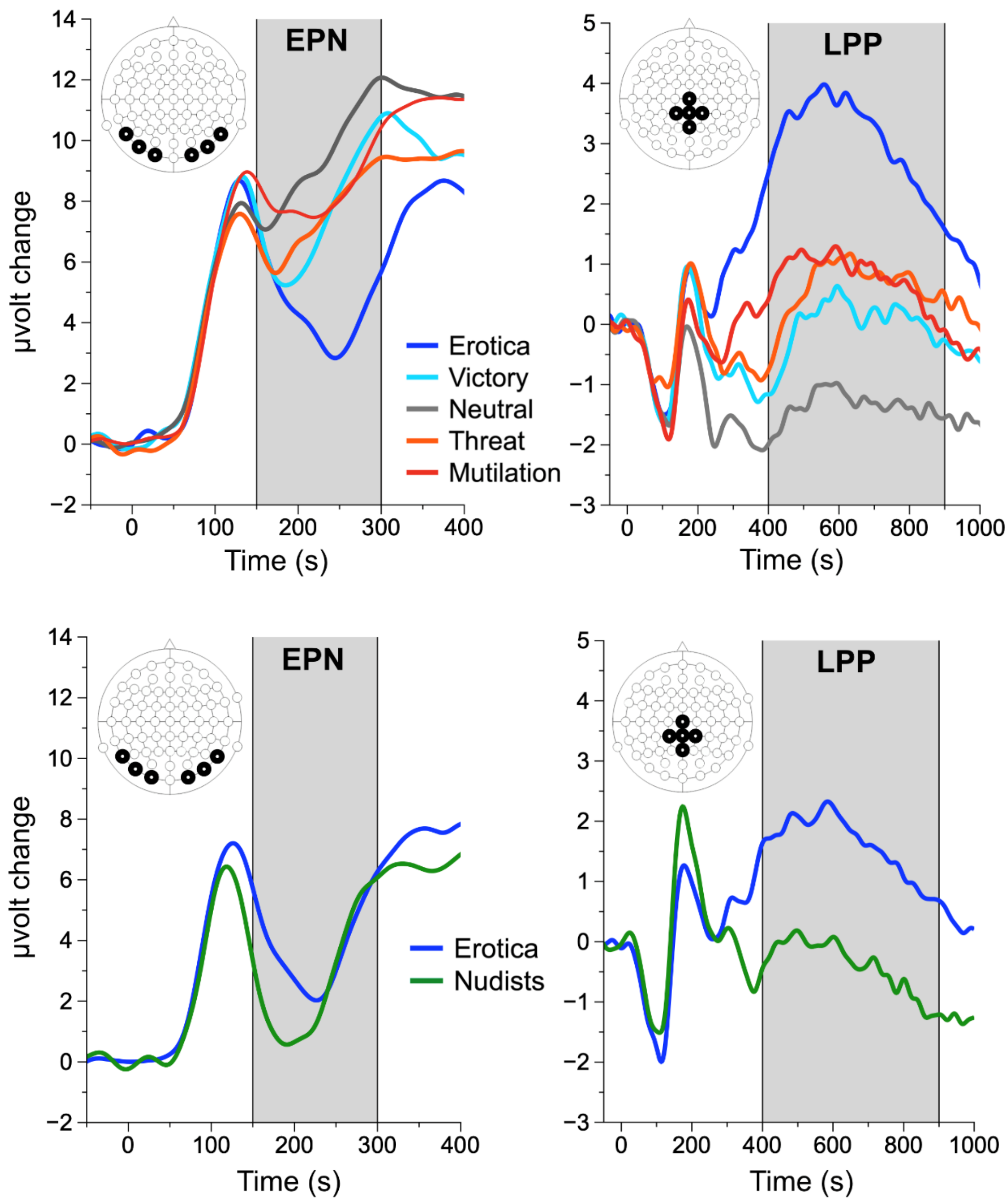


Figure 1. Summary waveforms of recent EPN and LPP study. The first study (presented in the first row) found erotic scenes elicit a greater EPN and LPP amplitude. The second study (second row) found nudists scenes that elicit lower self-reports of arousal surprisingly evoked a greater EPN modulation than erotic content (Farkas, et al., in revision).

While these recent results found evidence for body parts being a modulator of the EPN, these studies can be clarified with additional controls. A complication of the initial nudist study was that participants were only exposed to the two categories of nudists and erotica. Because the study only featured these two categories, we don't know how these EPN and LPP amplitudes would compare to other emotional content. Furthermore, participants may give more accurate ratings of how pleasant or arousing they find nudist scenes if they are self-reporting their feelings in comparison to other content that more effectively spans pleasantness and arousal dimensions. A second unanswered question is what features of nudist scenes allowed them to modulate the EPN more than erotica? Post-hoc visual inspection of individual nudist scenes that most modulated the EPN seemed to indicate that scenes with clearly unclothed and more normally oriented bodies led to the greatest EPN modulation

Here we attempt to explicitly examine these research questions and replicate the body exposure modulation effect on the EPN. The scene perception paradigm was used with a more complete scene set with nine scene categories including erotica, pleasant animals, victorious athletes, nudists, neutral animals, neutral people, threatening people, threatening animals, and mutilations. This scene set should accurately span the valence and arousal dimensions. The set also includes mostly unclothed categories of erotica, nudists, and mutilations that differ on valence and arousal as well as comparable categories that contain mostly clothed content of victorious athletes, neutral people, and threatening people. It also allows for testing of valence and arousal independently of human body part content with the pleasant animal, neutral animal, and threatening animal categories. Additionally, to examine the extent to which body exposure and body orientation in scenes predicted modulation of the EPN, we collected ratings of these dimensions. We also calculated the sum of pixels of exposed body parts that made up each scene to test whether it was associated with EPN modulation.

We hypothesized that the EPN would be most strongly modulated by nudist scenes. We also predicted that the nudist scenes would elicit more neutral self-reports of valence as well as less arousal than the six emotional categories. Furthermore, we expected the nudists scenes to be rated as having the highest body exposure and body orientation among the scene categories. We hypothesized that the EPN modulation for individual scenes will be better predicted by self-reports of highly exposed bodies and sum of exposed pixels of exposed body in contrast to self-reports of valence or arousal. We predicted the best multiple regression equation to predict the EPN will include the variables of body exposure and body orientation. For the LPP, we expect erotic scenes to elicit the largest amplitudes relative to all other scenes and nudist scenes would elicit modulation comparable to the other emotional categories. We expected the LPP for individual scenes would be best predicted by self-reported arousal.

Chapter 2

Literature Review

EEG and ERP Introduction

EEG is a method that records the summation of neuronal action potentials using electrodes attached to the scalp. The main neurons that contribute to EEG recordings are pyramidal neurons in the cortical layers two, three, and five. These pyramidal neurons make up most of the neurons in the brain (Elston, 2003). Furthermore, these neurons are oriented parallel to each other in the cortex. This mixed with the fact that their apical dendrites reach relatively far away into cortical layer one allows for a larger dipole during an action potential caused by synaptic transmission on these dendrites (Klein, 2006). When thousands of these neurons have action potentials in synchrony, they create a current that is conducted through the layers that surround the brain until it reaches the scalp (Nunez, 1981). Electrodes, fixed to the scalp with an elastic cap or glue, pick up these weak brain waves which are then amplified and recorded. However, EEG data can be noisy. Factors such as movement by the participant or current moving through wires in a room can contaminate the data.

The ERP method ameliorates many of the noise issues of EEG and allows for the isolation of activity related to a specific stimulus. This method involves repeating a stimulus presentation multiple times and averaging the EEG data recorded. The averaging of multiple trials cancels out random noise due to extraneous factors or brain activity not related to the event of interest. After averaging, the resulting data is known as an ERP. The ERP method has quickly become a staple of cognitive neuroscience because it allows noninvasive recording with great temporal resolution with a sampling rate of upwards of 1000Hz. This is incredibly fast compared to other methods such as fMRI which usually samples at a temporal resolution of 0.5Hz.

There are several limitations to the ERP method. ERPs have poor spatial resolution because as the current conducts toward the scalp it will inherently spread from the focal source. The folds that make up the brain also can affect the direction of conduction. These limitations with the ERP method contribute to the “inverse problem” in which many different neural sources could theoretically generate the same results. This problem can be lessened by careful research to eliminate alternative hypotheses and clever implementation of imaging methods with better spatial resolution such as fMRI or magnetoencephalography (MEG). Another limitation is that the numerous trials necessary to form an ERP, can mask habituation effects that could affect the validity of the results.

The Study of the Dimensional Model of Emotion and the LPP

Several popular theories aiming to explain emotion, argue emotion is organized along dimensional spectrums (Russell, 2003; Bradley, 2000). An influential model, sometimes referred to as the biphasic model of emotion, proposes that the two dimensions of valence and arousal organize emotion (Bradley, 2000a). The biphasic model of emotion was borne out by several studies that recorded peripheral and central neurophysiology (Bradley, 2000; Bradley & Lang, 2000). Much of this data was recorded using a scene presentation paradigm in which naturalistic emotional scenes theoretically engage emotional systems and reactions. By collecting self-reported emotional reactions to these scenes along the two bipolar dimensions of valence and arousal, researchers tried to understand how physiology changed with the ratings (Bradley et al., 2001). Often these studies utilized a standardized collection of scenes called the International Affective Picture System (IAPS; Lang, et al., 1997).

One of the earliest and most robust emotion ERPs studied using the IAPS was the Late Positive Potential (LPP; a variant of the P3b). The LPP can be observed as a positive deflection over midline parietal electrodes from 300ms after scene onset to scene offset. Extensive study of the LPP has found it will increase in positive amplitude to emotionally arousing scenes relative to neutral scenes. These findings suggest the LPP reflects motivated attention (Cuthbert et al., 2000; Schupp, 2007). Work using EEG and fMRI has implicated extrastriate cortical areas as well as limbic structures such as the amygdala and orbital frontal cortex as possible neural sources of the LPP (Sabatinelli et al., 2007; 2013). While self-reported feelings of arousal to scenes are loosely tided to LPP modulation, other work has shown specific content such as erotica and mutilation scenes modulate the LPP more than would be predicted by their arousal ratings (Weinberg & Hajcak, 2010). This may indicate that scenes depicting evolutionarily significant content (such as sexual opportunity and imminent threat) will have an outsized effect on the LPP despite reported participant arousal. The LPP also appears to be mostly driven by the arousing content and is relatively immune to scene complexity and color (Bradley, 2009; Miskovic et al., 2015).

Dimensional Emotion Model of the EPN

The EPN was first discovered and researched as a feature of motivated attention within the dimensional model of emotion (Junghöfer et al, 2001; Schupp, 2006a). The EPN is defined as a negative deflection occurring over posterior occipital areas starting around 150ms with a peak before 300ms (Schupp et al., 2004a). Topography, source localization, and convergent hemodynamic results indicate the source is most likely in lateral occipital cortices (Schupp et al., 2006b; Junghöfer et al., 2006). The EPN correlates with self-reported arousal to emotional scenes much like the LPP (Junghöfer et al., 2001). Furthermore, the EPN and LPP often correlate in studies of scene perception. The EPN appears to be immune to grayscale versus color scene presentation (Junghöfer et al., 2001). While the EPN was initially found to be elicited by emotional scenes relative to neutral, it can also be modulated by emotional faces (Schupp et al., 2004b), words (Kissler et al., 2007), and hand gestures (Flaisch et al., 2009) relative to perceptually similar neutral controls. However, a study in which an ERP that shares a similar topography and latency of the EPN, identified using spatial-temporal principal component analysis, was modulated more strongly by simple figure-ground scenes relative to complex scenes regardless of emotional self-reports (Bradley et al., 2007). This suggests that the EPN may be partially susceptible to the complexity of a scene, so stimuli should ideally be balanced for complexity through options such as JPEG files size (Donderi, 2006).

Theoretical Function of the EPN

An ERP known as a selection negativity (SN) may reflect a similar neural mechanism as the EPN. A SN is a diffuse negative deflection that begins around 160ms until 300ms over occipital-temporal areas like the EPN (Parasuraman et al., 1984). An SN occurs when participants are instructed to look a specific feature or object. Because the participant needs to be directed to look for a specific feature, it is also known as the early directing-attention negativity (EDAN). The negative deflection is best visualized by observing the difference between trials that featured the target stimuli versus those that did not. An SN can be found for various physical features such as spatial frequency (Martinez et al., 2001), color (Anllo-Vento et al. 1998), and movement (Valdes-Sosa et al., 1998). It has been found for participants looking for animals (Codispoti et al., 2006) as well as for faces and houses (Leuschow et al. 2004).

The SN appears to reflect activity in the ventral extrastriate cortices related to an early capture of attention by a stimulus. Positron emission tomography studies have shown that ventral areas specifically sensitive for the stimuli of interest are most involved in SN (Gazzaniga et al., 2002). For example, a participant looking for faces in a serial picture task may have extra activity in the fusiform gyrus which is known to be sensitive to faces from fMRI studies (Gazzaniga et al., 2002). Fahrenfort and colleagues (2007) presented evidence that an SN may represent “reentrant feedback” toward primary occipital areas vital for conscious perception. In a detection task, various square target figures made up of gradient patterns were presented for 16ms on half of the trials and then either masked with a different spatial frequency or weakly masked with a gray screen. They found that the mask made the target unperceivable with participants getting nearly 50% of the trials wrong when masked and 96.5% correct when unmasked. A Laplacian transform of the data revealed a positive feedforward activity occurring around 100ms on occipital temporal regions for all trials regardless of masking condition, while an SN was only found for unmasked trials. This may indicate that the SN reflects reentrant brain activity involved in early conscious awareness of relevant visual information.

Most research has studied the EPN under the assumption that it reflects early detection of emotionally relevant features possibly through a similar mechanism as the SN. This is because of the similarities in location and latency of the two potentials as well as the theoretical assumptions that they both represent early visual detection of something significant to the subject. Furthermore, the Fahrenfort (2007) findings that indicate the SN may represent a reentrant feedback fits with a prevailing theory that there are widespread reentrant effects in emotional scene perception (Frank & Sabatinelli, 2014; Keil et al., 2009; Lang, Bradley & Cuthbert, 1997; Sabatinelli et al., 2014; Vuilleumier & Driver, 2007). It has been theorized that the amygdala is the progenitor of a reentrant emotional modulation of ventral activity (Freese & Amaral, 2005; Amaral et al., 1992). If the theory is correct, the EPN may reflect an early sign of this reentrant feedback. In support of this possibility, intracranial recording of the amygdala in humans has observed discrimination of aversive scenes (Oya et al., 2002) and emotional faces (Murray et al., 2014) at 150 to 200ms, just prior to the EPN.

Specific Content Modulation of the EPN

Current research has scrutinized if specific scene content modulates the EPN differently. Four studies have reported an enhanced modulation for pleasant scenes over aversive (De Cesarei & Codispoti, 2006; Flaisch et al., 2008; Schupp et al., 2004a; Weinberg & Hajcak, 2010). However, many more studies have not found this bias (Sabatinelli et al., 2013). The studies that found a pleasure bias did not always control for the arousal ratings between categories. This makes it difficult to interpret the results because pleasantness self-reports were not independent of emotional arousal. However, a recent study investigating a pleasure bias of the EPN with complementary fMRI measures (Frank & Sabatinelli, 2019) found erotica and joy scenes (depicting content such as romantic couples and cute animals) modulated the EPN more than aversive mutilation scenes. A likely contributor to the EPN (lateral occipital cortex, measured with fMRI) was found to be similarly modulated in the same participants. Taken together, there is suggestive evidence in the literature that a pleasure bias can occur for the EPN.

There is also evidence for a more specific EPN bias for erotic and exposed body parts in scenes. Two studies by Schupp and colleagues (2006 & 2007) and one from Frank and Sabatinelli (2019) reported that erotica elicited a larger EPN than equivalently arousing mutilation scenes that also typically elicit the same magnitude of LPP amplitude. Furthermore, in our recent study that sought to isolate the effects of pleasantness versus body parts on the EPN, we found evidence body parts may be a potent modulator (Farkas, Oliver, & Sabatinelli, in revision). A summary of the results is presented in Figure 1. In the study, victorious sports scenes were rated as equivalently arousing as erotica, threatening people, and mutilation scenes were not able to match the amplitude of the EPN for erotica and were nearly equivalent to the modulation evoked by threat and mutilation scenes. This occurred even though the victory scenes were rated as more pleasant than those depicting erotic content. In the same study, nudist scenes elicited less self-reported arousal and pleasantness by participants, while modulating the EPN more so than the same erotic scenes that were compared to the victorious athlete scenes. However, the LPP was larger for erotic scenes than the nudist scenes which more closely aligned with the participants self-reported arousal.

An EPN sensitivity to unclothed bodies may be caused by a lateral occipital cortical area that is sensitive to the perception of body parts. Functional MRI studies have found an area of the lateral occipital cortex, coined the extrastriate body area (EBA), that is selectively activated by pictures of body parts (Downing et al., 2001; Peelen & Downing, 2007). The location of the EBA makes it a probable contributor to the EPN if visual information of body features, fed-forward by primary visual areas, activate this area within the EPN time window. Another line of research on the N170 ERP shows that nude bodies can greatly modulate this potential. The N170 is a negativity that peaks between 140-200ms over occipital temporal regions (generally more rostral then the EPN location) and is primarily studied as an integral process of forming a percept of facial stimuli (Bentin et al., 1996; Rossion et al., 2008). However, a research group has found robust N170 modulation using computer generated nude bodies relative to objects, faces, and clothed bodies (Hietanen et al., 2011; Hietanen et al., 2014; Alho et al., 2015). They found that along with the greater negative deflection, the N170 modulated by nude bodies had a more posterior topography and longer duration. It is possible that this extended and more posterior N170 could contribute to the EPN. However, in Hietanen et al. (2014) they treated the N170 and EPN as separate components that are differentially influenced by top down attention. Their research found both the EPN and N170 was greater for nude figures compared to clothed bodies and face stimuli. However, the EPN was more modulated when the participants were directed to attend more intensely to the stimuli, while target stimuli did not modulate the N170 than nontarget stimuli. Based on their findings that nude figures consistently modulate the N170, EPN, and LPP more that clothed figures and facial stimuli, this group proposes nude bodies have “privileged status” in the visual system that operates along a specialized brain network (Peelen & Downing, 2007; Minnebusch & Daum, 2009) that enhances processing and affective arousal (Hietanen et al., 2011; Hietanen et al., 2014).

Chapter 3

Methods

Sample

Fifty-seven participants were recruited from the University of Georgia student body and compensated with course credit. Seven participants were excluded from the sample after ERP preprocessing revealed excess movement leading to the loss of more than 50% of the trials from any scene category. Participants were between the ages of 18 to 26 (M = 19.7, SD = 1.40), with 28 identifying as female, and 22 as male. Participants were instructed not to sign up for the study if they were left-handed or a had a history of mental illness. All participants gave informed consent after receiving a form approved by the University of Georgia Human Subjects Institutional Review Board (IRB).

A separate 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 for 30 mins to 1 hour of work. Participants were presented with an informed consent document approved by the University of Georgia IRB. Mturk participants (n = 79) had to be from the United States and between the ages of 18 to 26. Seven participants consistently used the same number for every scene rating and were excluded from the sample. Two participants were extreme outliers and were excluded as well, leaving 70 in the final group.

Naturalistic Scenes

Nine categories of 135 naturalistic scenes were selected to best answer the research question of what modulates the EPN. We could partly predict how participants would rate the scenes because all scenes have been used in our lab for previous studies. A subset of the scenes was taken from the International Affective Picture System (IAPS; Lang, et al., 1997). Some scene categories are underrepresented in the IAPS, so additional scenes were found through internet searches. Scenes were 800 by 600 pixels and were kept or downgraded to 90% JPEG quality (https://JPEG.org). Luminance and complexity of the scenes were equivalent between categories as measure by an independent t-tests with p-values greater than 0.2. Scenes that were too bright or complex were edited with GNU Image Manipulation Program (GIMP, http://www.gimp.org/). Complexity was measured by the file size of the JPEG images at 90% quality, which has been reported as an accurate measure of complexity in human perception (Donderi, 2006). If a scene was too complex, a 1x1 pixel Gaussian blur was used, which has a negligible effect on perceived sharpness of the content.

The nine scene categories depicted erotica, pleasant animals, victorious athletes, nudists, neutral animals, neutral clothed people, threatening animals, threatening people, and mutilations. An example scene for each category can be seen if Figure 2. Erotica scenes depicted two attractive individuals (one male and one female) engaging in normative sexual activity. The pleasant animal category contained scenes of baby ducks, puppies, and kittens. Victorious athlete scenes depicted athletes expressing jubilation after winning a sports contest. Nudist scenes contained unclothed couples walking on beaches or parks and not engaging in sexual activity. The neutral animal category depicted animals deemed to be less cute, such as cows, squirrels, and chickens. The neutral people category depicted clothed people engaged in normal activities like sitting on busses or talking to each other. The threatening people category presented people with aggressive body positions and facial expressions while often brandishing weapons toward another person or the viewer. Some of these scenes depicted people harming others such as a man choking someone or a gunman with a woman hostage. Threatening animal scenes contain predators like wolves, jaguars, and snakes aggressively posturing or attacking the viewer. Mutilation scenes displayed graphic injuries of open wounds or disfigured body parts.

Figure 2. 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.

Scene categories were chosen to balance valence, arousal, as well as the specific contents of animals and body part exposure. Previous studies have shown that erotica, pleasant animals, and victorious athletes scenes elicit self-reports of pleasantness from participants, while threatening animals, threatening people, and mutilation scenes are self-reported as causing unpleasant feelings. Additionally, the neutral animals, neutral people, and nudist scenes have been reported as eliciting neither pleasant nor unpleasant feelings (Farkas et al., in revision). Previous studies have also found that the chosen pleasant and unpleasant categories elicit comparable high arousal self-reports than neutral categories. Category content was also 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 to the victorious athletes, neutral people, and threatening people categories which mostly contain clothed individuals. Additionally, the three animal categories allow for tests of valence and arousal ERP modulation effects independent of any human bodies being present in the scene.

Procedure

After informed consent, participants were brought into an electrically shielded chamber for EEG cap fitting. The 135 scenes were presented to each participant in a pseudorandom order. To keep scene categories evenly spread through the presentation order, scenes were arranged so that for every 18 scenes, two from each category were presented. Two different orders of the scene set were formed and assigned to each participant pseudorandomly. Each scene was presented for two seconds with an intertrial interval between 3.5 to 5.5 seconds. Scenes were presented on a Westinghouse 32-inch LCD monitor that occupies 31º of the horizontal visual field of view. After ERP data collection, the EEG cap was removed and participants were seated outside of the chamber in a quiet room. Here the participants self-reported their emotional reaction to each of the 135 scenes. Participants viewed a printed copy of each scene organized in a binder in another pseudorandom order. Participants were given a numbered worksheet to record their experienced valence and arousal.

Scene Self-reports

After ERP data collection, UGA participants self-reported how pleasant and aroused each scene made them feel on a 9-point scale using the Self-Assessment Manikin (SAM; Bradley & Lang, 1994). Participants were seated and read a slightly adjusted script from the initial SAM publication. Participants then viewed a printed version of each scene in a binder and recorded their responses on a worksheet. The worksheet had the SAM figures and scales with emotion nouns at the top of the page for participants to reference. Participants could use half increment values such as 1.5, 2.5, and so on.

To quantify if the additional scene features of body exposure and orientation, an online sample was recruited through Amazon Mechanical Turk (Mturk) to rate each scene on these dimensions. For this sample only the six human scene categories were used. Participants from the US and between the ages of 18-26 were able to click on the experiment to complete the task for $1.50 of compensation. Participants were instructed the study could last an hour, but most subjects finished around 30 minutes. Participants accessed the study through a Qualtrics link which presented the consent document and asked for their informed consent. If participants agreed to take part in the study, they began rating each scene by using a click and drag electronic scale that ranged from 1 to 9. Each scale was displayed one at a time underneath the scene the participant was self-reporting on. The marker started in the middle of the scale on the number 5, but participants had to click or 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., 1.0, 1.1,1.2). For the body exposure scale a written question asked, “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 asked participants, “How upright, or normally oriented are the people in the scene?” with the scale ranging from 1 upright to 9 unusually oriented. The scenes were presented in a pseudorandom order in a similar manner to how the scenes were organized for the UGA sample.

Quantifying Other Scene Features

To further identify if exposed body parts in scenes modulate the EPN, the sum of pixels containing exposed body parts was counted for each scene. Using GIMP, a transparent layer was made over each JPEG scene. On this layer, the lasso tool was used to trace around the exposed body parts in each scene. Body parts that were covered by clothes or accessories such as arm bands and sunglasses were not included. 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 in by the paint bucket tool. The sum of pixels containing exposed body parts for each scene could be compared because each scene was of equal size (800 by 600 pixels).

We also used JPEG file size and image-entropy to gauge the complexity of each scene. We included measures of complexity because previous studies have found evidence that the EPN could be modulated by the simplicity of a scene (Bradley et al., 2007). Although scene categories were altered to be statistically equivalent in JPEG file size as a straightforward means of controlling for complexity, the process of quantifying scene complexity is quite complicated and beyond the scope of this study (Donderi, 2006). However, to expand our assessment of scene complexity somewhat, entropy was also calculated for each scene. Also known as the Shannon information-entropy, this measure is found by using the first order histogram frequencies of grey values as probabilities. If every grey value is equally likely to occur, entropy is maximized, and if the scene contains only one color then entropy is minimized. Entropy values were found using the Matlab function “entropy”.

EEG Data Acquisition and Reduction

Continuous EEG data was recorded using a 64-channel BioSemi ActiveTwo system (BioSemi Amsterdam, Netherlands) which has pre-amplified electrodes positioned according to the 10/20 system. The electrode voltage was referenced to two additional common mode electrodes (CMS and DRL). The sampling rate was 512hz. The acquisition software (ActiView; actiview.org) was used to keep offsets between 50 to -50 millivolts during EEG set up and to monitor online data acquisition.

Offline, EEG data was preprocessed and segmented using the Electro Magnetic Encephalography Software (EMEGS; emegs.org; Peyk, De Cesarei, & Junghöfer, 2011) analysis package for MATLAB (Mathworks.com). Data was processed in close accordance with the guidelines of Junghöfer and colleagues (2000) through a method known as SCADS: statistical correction of artifacts in dense array studies. The data was adjusted using a low-pass Butterworth filter with a stopband of 40Hz and a passband of 30Hz to control for high frequency noise. A high-pass Butterworth filter was also implemented with a passband of 0.1Hz and stopband of 0.05Hz. Eye blinks were corrected in EMEGs by implementing the BIOSIG Matalb toolbox. Data were segmented from 100ms before scene onset to the scene's offset which occurred after 2000ms. The 100ms of data before scene onset was used to baseline the ERPs. Sensors and trials were screened for voltage artifacts that were unlikely to have occurred because of neural activity. These artifacts were found 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 was 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. Previous work has shown the spline interpolation can accurately replace missing data by purposely implementing the process on electrodes that were not actually missing (Junghöfer, et al., 2000). The data was kept in an average-reference which allows for easier visualization of the EPN which can be difficult to see with other references such as the mastoid reference (Junghöfer, et al., 2006).

After data were preprocessed, the ERPs for each participant were extracted for each scene and an averaged was calculated for each category. A participant was excluded if 50% of trials from a category were lost during the preprocessing due to artifacts. Seven participants were excluded for this reason. Electrodes and extraction times were kept the same as our previous study that used a similar scene presentation procedure (Farkas et al., in revision). The EPN was measured by extracting voltage from the lateral-posterior electrodes P7, PO7, O1, P8, PO8, and O2 from 150 to 300ms after scene onset (Figure 3). The LPP was recorded over midline parietal electrodes Cz, CPz, Pz, CP1, and CP2 from 400 to 900ms.

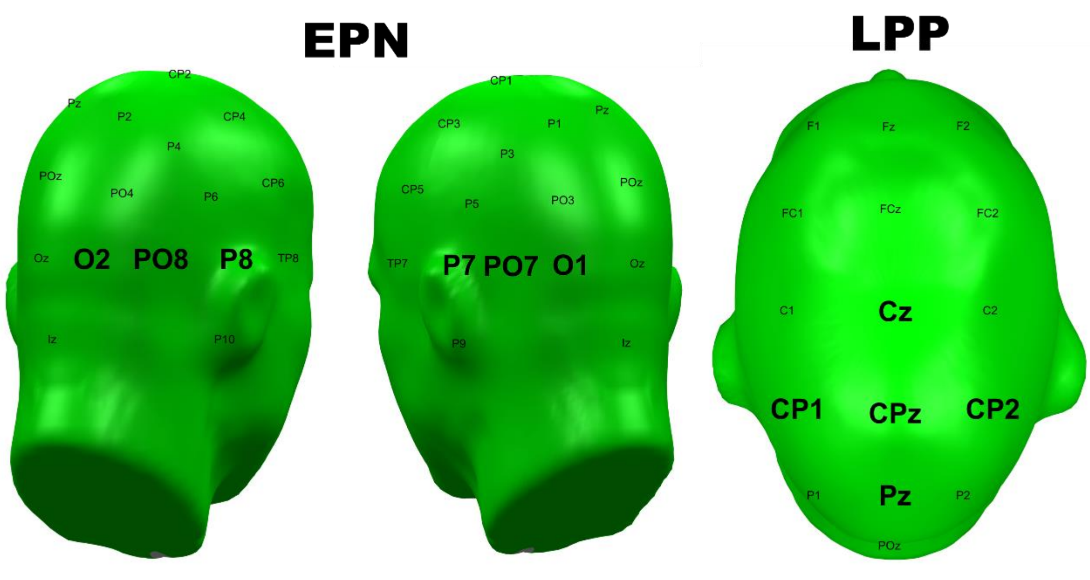


Figure 3. EPN and LPP electrode electrodes. Computer generated heads showing the electrode locations for the EPN and LPP. Bold letters indicate the electrodes where data was sampled. The EPN figures show views of posterior areas sampled. The LPP figure shows a top-down view of the head with the nose at the top of the page.

For data visualization purposes, the EPN and LPP were also transformed into z-score values for each participant (Appendix B). Thus, each participant's EPN values for each category were centered around zero with a standard deviation of one. This was also performed for the LPP (Appendix D). In ERP research, the difference from a modulatory amplitude and a participant's pre-stimulus baseline may differ between participants because of confounding factors such as skin density, hydration, or skull shape. Z-scoring allows for the between-subject category ERP differences to be minimized. To illustrate the robust within-subject effects, we present a line plot of each participants ERPs (Appendix A & C). Additional boxplots of z-scored ERP data are included to show the range of reactivity (Appendix B & D). Although the category differences look more striking in the z-scored boxplots as compared to the raw data boxplots (Figure 8 & 9), statistical tests for the differences between categories are consistent and thus are not reported. The statistical tests are similar because the within-subject variation is accounted for when using repeated measure ANOVAs and paired t-tests.

Statistical Procedures

Category differences for valence, arousal, rated body exposure, rated body orientation, EPN modulation, and LPP modulation were quantified by a repeated measure ANOVA and followed by paired t-tests to assess which categories were different. The software R (r-project.org) was also used to do an exploratory data analysis of correlation values between scene features and ERP modulation. Using the R function "pairs", a pairwise scatter plot figure was formed for scenes on the dimensions of EPN modulation, LPP modulation, valence, arousal, rated body exposure, rated body orientation, number of pixels of body exposure, size of JPEG file, and entropy. The “rcorr” function in the R Hmisc package was used to calculate Pearson’s R values for each association and the subsequent p-values (Harrell & Dupont, 2019). Only correlations between the EPN and the LPP with the independent variables related to our hypotheses for the study (valence, arousal, human scenes vs animal scenes, body exposure, and body orientation) are reported in the results section. However, Figures 10 and 11 display plots of all correlation possibilities and their associated statistical values can be seen in Tables 1 through 4.

To ultimately see which combination of scene features predicted EPN and LPP modulation, a best subset selection was implemented using the regsubsets function contained in the leaps package (Lumley, 2017). The algorithm performs an exhaustive search of every possible combination of independent variables to find the most predictive multiple regression for the desired dependent variable. The best subset selection was run twice on the 135 scene data set with one predicting the EPN and the other predicting the LPP with self-reported valence, arousal, a dummy coded variable indicating if a scene depicted humans or animals, JPEG file size, and entropy. Each multiple regression equation is then ranked based on Bayesian information criteria (BIC). Information criteria methods aim to balance the goodness of model fit while minimizing the complexity of the model. Models that use too many predictor variables are more likely to overfit to data used to form its parameters causing it to lose external validity and accuracy. BIC returns a value based on goodness of fit and a penalty term based on the number of observations and the number of predictors chosen. Lower BIC values indicate a well fit model that is relatively simple. Here we report the best simple regression model and multiple regression model based on BIC for the EPN and LPP for the complete 135 scene set and 90 human scenes. However, Appendix E through H display the complete residual sum of squares, R squared, BIC, and brick plots from the regsubsets function.

Chapter 4

Results

Self-reports Results by Scene Category

Self-reported valence was different between at least 2 of the 9 scene categories as found by a repeated measures ANOVA ($F(8,392) = 137.808$, $p < 0.001$; $\eta 2 = 0.738$). Figure 4 depicts a boxplot with an overlaid strip plot illustrating the distribution of the 50 UGA participants. Pleasant animal scenes elicited the most pleasant feelings ($M = 8.09$, $SE = 0.16$), and was different than the second most pleasant category of victorious athlete scenes ($M = 7.02$, $SE = 0.18$; $t(49) = 7.28$, $p < 0.001$, $d = 1.03$). Victorious athlete scenes elicited more pleasantness than the neutral animal category ($M = 5.86$, $SE = 0.10$; $t(49) = 6.48$, $p < 0.001$, $d = 0.92$). However, neutral animal scenes evoked equivalent pleasantness as the erotica scenes ($M = 5.64$, $SE = 0.24$). Erotic scenes made participants feel more pleasant that neutral people scenes ($M = 5.03$, $SE = 0.48$; $t(49) = 2.43$, $p = 0.019$, $d = 0.34$). Participants felt equivalently pleasant when viewing neutral people scenes as compared to nudist scenes ($M = 4.80$, $SE = 0.15$). Nudist scenes elicited less intense negative feelings than threatening animal scenes ($M = 4.27$, $SE = .15$; $t(49) = 2.77$, $p = 0.008$, $d = 0.39$). However, the threatening animals did not match the stronger unpleasant feelings of threatening people scenes ($M = 2.90$, $SE = 0.14$; $t(49) = 9.78$, $p < 0.001$, $d = 1.38$). Finally, mutilation scenes ($M = 2.40$, $SE = 0.18$) elicited the most unpleasant feelings even when compared to the second most unpleasant category of threatening people ($t(49) = 2.98$, $p =$, $d = 0.42$).

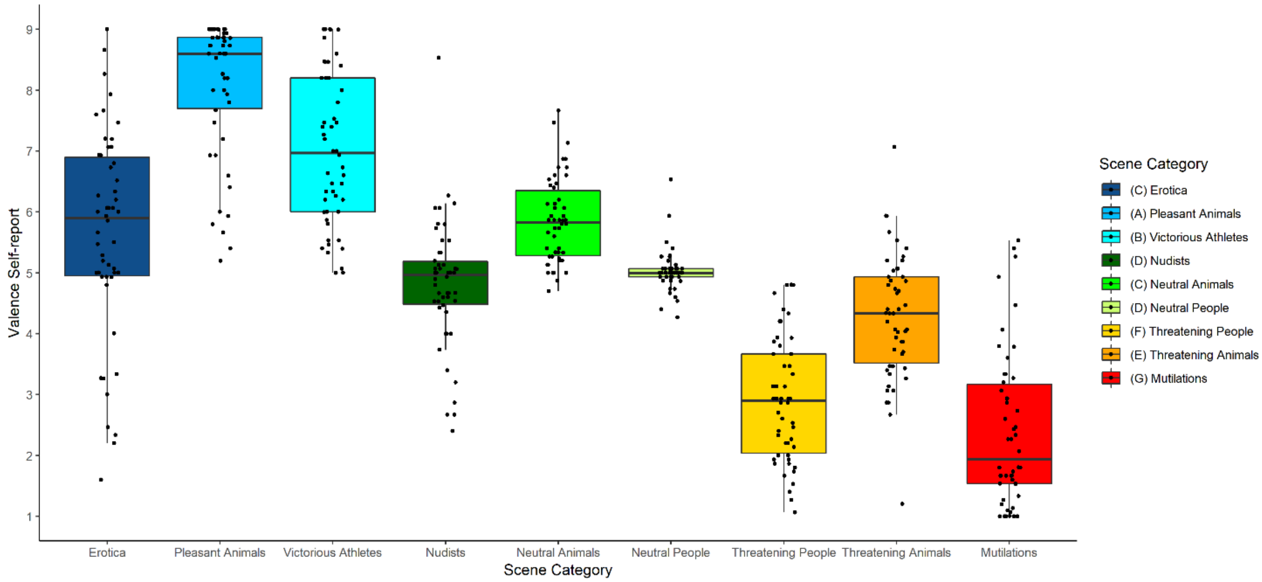


Figure 4. Valence self-reports by scene category. Each color represents a different scene category. Each black dot indicates one of the participant self-report for that scene category. Boxplots show information about the distribution of ratings for each scene. The line in the middle of each boxplot is the median self-report. Each end of the box indicates the inner quartile of the distribution. Outer whisker represent data within 1.5 times the inner and outer quartiles. Dots outside of the whisker can be considered an outlier. In the legend, letters next to each scene category indicate which groups are statistically equivalent. If a category shares a letter, they are not different. The letter "A" indicates the greatest category.

A repeated measures ANOVA was significant for the self-reports of experienced arousal between the nine scene categories ($F(8,392) = 25.021$, $p < 0.001$; $\eta 2 = 0.338$). A boxplot of the arousal ratings can be seen in Figure 3. Erotica scenes ($M = 6.52$, $SE = 0.20$) elicited the most arousal, but were statistically equivalent to the arousal experienced when viewing mutilation scenes ($M = 6.15$, $SE = 0.30$). Erotica scenes elicited more arousal than threatening animal scenes ($M = 6.03$, $SE = 0.18$; $t(49) = 2.51$, $p = 0.016$, $d = 0.35$), threatening people scenes ($M = 5.97$, $SE = 0.20$; $t(49) = 2.23$, $p = 0.030$, $d = 0.32$), and victorious athlete scenes ($M = 5.86$, $SE = 0.24$; $t(49) = 2.49$, $p = 0.016$, $d = 0.35$). However, the mutilation, threatening animals, threatening people, and victorious athletes scenes all elicited equivalent arousal in participants. Pleasant animal scenes ($M = 4.97$, $SE = 0.33$) evoked less arousal than victorious athlete scenes ($t(49) = 2.33$, $p = 0.024$, $d = 0.33$), but were equivalently arousing as nudist scenes ($M = 4.76$, $SE = 0.15$). Nudist scenes elicited more arousal than neutral animal scenes ($M = 4.07$, $SE = 0.18$, $t(49) = 3.39$, $p = 0.001$, $d = 0.48$). Lastly, participants reported neutral animal scenes were more arousing than the final category of neutral people scenes ($M = 3.80$, $SE = 0.17$; $t(49) = 2.45$, $p = 0.018$, $d = 0.35$).

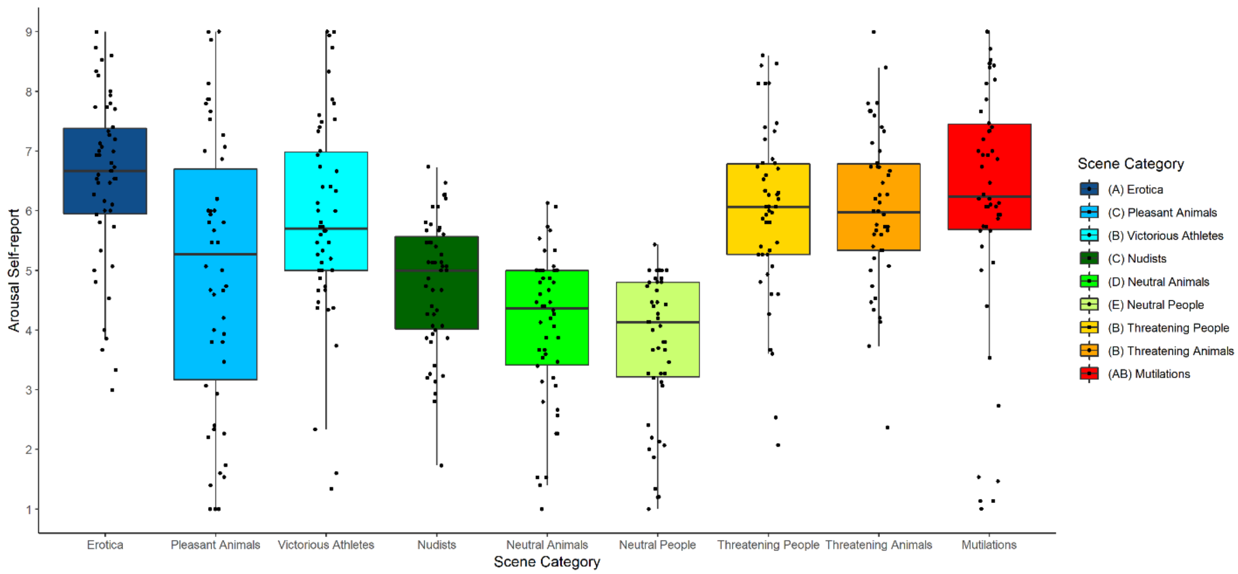


Figure 5. Arousal self-reports by scene category.

The Mturk sample reported the six human scene categories had a different amount of exposed body parts as found through a repeated measures ANOVA ($F(5, 345) = 857.16$, $p < 0.001$; $\eta 2 = 0.925$). Mturk ratings of body exposure and body orientation data can be seen in the corresponding boxplots (Figure 6 & 7). The nudist category ($M = 8.75$, $SE = 0.04$) was perceived as having the most exposed body parts and were significantly different than erotic scenes ($M = 8.48$, $SE = 0.05$; $t(69) = 6.30$, $p < 0.001$, $d = 0.75$). Erotic scenes were perceived as having more exposed body parts than mutilation scenes ($M = 6.30$, $SE = 0.21$; $t(69) = 10.93$, $p < 0.001$, $d = 1.31$). Participants felt mutilation scenes had more body part exposure than victorious athlete scenes ($M = 3.85$, $SE = 0.13$; $t(69) = 12.25$, $p < 0.001$, $d =1.46$). In turn, victorious athlete scenes were rated as including less exposed body than threatening people scenes ($M = 2.17$, $SE = 0.09$; $t(69) = 19.30$, $p < 0.001$, $d = 2.31$). Threatening people scenes were reported as more clothed then the final category of neutral people ($M = 1.88$, $SE = 0.10$; $t(69) = 6.51$, $p < 0.001$, $d = 0.78$).

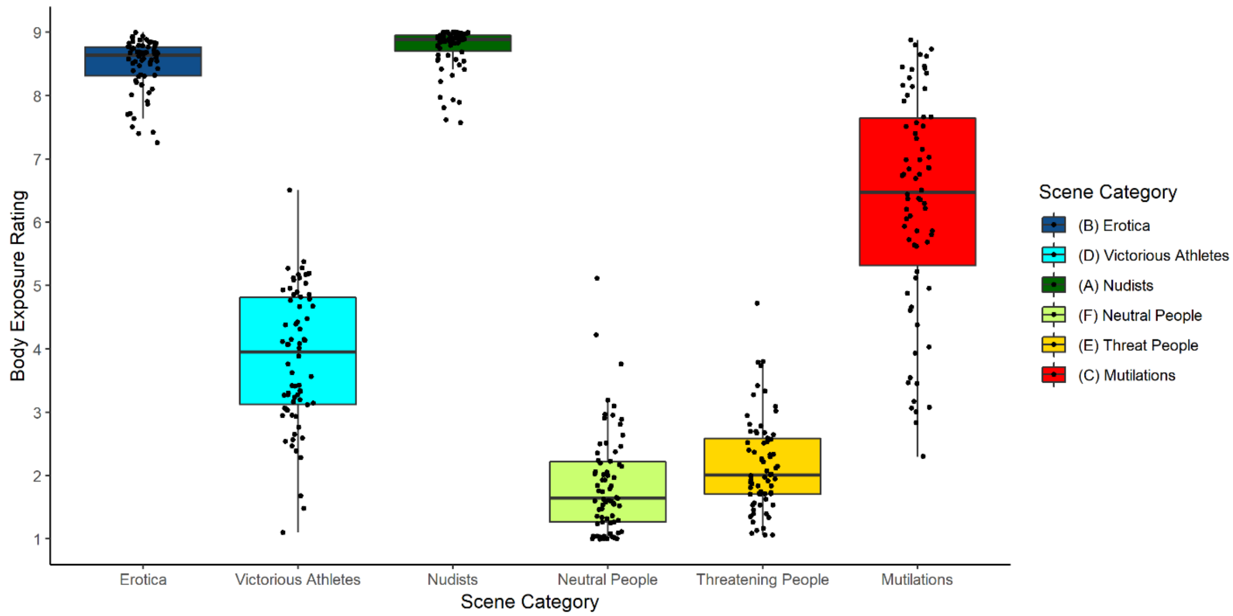


Figure 6. Body exposure self-reports by scene category.

Mturk reports of body orientation were different between scene categories ($F(5,345) = 167.66$, $p < 0.001$, $\eta 2 = 0.708$). Participants rated the nudist category (M = 7.79, SE = 0.21) as having the most normally oriented depicted people, but the nudists scenes were statistically equivalent to the second highest rated category of victorious athletes (M = 7.51, SE = 0.15). Nudist scenes were more normally oriented than neutral people scenes (M = 7.30, SE = 0.13; $t(69) = 2.16$, $p = 0.034$, $d = 0.26$), but victorious athlete scenes were rated as just as normally oriented as the neutral people category. The neutral people were more normally oriented than the threatening people scenes (M = 5.99, SE = 0.25; $t(69) = 5.26$, $p < 0.001$, $d = 0.63$). The threatening people category was rated higher than the erotic scenes (M = 3.63, SE = .20; $t(69) = 7.77$, $p < 0.001$, $d = 0.93$). Finally, the erotic scenes were reported as less unusually oriented as the people in the mutilation scenes (M = 3.21, SE = 0.14; $t(69) = 2.18$, $p = 0.033$, $d = 0.26$).

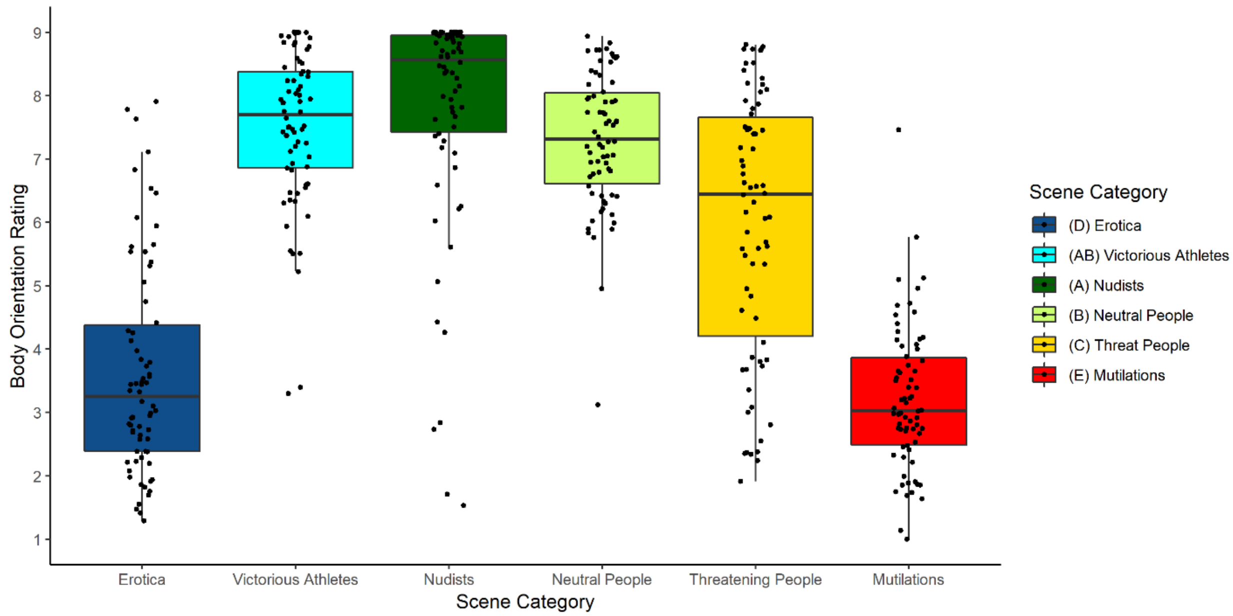


Figure 7. Body exposure self-reports by scene category.

EPN and LPP Results by Scene Category

A repeated measure ANOVA found significance for EPN modulation for the nine scene categories ($F(8,392) = 55.658$, $p < 0.001$; $\eta 2 = 0.532$). EPN category waveform and boxplot results can be seen in Figure 8. As stated in the methods section, a z-score boxplot figure is also shown in Appendix B. The z-scored data highlights the consistent pattern of modulation of the EPN and LPP within each participant, however the inferential statistics are similar so only statistical test results for raw ERPs are reported here. Nudist scenes (M = 2.54µV, SE = 0.64) modulated the EPN the most and was significantly different than modulation evoked by erotic scenes (M = 3.93µV, SE = 0.68; $t(49) = 4.41$, $p < 0.001$, $d = 0.62$). EPN modulation from erotic scenes was greater than modulation elicited by victorious athletes (M = 6.89µV, SE = 0.58; $t(49) = 8.00$, $p < 0.001$, $d = 1.13$), threatening animals (M = 6.91µV, SE = 0.64; $t(49) = -7.50$, $p < 0.001$, $d = 1.06$), and threatening people scenes (M = 7.11µV, SE = 0.60; $t(49) = 8.59$,$p < 0.001$, $d = 1.21$). However, the three categories of victorious athletes, threatening animals, and threatening people all modulated the EPN equivalently. Pleasant animal scenes (M = 7.82µV, SE = 0.57) modulated the EPN less than victorious athlete scenes ($t(49) = 2.61$, $p = 0.012$, $d = 0.37$) and the threatening animal scenes ($t(49) = 2.54$, $p = 0.014$, $d = 0.36$). However, the pleasant animal, threatening people, and mutilation scenes (M = 7.97µV, SE = 0.63) all modulated the EPN to a statistically equivalent amplitude. Mutilation scenes modulated the EPN more than neutral animals (M = 8.87µV, SE = 0.62; $t(49) = 2.34$, $p = 0.023$, $d = 0.33$) and neutral people scenes (M = 9.08µV, SE = 0.58; $t(49) = 2.45$, $p = 0.018$, $d = 0.35$). Neutral animal and neutral people scenes elicited equivalent EPN modulation.

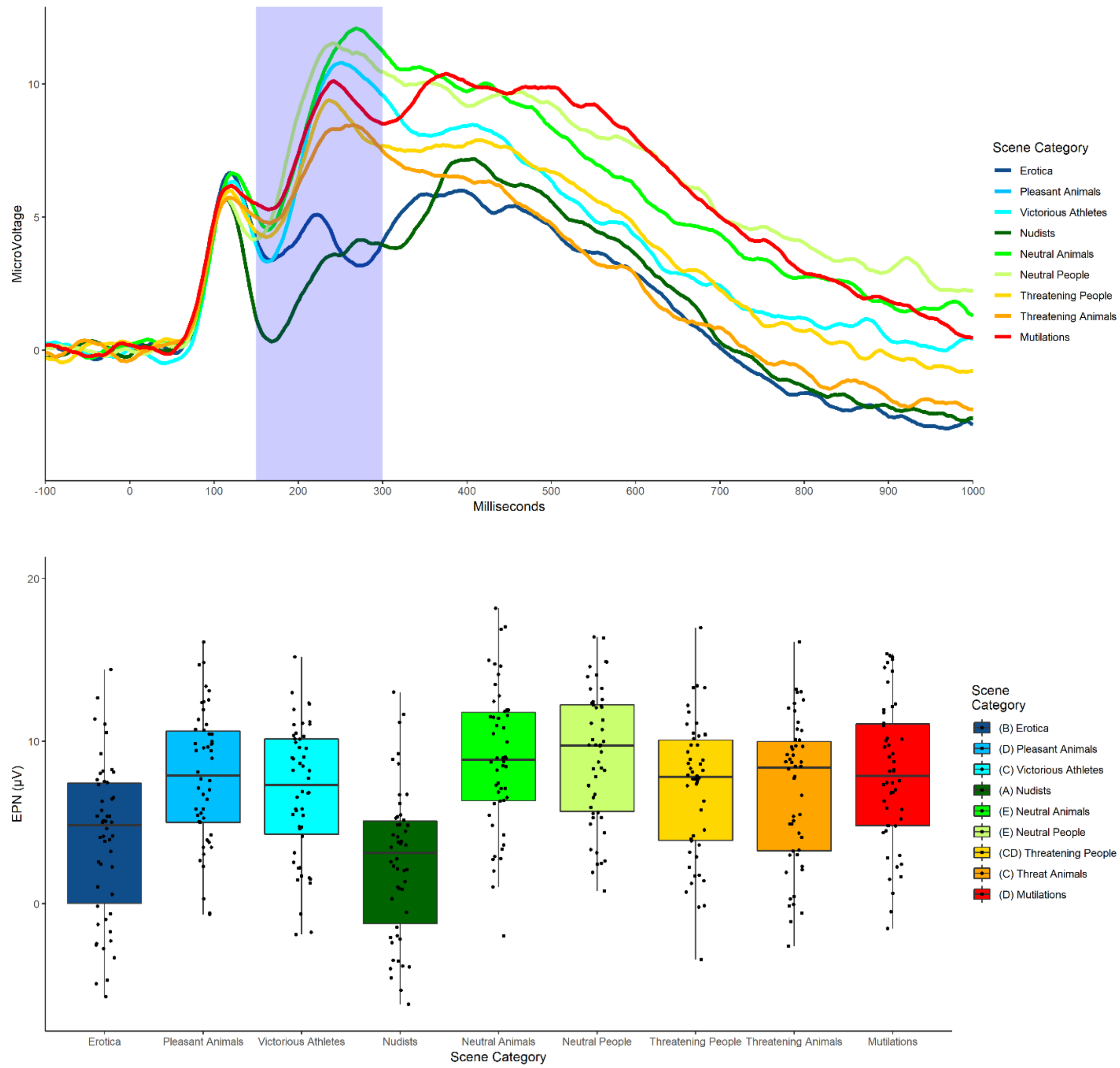


Figure 8. EPN waveform and results by category. Top figure depicts the average waveforms of EPN electrodes for each category. The transparent blue rectangle represents where the EPN was extracted (150-300ms). The bottom figure is the results from each participant's modulated EPN amplitude by scene category.

A repeated measure ANOVA found a difference in LPP modulation for the nine scene categories ($F(8,392) = 46.751$, $p < 0.001$; $\eta 2 = 0.488$). LPP category results can be seen in Figure 9. Erotic scenes modulated the LPP the most ($M = 4.96\mu V$, $SE = 0.43$). LPP modulation by erotic scenes was greater than the next most potent scene category of nudists ($M = 3.06\mu V$, $SE = 0.44$; $t(49) = 6.11$, $p < 0.001$, $d = 0.86$). Nudists scenes modulated the LPP more than mutilation ($M = 1.93\mu V$, $SE = 0.44$; $t(49) = 2.94$, $p = 0.005$, $d = 0.42$) and threatening animal scenes ($M = 1.56\mu V$, $SE = 0.36$; $t(49) = 3.21$, $p = 0.002$, $d = 0.45$). However, mutilation and threatening animal scenes statistically elicited the same LPP amplitude. Mutilation scenes evoked more LPP modulation than threatening people scenes ($M = 1.07\mu V$, $SE = 0.34$; $t(49) = 2.85$, $p = 0.006$, $d = 0.40$) and pleasant animals scenes ($M = 1.03\mu V$, $SE = 0.24$; $t(49) = 2.14$, $p = 0.037$, $d = 0.30$). Threatening animal modulation was equivalent to the modulation of threatening people and pleasant animal categories. Neutral animal scenes ($M = 0.47\mu V$, $SE = 0.34$) elicited less LPP modulation than the threatening animal scenes ($t(49) = 2.82$, $p = 0.007$, $d = 040$), but the neutral animals elicited statistically equivalent modulation as threatening people and happy animal scenes. Victorious athlete scenes ($M = 0.40\mu V$, $SE = 0.30$) modulated the LPP less than threatening people ($t(49) = 2.15$, $p = 0.37$, $d = 0.30$) and threatening animal scenes ($t(49) = 3.29$, $p = 0.002$, $d = 0.46$), while the victorious athlete scenes were equivalent to modulation by neutral animal scenes. Neutral people scenes ($M = -1.54\mu V$, $SE = 0.26$) modulated the LPP less than all other categories including the next closest category of victorious athletes ($t(49) = 7.30$, $p < 0.001$, $d = 1.03$).

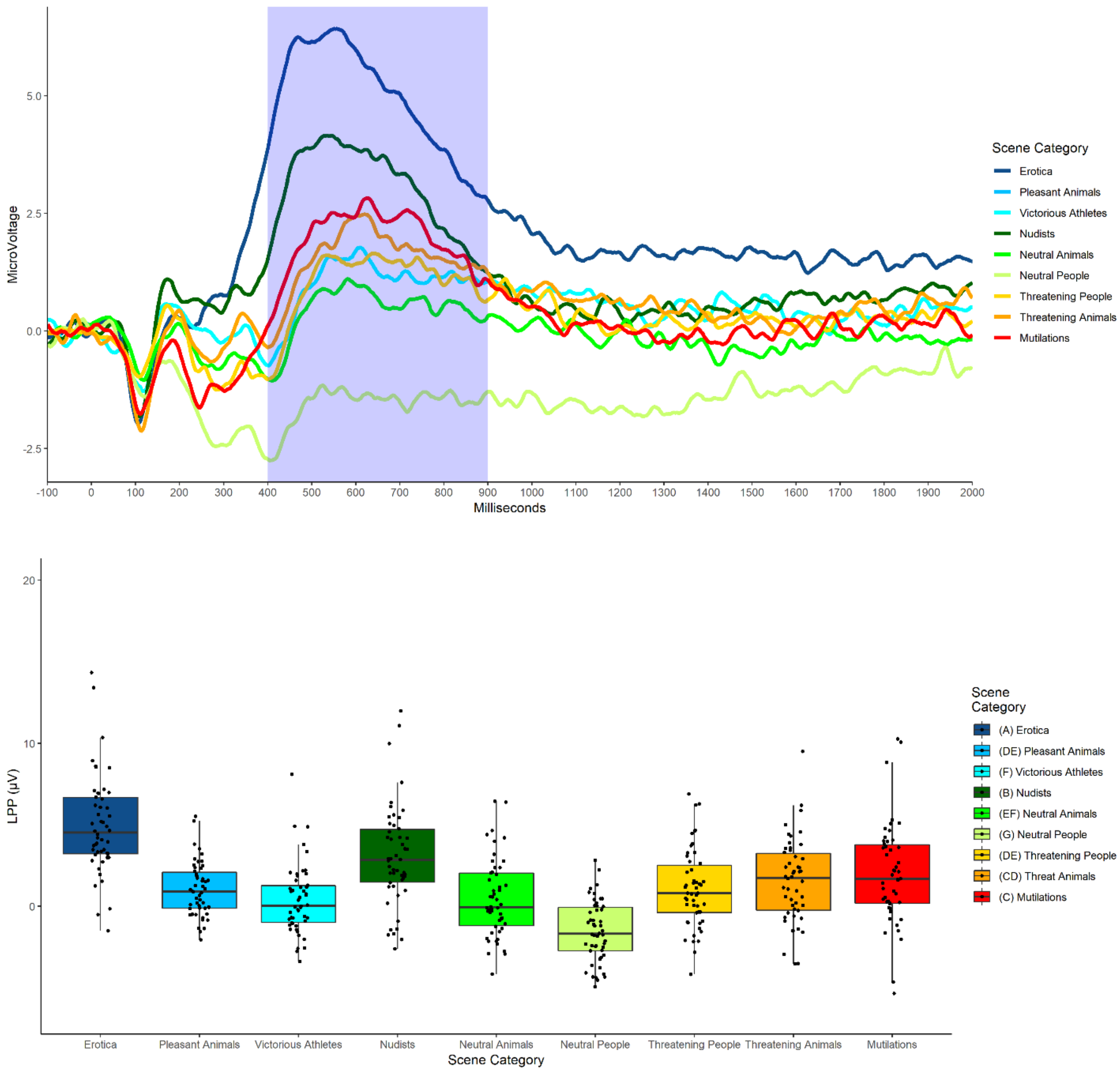


Figure 9. LPP waveform and results by category. The top figure is the average waveform of the LPP electrodes by category. The transparent blue rectangle represents where the was extracted LPP (400-900ms). The bottom figure is the results from each participant's modulated LPP amplitude by scene category.

Scene Correlations

For the complete 135 scene set, the independent variables of interest were correlated with the EPN and LPP. A complete pairwise scatter plot of all correlations can be seen in Figures 10 and 11 with associated Pearson R and p-values in Tables 1 through 4. For the EPN modulation, there was no association for scene valence ($r = 0.04$, $p = 0.62$). There was a greater EPN modulation for scenes that induced higher self-reported arousal ($r = -0.25$, $p = 0.003$). For this scene set, human scenes ($M = 6.23$, $SE = 0.29$) predicted more EPN modulation through an independent t-test than animal scenes ($M = 7.81$, $SE = 0.26$, $t(133)$, $p = 0.001$, $d = 0.69$). This was also true for a statistically equivalent correlation using a dummy coded variable indicating if the scene depicted people or animals ($r = -0.29$, $p = 0.001$). For the LPP, valence did not predict modulation strength ($r = -012$, $p = 0.17$). More arousing scenes did have increased LPP modulation ($r = 0.51$, $p < 0.001$). Human scenes did not have greater LPP modulation than animal scenes as measured with an independent t-test ($t(133) = -1.73$, $p = 0.086$, $d = 0.34$) or a correlation with a dummy coded categorical variable ($r = 0.15$, $p = 0.086$).

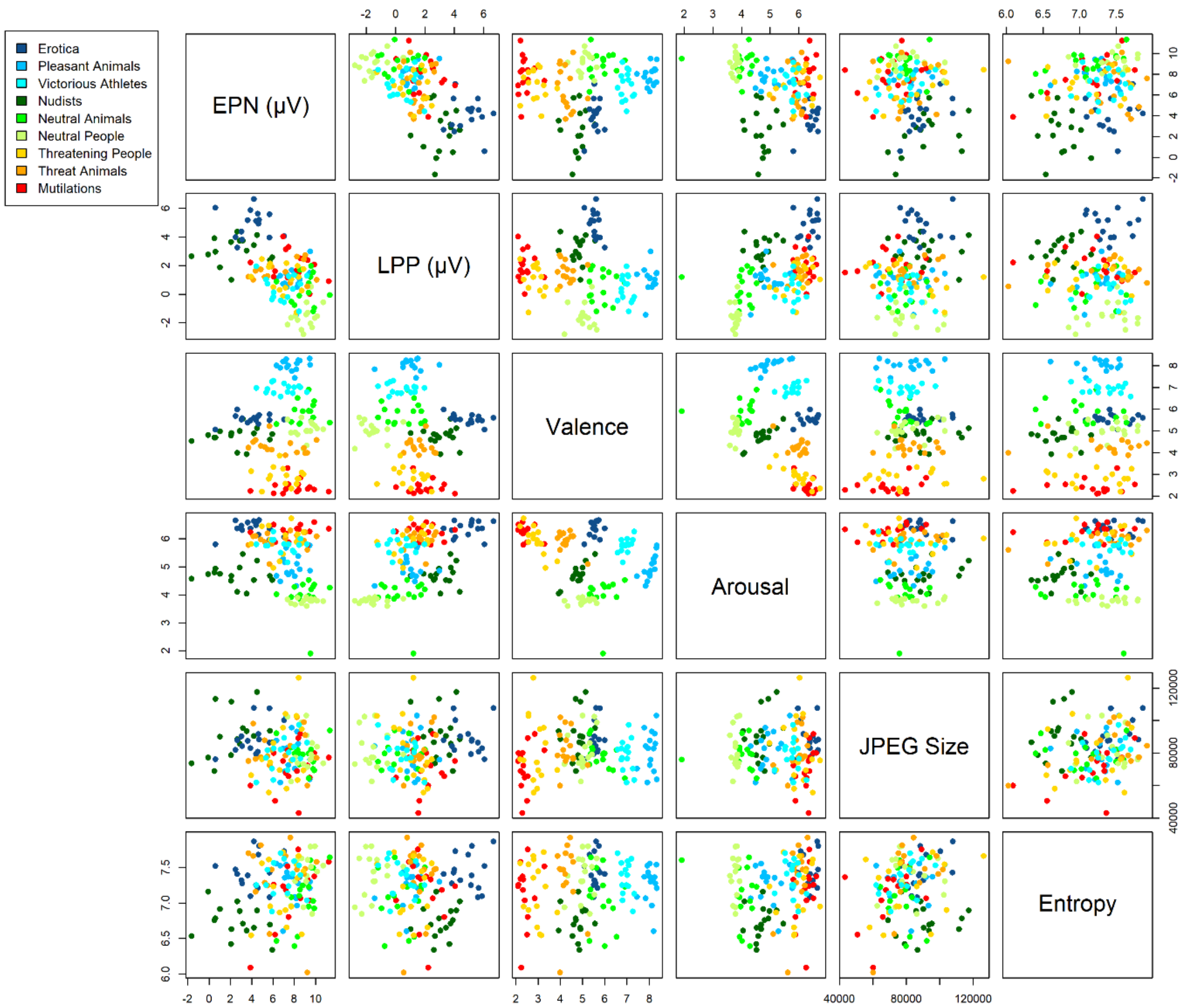


Figure 10. Pair-wise scatter plot for all 135 scenes. Colors indicate the scene category. The Diagonal indicates the variable. For each row, the variable in that row acts as the dependent variable and is the y-axis. For each column, the variable acts as the independent x-axis.

Table 1 & 2. Correlation results from the complete 135 scene set. The top table shows Pearson R values. The bottom table shows the association's p-value.

	EPN	LPP	Human Content	Valence	Arousal	JPEG Size	Entropy
EPN	1.0000000	-0.5861948	-0.2912606	0.0425978	-0.2498056	-0.1270419	0.2536429
LPP	-0.5861948	1.0000000	0.1482225	-0.1200974	0.5117314	0.1115902	-0.0629057
Human Content	-0.2912606	0.1482225	1.0000000	-0.3989289	0.2368289	0.0438778	-0.0412778
Valence	0.0425978	-0.1200974	-0.3989289	1.0000000	-0.3049697	0.0982664	0.0963144
Arousal	-0.2498056	0.5117314	0.2368289	-0.3049697	1.0000000	-0.0188942	0.1632641
JPEG Size	-0.1270419	0.1115902	0.0438778	0.0982664	-0.0188942	1.0000000	0.1602162
Entropy	0.2536429	-0.0629057	-0.0412778	0.0963144	0.1632641	0.1602162	1.0000000

	EPN	LPP	Human Content	Valence	Arousal	JPEG Size	Entropy
EPN	NA	0.0000000	0.0006096	0.6237361	0.0034783	0.1420162	0.0029939
LPP	0.0000000	NA	0.0862233	0.1653023	0.0000000	0.1975608	0.4685628
Human Content	0.0006096	0.0862233	NA	0.0000016	0.0056823	0.6133368	0.6345393
Valence	0.6237361	0.1653023	0.0000016	NA	0.0003225	0.2568440	0.2664599
Arousal	0.0034783	0.0000000	0.0056823	0.0003225	NA	0.8278123	0.0584866
JPEG Size	0.1420162	0.1975608	0.6133368	0.2568440	0.8278123	NA	0.0634189
Entropy	0.0029939	0.4685628	0.6345393	0.2664599	0.0584866	0.0634189	NA

We performed the same process on the 90 human scenes and incorporated our Mturk self-reports of body exposure, body orientation, as well as the sum of pixel in each scene that contained exposed body parts. Valence did not predict the scene modulation of the EPN ($r = 0.04$, $p = 0.62$). The EPN modulation was associated with more arousing human scenes ($r = -0.24$, $p = 0.003$). The higher sums of pixels that contained exposed body parts strongly predicted more EPN modulation ($r = -0.42$, $p < 0.001$). Mturk ratings of more body exposure strongly predicted EPN modulation ($r = -0.66$, $p < 0.001$). Mturk ratings of body orientation did not predict EPN modulation ($r = -0.05$, $p = 0.67$). For the LPP modulation, valence did not predict the LPP amplitude for human scenes ($r = -0.12$, $p = 0.17$). Arousal did have a positive association with the LPP amplitude ($r = 0.51$, $p < 0.001$). Scenes with a higher sum of pixels containing exposed body parts had more LPP modulation ($r = 0.53$, $p < 0.001$) . Mturk ratings of more exposed body parts also predicted a larger LPP amplitude ($r = 0.79$, $p < 0.001$). In contrast to the EPN, less normally oriented bodies had more LPP modulation ($r = -0.46$, $p < 0.001$).

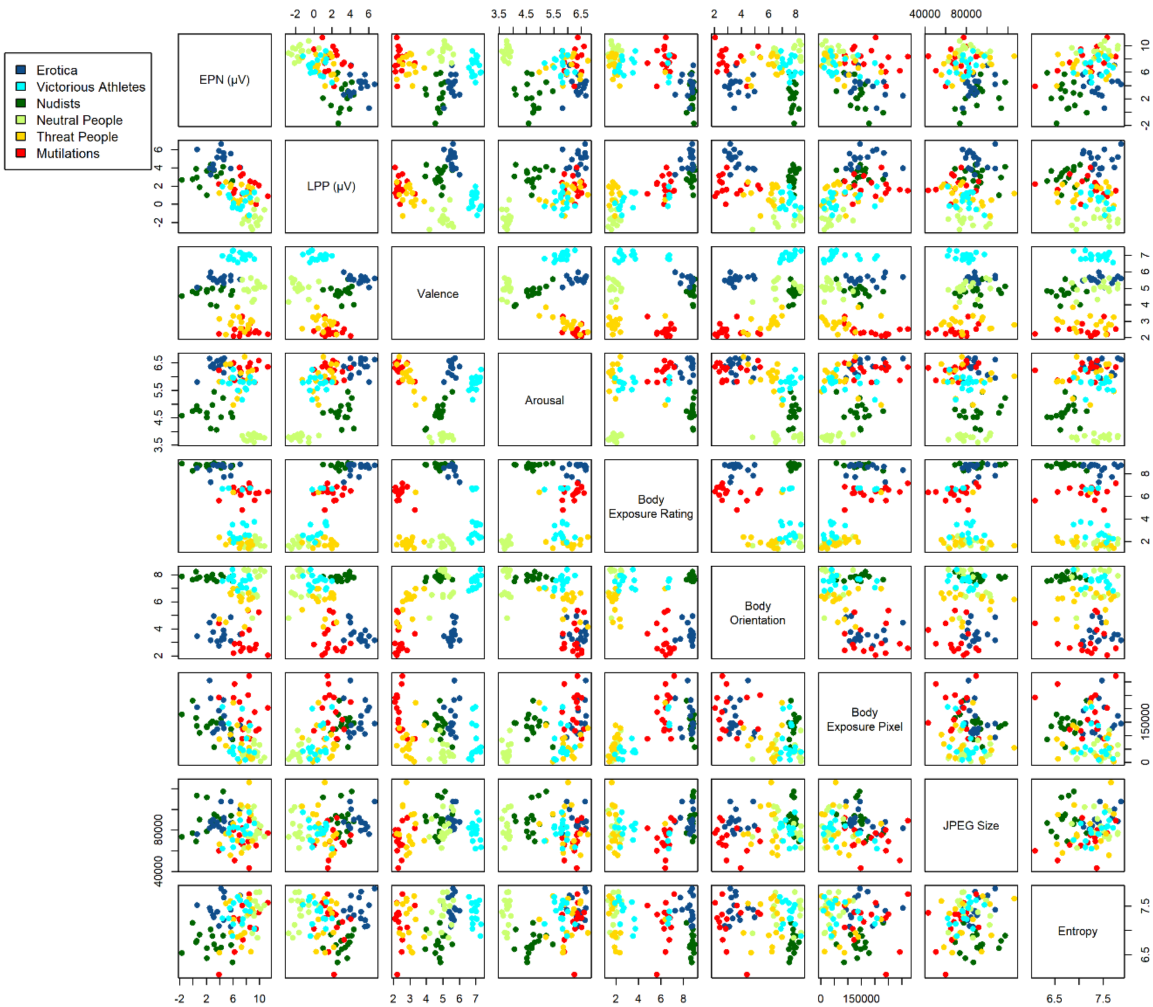


Figure 11. Pairwise scatter plot for the 90 human scenes.

Table 3 & 4. Correlation results for the 90 human scenes. The top table shows Pearson R values. The bottom table shows the association's p-value.

	EPN	LPP	Valence	Arousal	Body Exposure Rating	Body Orientation	Body Exposure Pixels	JPEG File	Entropy
EPN	1.0000000	-0.5861948	0.0425978	-0.2498056	-0.6585593	-0.0459757	-0.4222731	-0.1270419	0.2536430
LPP	-0.5861948	1.0000000	-0.1200974	0.5117314	0.7898256	-0.4616126	0.5274244	0.1115902	-0.0629056
Valence	0.0425978	-0.1200974	1.0000000	-0.3049698	0.0637156	0.4569896	-0.2379656	0.0982664	0.0963144
Arousal	-0.2498056	0.5117314	-0.3049698	1.0000000	0.2678885	-0.6420979	0.3640382	-0.0188942	0.1632642
Body Exposure Rating	-0.6585593	0.7898256	0.0637156	0.2678885	1.0000000	-0.3031154	0.6839297	0.1629133	-0.2666624
Body Orientation	-0.0459757	-0.4616126	0.4569896	-0.6420979	-0.3031154	1.0000000	-0.4645934	0.0899124	-0.1735349
Body Exposure Pixels	-0.4222731	0.5274244	-0.2379656	0.3640382	0.6839297	-0.4645934	1.0000000	-0.1488121	-0.1315965
JPEG File	-0.1270419	0.1115902	0.0982664	-0.0188942	0.1629133	0.0899124	-0.1488121	1.0000000	0.1602161
Entropy	0.2536430	-0.0629056	0.0963144	0.1632642	-0.2666624	-0.1735349	-0.1315965	0.1602161	1.0000000

	EPN	LPP	Valence	Arousal	Body Exposure Rating	Body Orientation	Body Exposure Pixels	JPEG File	Entropy
EPN	NA	0.0000000	0.6237361	0.0034783	0.0000000	0.6669812	0.0000339	0.1420162	0.0029939
LPP	0.0000000	NA	0.1653023	0.0000000	0.0000000	0.0000047	0.0000001	0.1975608	0.4685631
Valence	0.6237361	0.1653023	NA	0.0003225	0.5507636	0.0000060	0.0239125	0.2568440	0.2664602
Arousal	0.0034783	0.0000000	0.0003225	NA	0.0106883	0.0000000	0.0004201	0.8278122	0.0584864
Body Exposure Rating	0.0000000	0.0000000	0.5507636	0.0106883	NA	0.0036836	0.0000000	0.1249814	0.0110662
Body Orientation	0.6669812	0.0000047	0.0000060	0.0000000	0.0036836	NA	0.0000040	0.3993575	0.1018983
Body Exposure Pixels	0.0000339	0.0000001	0.0239125	0.0004201	0.0000000	0.0000040	NA	0.1615647	0.2163219
JPEG File	0.1420162	0.1975608	0.2568440	0.8278122	0.1249814	0.3993575	0.1615647	NA	0.0634190
Entropy	0.0029939	0.4685631	0.2664602	0.0584864	0.0110662	0.1018983	0.2163219	0.0634190	NA

Best Subset Multiple Regressions

Using all 135 scenes, the best subset selection method was used to find the best predictors of the EPN and the LPP. The independent variables of self-reported valence, arousal, a dichotomous variable indicating if the scene depicted humans or animals, JPEG file size, and entropy. Here we report the simple regression and the best multiple regression equation based on BIC values. Complete regsubsets output can be see in Appendices E, F, G, and H. The best simple linear regression for the EPN used the dummy coded variable for human or animals scenes with human scenes predicting more modulation of the EPN ($\beta = -1.56$, $p = 0.001$); $F(1, 133) = 12.33$, $p = 0.001$, $R^2 = 0.085$, adjusted $R^2 = 0.078$, and BIC = -2.16. The best model selected included the four variables of arousal ($\beta = -0.66$, $p = 0.002$), the dichotomous indicator of human or animal scenes ($\beta = -1.14$, $p = 0.009$), scene size ($\beta = 3.31 \times 10^{-5}$, $p = 0.029$) , and entropy ($\beta = 2.068$, $p < 0.001$); $F(4,130) = 9.519$, $p < 0.001$, $R^2 = 0.227$, adjusted $R^2 = 0.203$, and BIC = -10.15. For the LPP, the one variable simple regression utilizing self-reported arousal ($\beta = 1.01$, $p < 0.001$) was also the model with the best BIC value; $F(1, 133) = 47.19$, $p < 0.001$, $R^2 = 0.262$, adjusted $R^2 = 0.256$, and BIC = -31.18.

A best subset selection was also used for the EPN and LPP of the 90 human scenes with the seven predictors of valence, arousal, Mturk reported body exposure, Mturk reported body orientation, sum of pixels containing exposed body parts, JPEG file size, entropy. The simple regression for EPN used Mturk body exposure rating ($\beta = -0.61$, $p < 0.001$) in which more exposed bodies increase EPN modulation; $F(1, 88) = 67.40$, $p < 0.001$, $R^2 = 0.434$, adjusted $R^2 = 0.427$, and BIC = -42.18. The best multiple regression used the two variables of rated body exposure ($\beta = -0.69$, $p < 0.001$) and body orientation ($\beta = -0.37$, $p = 0.001$); $F(2, 87) = 43.52$, $p < 0.001$, $R^2 = 0.500$, adjusted $R^2 = 0.489$, and BIC = -48.91. Using the LPP as the dependent variable, the best simple regression also used rated body exposure ($\beta = 0.60$, $p < 0.001$) with more perceived body exposure predicting greater LPP amplitude; $F(1, 88) = 145.93$, $p < 0.001$, $R^2 = 0.624$, adjusted $R^2 = 0.620$, and BIC = -78.99. The best combination of independent variables included the two variables of rated body exposure ($\beta = 0.53$, $p < 0.001$) and self-reported arousal ($\beta = 0.82$, $p < 0.001$); $F(2, 87) = 124.40$, $p < 0.001$, $R^2 = 0.741$, adjusted $R^2 = 0.735$, and BIC = -108.05.

Chapter 5

Discussion

Results Overview

In this study, we attempted to define the extent to which body exposure modulates the EPN. Results from a previous study found nudist scenes modulated the EPN more than erotica despite self-reports indicating nudist content was less pleasant and arousing (Farkas et al., in revision). Here we further tested if scenes featuring more body part exposure would modulate the EPN by using the same nudist and erotica scenes as well as seven other categories that spanned the pleasantness and arousal dimensions. The categories were also chosen to test if body exposure explained EPN modulation in addition to self-reports of valence and arousal. Perception of body exposure and body orientation were quantified by participants using a nine-point scale. Body exposure was also operationalized by calculating the sum of pixels that contained exposed body parts in each scene. Category differences were quantified using repeated measures ANOVAs and paired t-tests. We also analyzed the effects of individual scene stimuli to understand which dimensions best predicted the EPN. We then consolidated our results by using a best subset selection algorithm to find the most predictive multiple regression equations for ERP modulation based on BIC.

Overall, we found that measures of body exposure best explain EPN and LPP modulation for our scene stimuli. Nudists scenes elicited neutral valence and low arousal self-reports, but these scenes were rated as having the most body exposure and subsequently modulated the EPN more than all other categories. Erotica modulated the EPN the second most and elicited the largest LPP amplitude. Nudist scenes modulated the LPP more than all other scenes besides erotica. Analysis of individual scenes results found additional evidence that body exposure can predict EPN and LPP modulation. Valence did not predict EPN modulation although arousal moderately did while accounting for 6% of the variance. For the LPP, again valence did not predict modulation, while we saw typical arousal modulation with a Pearson's R of 0.51. Correlations for the 90 human scenes found similar associations between the EPN and the predictors of valence and arousal. However, rated body exposure ($R^2 = 0.43$) and the sum of pixels containing exposed body parts ($R^2 = 0.18$) better predicted the EPN. Similarly, the body exposure metrics also accounted for more variance than arousal for the LPP. For the 135 total scenes, the multiple regression with the best BIC indicated a combination of arousal, complexity, and the depiction of humans predicted EPN modulation with a R^2 of 0.23. However, the addition of the new body measures into the best subset algorithm found the two variables of body exposure and body orientation best predicted EPN modulation and accounted for 50% of the variance. For the LPP, arousal best predicted modulation for the 135 scenes while body exposure did better for the subset of 90 human scenes. The best multiple regression for the LPP used the independent variables of arousal and body exposure and accounted for 74% of the variance.

These results replicated many past findings and extended our understanding of how body part perception affects the emotion-modulated ERPs. We replicated past findings that erotica will modulate the EPN more than mutilation scenes (Farkas et al, in revision; Frank & Sabatinelli, 2019; Schupp et al., 2006; Schupp et al., 2007). We also replicated our findings that nudist scenes will modulate the EPN more than erotic content (Farkas et al., in revision). Furthermore, we again found a disassociation between the EPN and LPP (Farkas et al., in revision). This difference in sensitivities between the EPN and LPP is demonstrated by the nudist scenes (with the highest body exposure) being more influential for the EPN, while high arousal categories like erotica and mutilation were more able to modulate the LPP. These differences between the ERPs seem to indicate scenes with easy to perceive body parts are more potent for the EPN, while the most arousing scenes will have a greater impact on the LPP. However, we learned that body exposure may also play a role in the LPP with the scenes containing the most unclothed body parts also predicting greater amplitudes.

Body Exposure and the EPN

In this study we found strong confirmatory evidence that the EPN can be modulated by scenes depicting body parts. Furthermore, our evidence indicates body parts are especially potent to the EPN if the bodies are oriented in upright positions. These findings do not invalidate the existence of an EPN arousal effect. Numerous studies have found arousing content will modulate the EPN more than neutral content (Flaisch et al., 2009; Junghöfer et al., 2001; Kissler et al., 2007; Schupp et al., 2004). In fact, this present study found an arousal effect for emotional categories of clothed people (victorious athletes and threatening people) and animals (pleasant animals and threatening animals) relative to their neutral counterparts (neutral people and neutral animals). However, despite the existence of an arousal effect for the EPN, our results imply a stronger predictor of the EPN is the presence of unclothed body parts in scenes, independent of arousal ratings.

Normally oriented body parts may modulate the EPN so effectively because they represent a class of objects that humans have a great deal of experience processing, and that are strongly associated with motivational demands. The EPN is a brief ERP with relatively early latency. In ERP research, later components often capture activity from numerous brain regions and localized neural processes can be disguised by a collection of overlapping neuronal generators. A scene that is rated as mostly filled with upright bodies may be easy to interpret by the brain, quickly giving the scene a modulatory advantage and enhancing the EPN. For example, a typical nudist scene that displays two upright people may be easier to process than an erotic scene depicting two individuals intertwined in an unusual position. The neuronal activity evoked by a more perceptually difficult erotic scene may cause similar activity but over a greater duration, leading to a potential that would be difficult to see as more brain areas become active. However, in ERP research latency differences can be difficult to separate from differences in amplitude. This explanation also does not answer why body parts seem to be so important to the EPN. One possibility is the EPN partially reflects the EBA becoming active because this cortical area stores semantic information about bodies (Schwoebel & Coslett, 2005). This perspective mechanism would mean the nudist scenes are generating a response independent to emotion processes. Another possibility is the nudist scenes are acting as a sexual cue in early visual processing, but don’t evoke a large degree of affective arousal past the EPN time window once the scene has been more fully perceived by the participant. This would explain why the LPP and arousal ratings are larger for erotica than the nudist scenes. It is also possible both semantic and emotional activations are happening concurrently.

Future studies could further understand if there are distinct neuronal generators by utilizing the more spatially precise technique of MEG. In comparison to EEG, MEG has similar temporal resolution with improved spatial resolution. A study comparing nudist and erotic scenes could potentially highlight semantic activations versus emotional processes. Alho and colleagues (2015), in a MEG study found computerized nude figures activated cortical areas known to be sensitive to body parts between 100-200ms with more emotion related structures activating between 200-300ms. A MEG study with our current set of scenes may reveal if nudists scenes are primarily driving an early response in body sensitive cortices or later in emotion-associated structures. This could illuminate if the nudists scenes are motivationally significant and if there are separable perceptual processes that make up the EPN.

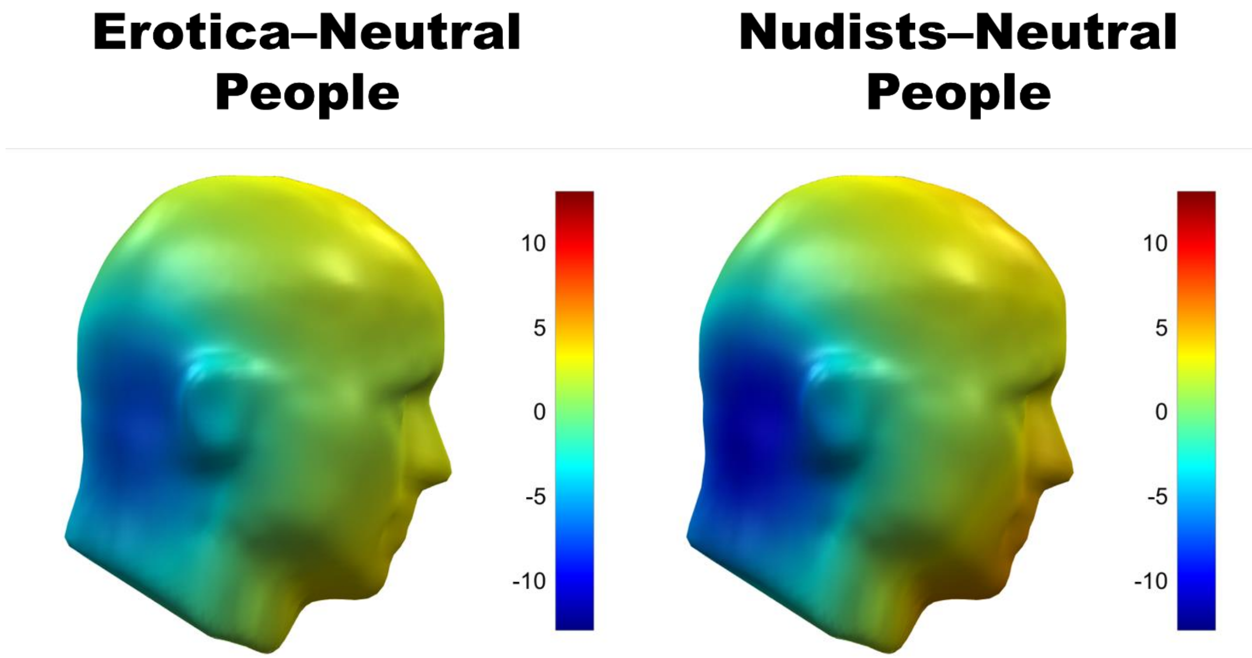


Figure 12. EPN topography for erotica and nudists scenes. The figures represent difference in microvoltage for the scene categories from neutral people scenes. The color represents the average microvoltage within 150-300ms after scene presentation.

Body Exposure and the LPP

A surprising finding was the LPP, which has been strongly tied to emotional arousal, also appears to be sensitive to body exposure. Weinberg and Hajcak (2010) found that the LPP modulation for erotica and mutilation scenes was larger than arousal ratings would predict. The researchers claimed their results showed content tied to sex or danger, that would be important to our evolutionary ancestors, would modulate the LPP greater than other categories. There is reason to believe a perceptual system fine-tuned to human bodies would be evolutionarily adaptive beyond recognizing sexual and dangerous situations. Extracting information from body positions and movement is used in perceptual learning (Grossman, Blake, and Kim, 2004) and crucial to social communication (Slaughter, Stone, & Reed, 2004). Furthermore, there is evidence that humans traversed our environments naked for a large portion of our early history (Kitter, Kayser, & Stoneking, 2003). Altogether, this means human brains may have been adaptively tuned to attend to unclothed bodies through natural selection. This theory could explain why a nudist scene does not seem arousing in comparison to a scene depicting a person wearing a ski mask and brandishing a gun, but will subsequently generate a larger LPP amplitude.

Do Body Parts Hold a Privileged Status in Visual Perception?

The modulatory effects of body parts on the EPN and LPP strengthen a theory that body parts hold a “privileged status” in visual perception (Alho et al., 2015). Our findings add to accumulating evidence that bodies seem to have widespread importance in the human visual system (Hietanen & Nummenmaa, 2011). A hypothesized brain circuit of the EBA, fusiform body area, and posterior inferior temporal cortex is specifically tuned for the perception of bodies (Peelen & Downing, 2007). However, many researchers believe the evolutionary origins of this visual circuit was to identify conspecifics and increase affective arousal with the ultimate purpose of copulation (Hietanen et al., 2014). With our supposedly emotional neutral nudist scenes also eliciting large ERPs, it may be possible bodies modulate these ERPs for reasons unrelated to arousal or sexual activity.

Future research could use measures of the sympathetic nervous system to assess if our body exposure metrics are associated with elevated arousal. While the body exposure of a scene predicted larger ERP amplitudes, it may not be necessarily correlated with physiological responses that can be modulated by emotional scenes. The measures of skin conductance and heart rate acceleration are known to increase when participants are shown emotionally arousing scenes (Bradley, 2000; Bradley & Lang, 2000). While in our study body exposure ratings ($r = 0.27$, $p = 0.011$) and the sum of pixels containing exposed bodies ($r = 0.36$, $p < 0.001$) were associated with self-reported arousal (Figure 11, Table 3, and Table 4), we do not know if body exposure ratings predict measures such as skin conductance or heart rate acceleration. We would specifically be interested if the nudist scenes, that elicited high ratings of body exposure and low arousal self-reports, would show sympathetic nervous system activity. If the nudists scenes do not elicit peripheral nervous system activity associated with arousal, then this would be more evidence that emotion-related ERPs may not always be tied to arousal. If we do see sympathetic nervous system activity to nudist scenes, then the scenes may be arousing while semantically participants feel they are not.

Mutilation ERP Results

Although mutilation scenes often display a large portion of unclothed body parts, they did not modulate the ERPs as much as erotica and nudist scenes. Mutilation scenes are often used in conjunction with erotica scenes because they typically elicit equivalent arousal while being on opposite ends of the valence spectrum. The two categories often elicit similar LPP modulation as well. However, a growing number of studies have found erotica may be more potent for both the LPP and the EPN (Farkas et al., in revision; Frank & Sabatinelli, 2019; Schupp et al., 2006; Schupp et al., 2007). The scenes chosen for this study may display clearer depictions of erotic content than previous studies. Future studies could examine if erotic scenes, that did not elicit a larger amplitude than mutilation scenes, are more complex based on our measures of JPEG file size or entropy.

The composition of mutilation scenes may also explain why they led to less modulation than erotica and nudist scenes. Although mutilation scenes had a comparable number of pixels that contained exposed body parts to erotica and nudist scenes, the mutilation scenes elicited much lower perceptual ratings of body exposure. Participants may have rated that mutilation scenes have less exposed body parts because the bodies depicted are obstructed by blood or missing skin. The mutilation scenes were also rated as having the most unusual body orientations, which could influence the scenes modulatory potential. Furthermore, mutilation scenes of mangled limbs could affect the holistic processing of body parts that would make them more difficult to perceive quickly.

Valence and EPN Modulation

This study found strong evidence against an EPN valence bias. The most pleasant scenes of victorious athletes and pleasant animals had similar EPN modulation to their unpleasant counterpart of threatening animals, threatening people, and mutilation scenes. Furthermore, victorious athlete scenes were equivalent in self-reported arousal to our three unpleasant categories which should have allowed for an independent test of pleasantness. Past findings of an EPN pleasure bias could be the categories were not balanced for body exposure (Farkas et al., in revision). To understand if valence modulates the EPN, future studies could use a large diverse set of scenes and statistically control for body exposure.

Limitations

A possible limitation of this study is the set of categories were chosen to highlight body exposure as a modulator of the ERPs. The scenes within each category were curated to be as similar as possible. This was mostly successful, because scenes within each category elicited similar self-reports and ERP modulation. This homogeneity within each category allowed us to clearly analyze content differences between ERPs and self-reports. However, similarity within each category makes it difficult to understand if our overall finding, that body parts modulate our ERPs of interest, is true within each category. For example, within the nudists category a scene depicting more exposed body parts should have the largest EPN amplitude. However, with only 15 scenes that are so semantically similar, we do not have enough statistical power to understand if this is true. Future research could quantify exposure and record ERPs for a larger and more diverse set of scenes.

Conclusions

In the present study we attempted to understand what modulates the EPN by using a set of scenes that spanned the relevant dimensions of arousal, valence, and body exposure. We replicated past findings that arousal and to a greater degree body exposure will increase EPN amplitude (Farkas et al., in revision). We did this by quantifying body exposure with self-report ratings and quantifying exposed body parts in each scene stimulus. These body part measures explained a larger portion of variance for EPN modulation than rated arousal. Additionally, the study found evidence that a valence bias for the EPN was not evident after controlling for body exposure. We also observed an unexpected finding that the LPP may have a sensitivity to body exposure in addition to its well-known association with arousal. A complete interpretation of the results suggest that the EPN and LPP may be especially modulated by nude bodies independent of rated pleasantness and arousal. Theoretically, a body part effect on these ERPs may reflect the fact that the perception of human bodies was important in our evolutionary history. It is still unclear if a neuronal circuit specialized for bodies is contributing to the EPN. More research is needed to understand if ERP activity related to nude bodies is because of their semantic content or an evolutionary process to evoke attention and sexual preparation. Additionally, peripheral nervous system measures that index arousal could be implemented to understand if they are associated with ERP modulation to high body exposure scenes. Future research could also utilize more spatially precise methods such as MEG and fMRI to understand activation during the viewing of naturalistic nudist and erotic scenes. MEG would be especially useful because it has equal temporal resolution to EEG yet greater spatial resolution, thus researchers could more accurately assess which visual cortical subareas are active during the EPN time window.

References

Alho, J., Salminen, N., Sams, M., Hietanen, J. K., & Nummenmaa, L. (2015). Facilitated early cortical processing of nude human bodies. *Biol Psychol, 109*, 103-110. Doi:10.1016/j.biopsycho.2015.04.010

Amaral, D., Capitanio, J., Jourdain, M., Mason, W., Mendoza, S., & Prather, M. (1992). The amygdala. *Neuropsychologia*, *41*(2), 235-240.

Anllo-Vento, L., Luck, S. J., & Hillyard, S. A. . (1998). Spatio-temporal dynamics of attention to color: Evidence from human electrophysiology. *Human brain mapping, 6*(4), 216-238.

Bradley, M. M., and Lang, P. J. . (1994). Measuring Emotion: The Self-Assessment Manikin and the Semantic Differential. *Journal of behavior therapy and experimental psychiatry, 25*(1), 49-59.

Bradley, M. M., & Lang, P. J. (2000). Measuring emotion: Behavior, feeling, and physiology. *Cognitive neuroscience of emotion, 25*, 49-59.

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion, 1*(3), 276-298. Doi:10.1037//1528-3542.1.3.276

Bradley, M. M., Hamby, S., Low, A., & Lang, P. J. (2007). Brain potentials in perception: picture complexity and emotional arousal. *Psychophysiology, 44*(3), 364-373. Doi:10.1111/j.1469-8986.2007.00520.x

Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology, 46*(1), 1-11.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G. (1996) Electrophysiological studies of face perception in humans. *J Cogn Neurosci 8*: 551–565.

Codispoti, M., Ferrari, V., Junghöfer, M., & Schupp, H. T. (2006). The categorization of natural scenes: brain attention networks revealed by dense sensor ERPs. *Neuroimage, 32*(2), 583-591. Doi:10.1016/j.neuroimage.2006.04.180

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biological Psychology, 52*(2), 95-111.

De Cesarei, A., & Codispoti, M. (2006). When does size not matter? Effects of stimulus size on affective modulation. *Psychophysiology, 43*(2), 207-215. Doi:10.1111/j.1469-8986.2006.00392.x

Dien, J. (2010). The ERP PCA Toolkit: an open source program for advanced statistical analysis of event-related potential data. *J Neurosci Methods, 187*(1), 138-145. Doi:10.1016/j.jneumeth.2009.12.009

Donderi, D. C. (2006). Visual Complexity: A Review. *Psychological bulletin, 132*, 73-97.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. . (2001). A Cortical Area Selective for Visual Processing of the Human Body. *Science, 293*(5539), 2470 – 2473.

Elston, G. N. (2003). Cortex, cognition and the cell: new insights into the pyramidal neuron and prefrontal function. *Cereb Cortex, 13*(11), 1124-1138. Doi:10.1093/cercor/bhg093

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2007). Masking Disrupts Reentrant Processing in Human Visual Cortex. *Journal of Cognitive Neuroscience, 19*(9), 1488 – 1497.

Farkas, A. H., Oliver, K. I., & Sabatinelli, D. (In revision). Emotional and feature-based modulation of the early posterior negativity. *Psychophysiology.*

Flaisch, T., Schupp, H. T., Renner, B., & Junghöfer, M. (2009). Neural systems of visual attention responding to emotional gestures. *Neuroimage, 45*(4), 1339-1346. Doi:10.1016/j.neuroimage.2008.12.073

Flaisch, T., Stockburger, J., & Schupp, H. T. (2008). Affective prime and target picture processing: an ERP analysis of early and late interference effects. *Brain Topogr, 20*(4), 183-191. Doi:10.1007/s10548-008-0045-6

Frank, D. W., & Sabatinelli, D. (2014). Human thalamic and amygdala modulation in emotional scene perception. *Brain Res, 1587*, 69-76. Doi:10.1016/j.brainres.2014.08.061

Frank, D. W., & Sabatinelli, D. (2019). Hemodynamic and electrocortical reactivity to specific scene contents in emotional perception. *Psychophysiology*, e13340. Doi:10.1111/psyp.13340

Freese, J. L., & Amaral, D. G. (2005). The organization of projections from the amygdala to visual cortical areas TE and V1 in the macaque monkey. *Journal of Comparative Neurology*, *486*(4), 295-317.

Gazzaniga MS , Ivry RB , Mangun GR . (2002). Cognitive neuroscience: the biology of the mind. New York: W. W. Norton.

Grossman, E. D., Blake, R., & Kim, C. Y. (2004). Learning to see biological motion: brain activity parallels behavior. *J Cogn Neurosci, 16*(9), 1669-1679. Doi:10.1162/0898929042568569

Harrell Jr, F. E., Dupont, C. (2019). Hmisc: Harrell Miscellaneous. R package version 4.2-0. https://CRAN.R-project.org/package=Hmisc

Hietanen, J. K., Kirjavainen, I., & Nummenmaa, L. (2014). Additive effects of affective arousal and top-down attention on the event-related brain responses to human bodies. *Biol Psychol, 103*, 167-175. Doi:10.1016/j.biopsycho.2014.09.003

Hietanen, J. K., & Nummenmaa, L. (2011). The naked truth: the face and body sensitive N170 response is enhanced for nude bodies. *PloS One, 6*(11), e24408. Doi:10.1371/journal.pone.0024408

Junghöfer, M., Elbert, T., Tucker, D. M., & Rockstroh B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology, 37*(4), 523-532.

Junghöfer, M., Sabatinelli, D., Bradley, M. M., Schupp, H. T., Elbert, T. R., and Lang, P. J. . (2006). Fleeting images: rapid affect discrimination in the visual cortex. *Neuroreport, 17*, 225-229.

Junghöfer, M., Peyk, P., Flaisch, T., & Schupp, H. T. (2006). Neuroimaging methods inaffective neuroscience: Selected methodological issues. *Progress in BrainResearch, 156*, 123-143.

Junghöfer, M., M., B. M., Elbert, T. R., & J., L. P. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology, 38*(2), 175-178. Doi:DOI: 10.1017/S0048577201000762

Keil, A., Sabatinelli, D., Ding, M., Lang, P. J., Ihssen, N., & Heim, S. (2009). Re-entrant projections modulate visual cortex in affective perception: evidence from Granger causality analysis. *Hum Brain Mapp, 30*(2), 532-540. Doi:10.1002/hbm.20521

Klein, S.; Thorne, B. M. (3 October 2006). Biological psychology. New York, N.Y.: Worth. ISBN 978-0-7167-9922-1.

Kissler, J., Herbert, C., Peyk, P., & Junghöfer, M. (2007). Buzzwords: early cortical responses to emotional words during reading. *Psychological Science, 18*(6), 475-480.

Kittler, R., Kayser, M., & Stoneking, M. (2003). Molecular Evolution of Pediculus humanus and the Origin of Clothing. *Current Biology, 13*(16), 1414-1417. Doi:10.1016/s0960-9822(03)00507-4

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). International Affective Picture System (IAPS): Technical Manual and Affective Ratings. *Institute of Mental Health Center for the Study of Emotion and Attention,Gainesville, FL).*

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. *Attention and orienting: Sensory and motivational processes*, 97-135.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. *Technical report A-8*.

Lueschow, A., Sander, T., Boehm, S. G., Nolte, G., Trahms, L., & Curio, G. (2004). Looking for faces: Attention modulates early occipitotemporal object processing. *Psychophysiology, 41*(3), 350-360.

Lumley, T. (2017). Leaps: Regression Subset Selection. R package version 3.0. https://CRAN.R-project.org/package=leaps

Martınez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. . (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

Michalowski, J. M., Pane-Farre, C. A., Low, A., & Hamm, A. O. (2015). Brain dynamics of visual attention during anticipation and encoding of threat- and safe-cues in spider-phobic individuals. *Soc Cogn Affect Neurosci, 10*(9), 1177-1186. Doi:10.1093/scan/nsv002

Minnebusch, D. A., & Daum, I. (2009) Neuropsychological mechanisms of visual face and body perception. *Neurosci Biobehav Rev 33*: 1133–1144.

Miskovic, V., Martinovic, J., Wieser, M. J., Petro, N. M., Bradley, M. M., & Keil, A. (2015). Electrocortical amplification for emotionally arousing natural scenes: the contribution of luminance and chromatic visual channels. *Biol Psychol, 106*, 11-17. Doi:10.1016/j.biopsycho.2015.01.012

Murray, R. J., Brosch, T., & Sander, D. (2014). The functional profile of the human amygdala in affective processing: insights from intracranial recordings. *Cortex*, *60*, 10-33.

Nunez PL, Srinivasan R (1981). Electric fields of the brain: The neurophysics of EEG. Oxford University Press.

Oya, H., Kawasaki, H., Howard, M. A., & Adolphs, R. (2002). Electrophysiological responses in the human amygdala discriminate emotion categories of complex visual stimuli. *Journal of Neuroscience*, *22*(21), 9502-9512.

Parasuraman, R., & Davies, R. (1984). Varieties of attention. *New York: Academic.*

Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nat Rev Neurosci, 8*(8), 636-648. Doi:10.1038/nrn2195

Peyk, P., De Cesarei, A., & Junghöfer, M. (2011). ElectroMagnetoEncephalography software: overview and integration with other EEG/MEG toolboxes. *Comput Intell Neurosci, 2011*, 861705. Doi:10.1155/2011/861705

Robinson, J. D., Versace, F., Engelmann, J. M., Cui, Y., Gilbert, D. G., Waters, A. J., . . . Cinciripini, P. M. (2016). Attentional bias to smoking and other motivationally relevant cues is affected by nicotine exposure and dose expectancy. *Journal of Psychopharmacology, 30*(7), 627-640.

Rossion, B., Jacques, C. (2008) Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage 39*: 1959–1979.

Sabatinelli, D., Bradley, M. M., Lang, P. J., Costa, V. D., & Versace, F. (2007). Pleasure rather than salience activates human nucleus accumbens and medial prefrontal cortex. *J Neurophysiol, 98*(3), 1374-1379. Doi:10.1152/jn.00230.2007

Sabatinelli, D., Frank, D. W., Wanger, T. J., Dhamala, M., Adhikari, B. M., & Li, X. (2014). The timing and directional connectivity of human frontoparietal and ventral visual attention networks in emotional scene perception. *Neuroscience, 277*, 229-238. Doi:10.1016/j.neuroscience.2014.07.005

Sabatinelli, D., Keil, A., Frank, D. W., & Lang, P. J. (2013). Emotional perception: correspondence of early and late event-related potentials with cortical and subcortical functional MRI. *Biol Psychol, 92*(3), 513-519. Doi:10.1016/j.biopsycho.2012.04.005

Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., and Hamm, A. O. . (2007). Selective Visual Attention to Emotion. *The Journal of Neuroscience, 27*(5), 1082-1089. Doi:10.1523/JNEUROSCI.3223-06.2007

Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006a). Emotion and attention: event-related brain potential studies. *Progress in brain research, 156*, 31-51.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: an ERP analysis. *Psychophysiology, 41*(3), 441-449. Doi:10.1111/j.1469-8986.2004.00174.x

Schupp, H. T., Ohman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion, 4*(2), 189-200. Doi:10.1037/1528-3542.4.2.189

Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2006b). Stimulus novelty and emotion perception: the near absence of habituation in the visual cortex. *Neuroreport, 17*(4), 365-369.

Schwoebel, J., & H., C. B. (2005). Evidence for Multiple, Distinct Representations of the Human Body. *Journal of Cognitive Neuroscience, 17*(4), 543-553.

Slaughter, V., Stone, V. E., & Reed, C. Perception of Faces and Bodies. *Current Directions in Psychological Science, 13*(6), 219-223.

Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight: Object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience, 10*(1), 137-151.

Versace, F., Kypriotakis, G., Basen-Engquist, K., & Schembre, S. M. (2016). Heterogeneity in brain reactivity to pleasant and food cues: evidence of sign-tracking in humans. *Soc Cogn Affect Neurosci, 11*(4), 604-611. Doi:10.1093/scan/nsv143

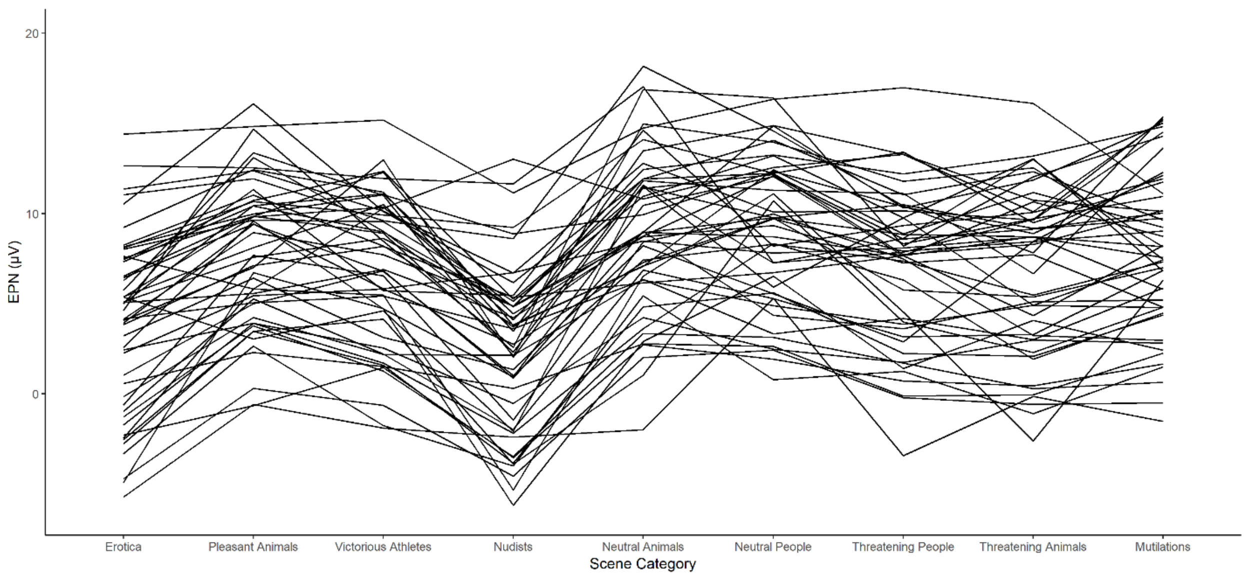
Vuilleumier, P., & Driver, J. (2007). Modulation of visual processing by attention and emotion: windows on causal interactions between human brain regions. *Philos Trans R Soc Lond B Biol Sci, 362*(1481), 837-855. Doi:10.1098/rstb.2007.2092

Weinberg, A., & Hajcak, G. (2010). Beyond good and evil: the time-course of neural activity elicited by specific picture content. *Emotion, 10*(6), 767-782. Doi:10.1037/a0020242

Weinberg, A., & Hajcak, G. (2011). Electrocortical evidence for vigilance-avoidance in Generalized Anxiety Disorder. *Psychophysiology, 48*(6), 842-851. Doi:10.1111/j.1469-8986.2010.01149.x

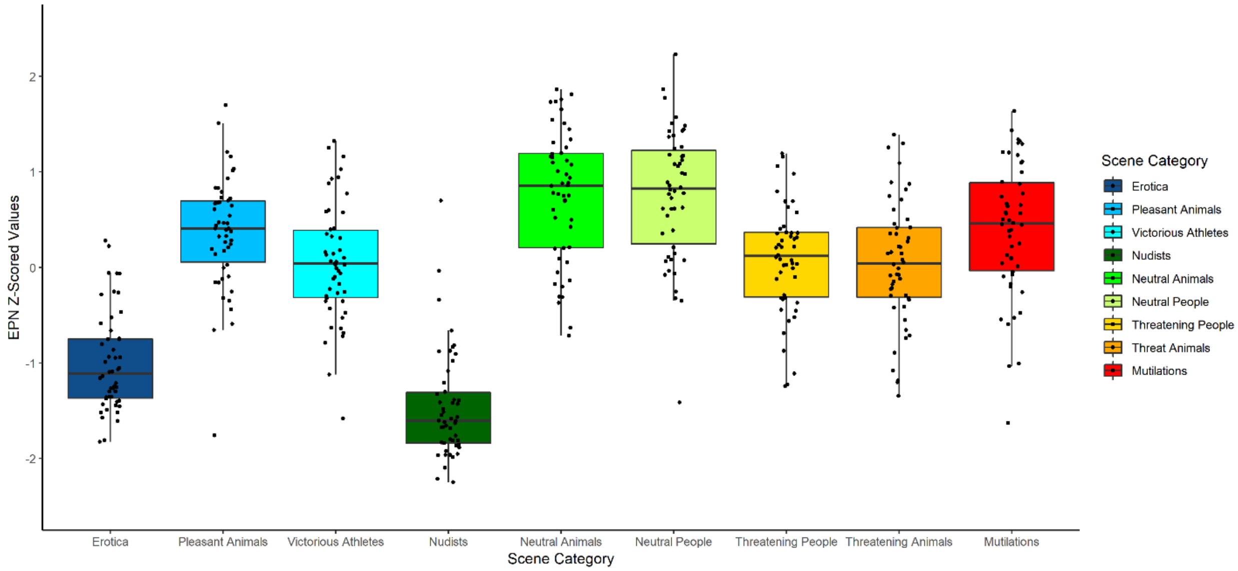
Appendices

Appendix A



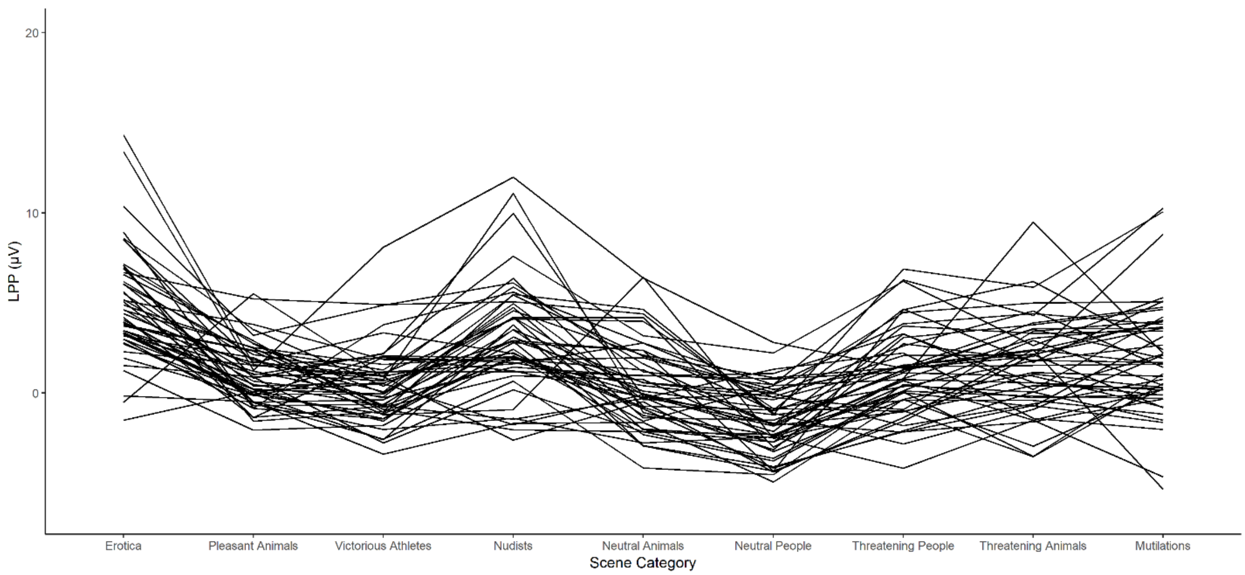
Line plot of EPN amplitudes for each scene category. Each line represents a participant.

Appendix B



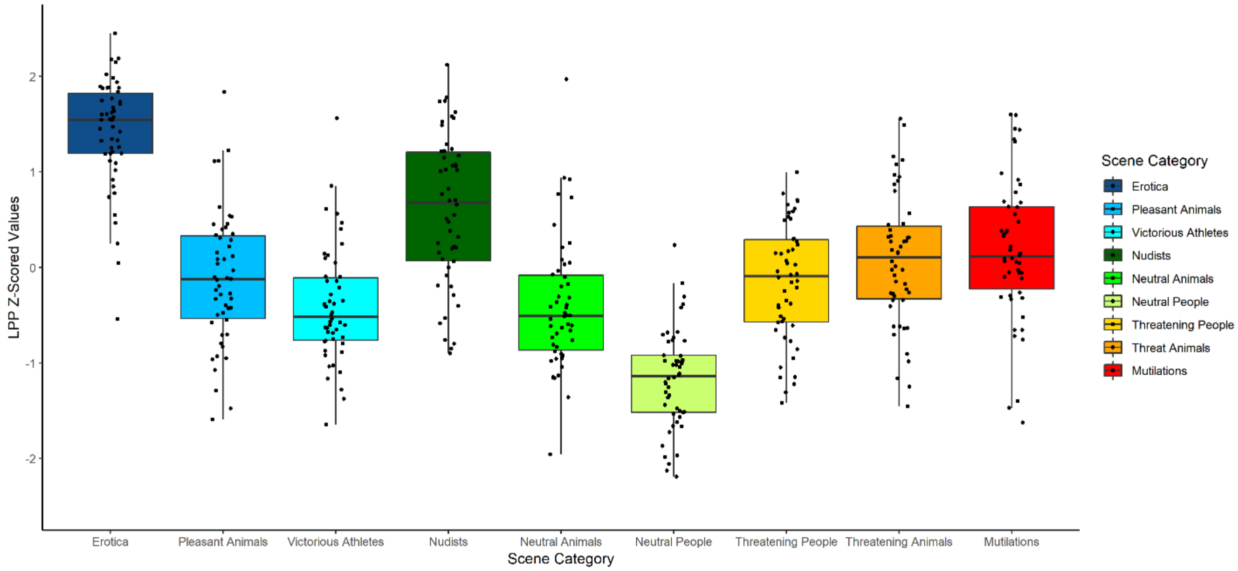
Z-scored results of the EPN values by category.

Appendix C



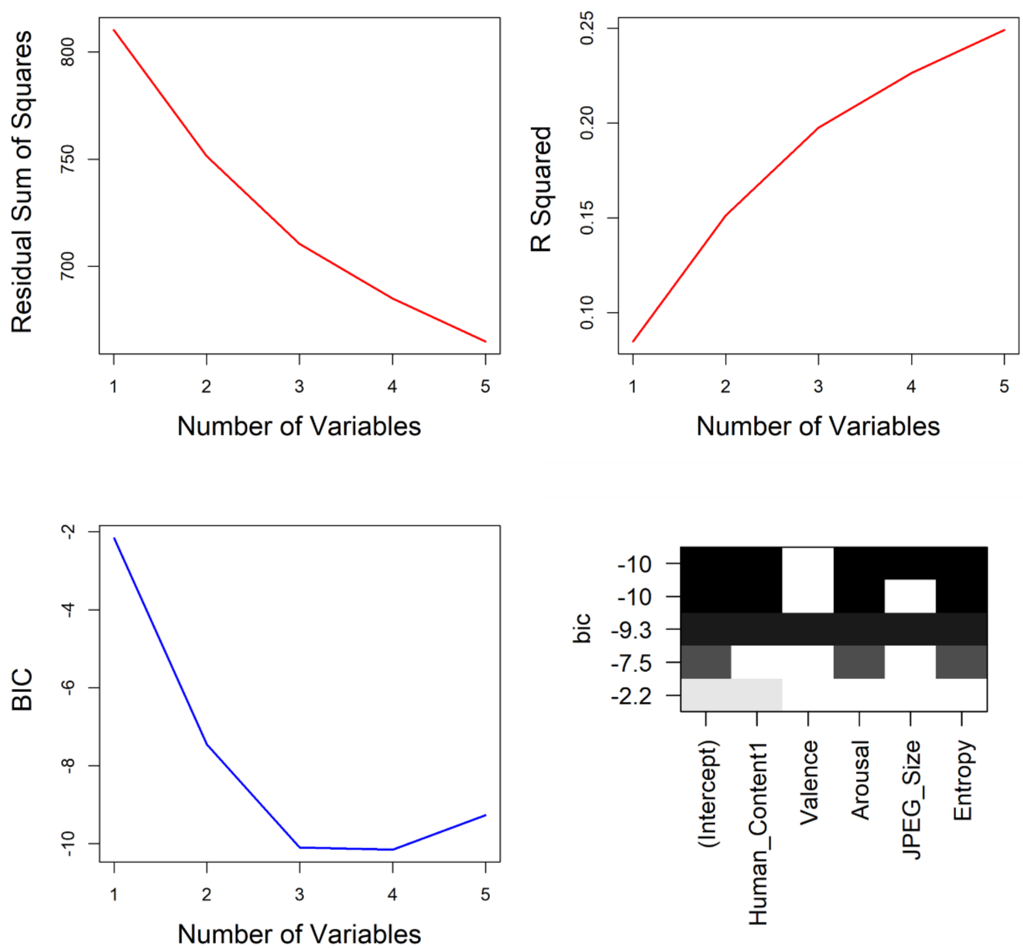
Line plot of LPP amplitudes. Each line represents a participant.

Appendix D



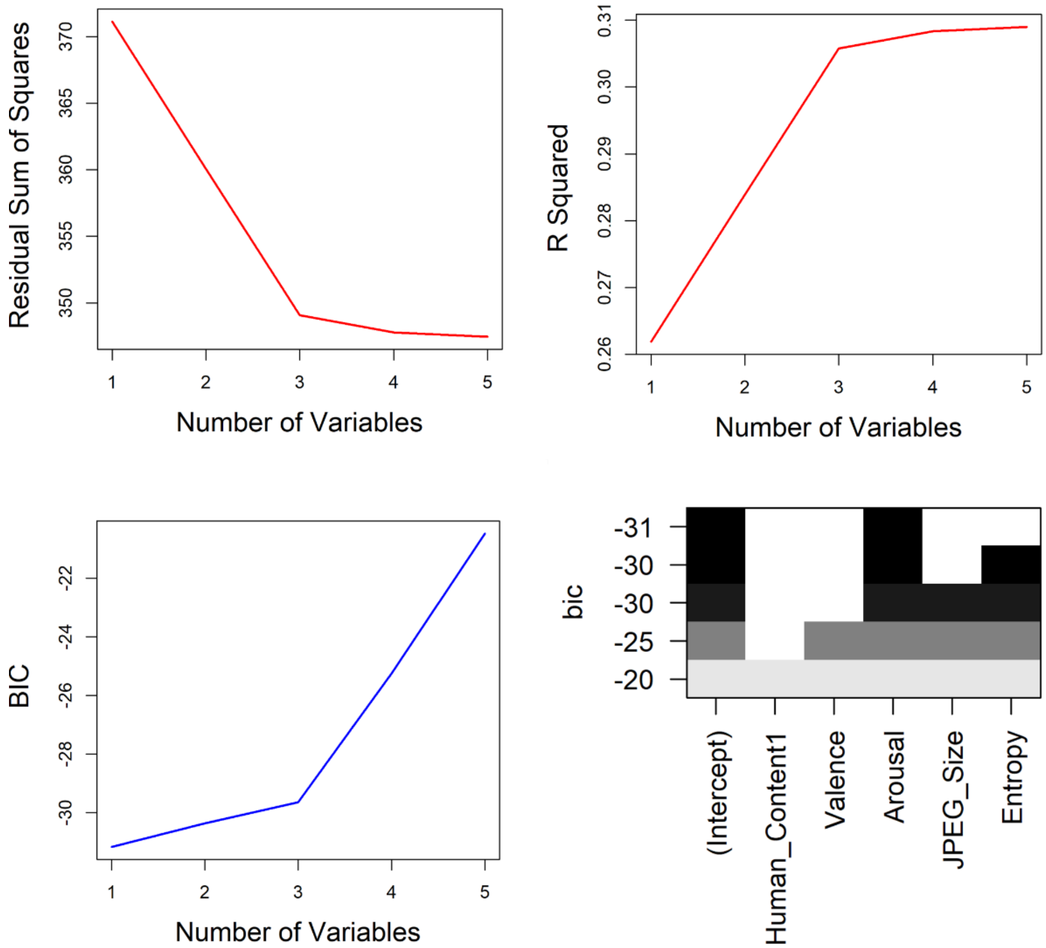
Z-scored results of the LPP values.

Appendix E



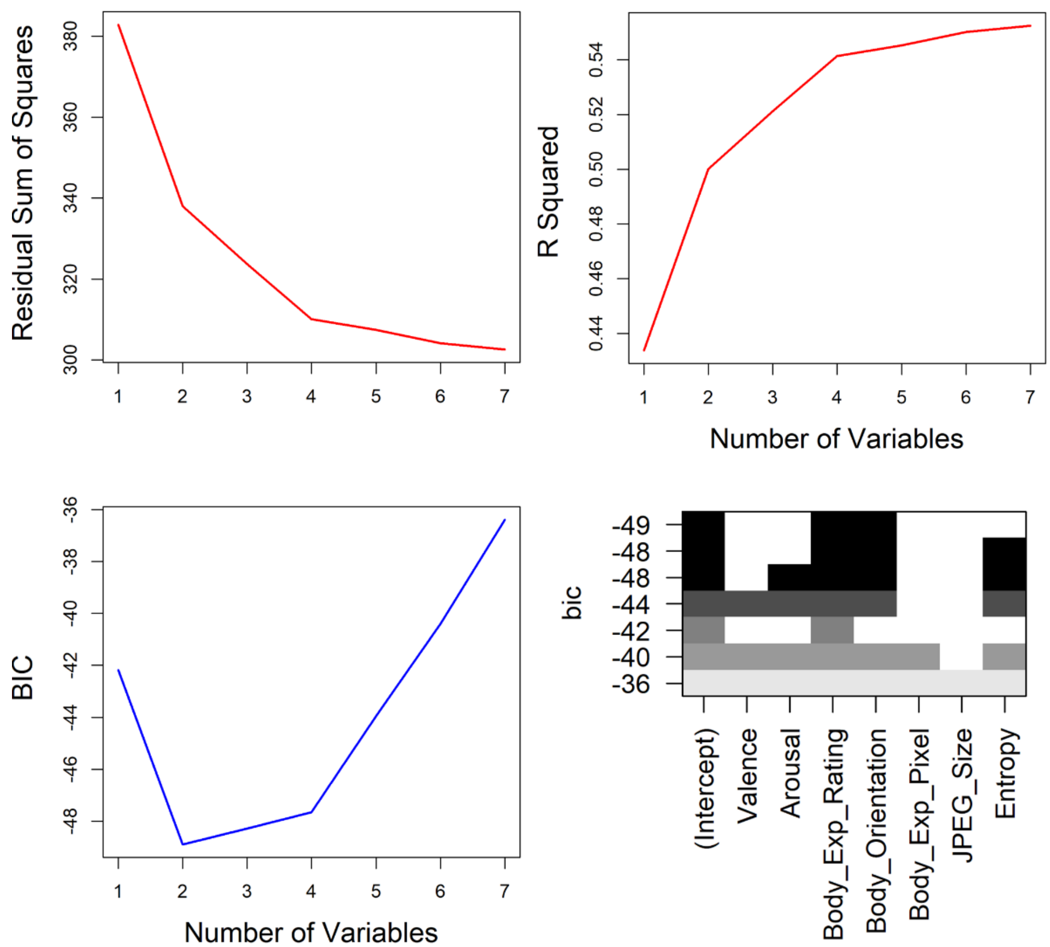
Output from regsubsets function that implements the best subset algorithm for the EPN and relevant independent variables for the complete 135 scene set. The best subset selection algorithm does an exhaustive search for the multiple regression equation with the lowest residual sum of squares. It then returns the best model that includes one variable, two variables, and so on. The top two figures show the residual sum of squares and the R squared for each multiple regression equation. The bottom left figures show the BIC value for each model. The models are then ordered in the brick plot.

Appendix F



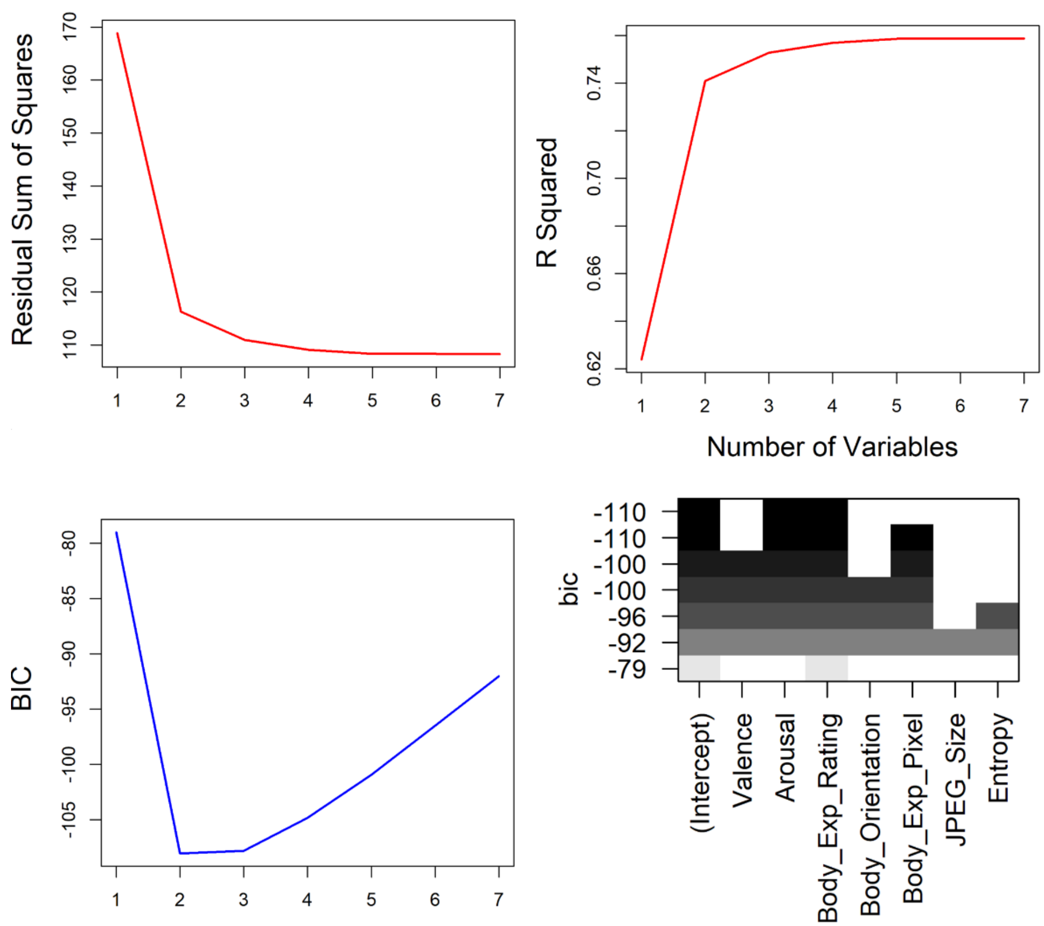
Results from the regsubsets function for the LPP and relevant independent variables from the 135 scene set.

Appendix G



Results from the regsubsets function for the EPN from the 90 human scene set.

Appendix H



Results from the regsubsets function for the LPP using the data from the 90 human scene set.