



Deconstructing threat: Rethinking the interplay between biological and social relevance in the emotional salience of unpleasant images



Rosemaree Kathleen Miller*, Frances Heritage Martin

The University of Newcastle, 10 Chittaway Road, Ourimbah, New South Wales, 2258, Australia

ARTICLE INFO

Keywords:

Unpleasant images
Defensive motivation
ERP
Late positivity
LPC
EPN

ABSTRACT

The type of threat shown in an image influences the emotional salience of unpleasant images. Seventy-four participants (21 male) rated high threat, moderate threat, and neutral images featuring reptiles, firearms, or humans as electroencephalographic activity was recorded. The magnitude of P3b amplitudes coincided with the threat level of firearm and human images, whereas scenes of attacking snakes and aimed handguns evoked more positive late positive component (LPC) activity than non-attacking or neutral versions of these same stimuli. The lateralised early posterior negativity (EPN) in temporal occipital regions was most negative for firearms, followed by reptiles, and then humans, while the midline EPN in occipital regions was most negative for reptiles, followed by firearms, and then humans. These findings imply late event-related potential positivity is influenced by social relevance (the P3b) or the level of aggression displayed by the stimulus (the LPC), whereas stimulus type may be indexed by EPN modulation.

1. Introduction

Threat remains one of the most intriguing aspects of the negativity bias in picture processing, as behavioural and neural responses to these types of stimuli index defensive motivation. Defensive motivation refers to the instigation of physiological states that facilitate approach and avoidant behaviours, such as attack, withdrawal, and self-protection (Bradley, Sabatinelli, & Lang, 2014; Lang & Bradley, 2013; LeDoux, Moscarello, Sears, & Campese, 2017). All negative stimuli, to varying degrees, pose a threat to one's emotional, physical, or mental well-being, and yet specific types of content are repeatedly shown in the most aversive images (e.g., attack, injury/mutilation). Similar parallels have been observed in relation to pleasant images and appetitive motivation (e.g., erotica, sex-related content), suggesting that the emotional salience of unpleasant and pleasant images is driven by factors other than valence (i.e., pleasantness) and arousal (i.e., intensity). The two strongest candidates for this perspective are biological and social relevance. Biological relevance refers to the emotional salience of a naturalistic scene related to evolutionary significance, while social relevance denotes the presence of members from one's own species. The dilemma is that the probability of a stimulus being hazardous is also signalled by signs of imminent violence (i.e., threat), indicating that this is the element that differentiates negative from more positive and neutral stimuli during picture processing.

1.1. The status of threat in picture processing

Threats can be defined as any organism, object, event, or other stimulus that endangers, or is perceived to endanger, an individual. The attribution of threat is a complex process requiring the integration of input from multiple brain and body regions, and the unconscious processes that facilitate defensive behaviours are not necessarily interchangeable with the feelings elicited or associated with threat (e.g., fear, anxiety, anger; LeDoux, 2012). The mere presence of a threat, whether real or inferred, is also presumed a trigger for defensive motivation. Picture processing is a useful way to examine defensive motivation, as images can be employed to represent small-scale versions of an encounter with a motivationally salient stimulus, such as a threat, in real life (Lang, Greenwald, Bradley, & Hamm, 1993). In the present context, the appetitive (or reward-based) and defensive motivation indexed by picture processing will be referred to as emotional salience (also see Bradley et al., 2014). Event-related potentials (ERP) are an ideal tool with which to characterise emotional salience as ERPs index the temporal course of brain activity and physiological arousal elicited by images (Hajcak, Weinberg, MacNamara, & Foti, 2012; Olofsson, Nordin, Sequeira, & Polich, 2008).

Numerous EEG studies demonstrate that unpleasant and pleasant images are differentiated from more neutral stimuli in ERP activity. Examples include ERP modulation indexing the late positive

* Corresponding author at: School of Psychology, The University of Newcastle, Ourimbah, New South Wales, 2258, Australia.

E-mail addresses: Rosemaree.Miller@uon.edu.au (R.K. Miller), Frances.Martin@newcastle.edu.au (F.H. Martin).

components (e.g., late positive potential [LPP], late positive component [LPC], P300, P3b) and the early posterior negativity (EPN; Hajcak et al., 2012; Olofsson et al., 2008; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Later-occurring positive ERP components, between 250–500 ms and beyond, such as the P3, the LPC and the LPP, are linked to the integration of several cognitive, psychological, and emotional processes (e.g., Hajcak et al., 2012; Matsuda & Nittono, 2015; Polich, 2007, 2012), as well as the allocation of attentional resources (Kok, 1997). In addition to indexing emotional salience, EPN modulation (est. 150–300 ms) is also associated with biological relevance (e.g., Schupp et al., 2006; van Strien, Franken, & Huijding, 2014). However, ERP modulation during picture processing is not confined to late positivity and the EPN. Activity indexing short latency ERP components, such as the P1 and N1 (est. 100–200 ms), have been linked with emotional salience (Olofsson et al., 2008). ERP modulation by way of emotional salience has also been observed for the middle latency components, including the P2 (est. 150–250 ms) and the N2 (est. 200–300 ms; Hajcak et al., 2012).

1.2. The negativity bias in picture processing

To clarify whether defensive motivation is unique to ERP activity elicited by negative stimuli would require investigation of the specific factors that differentiate unpleasant from pleasant and neutral images. The idea that negativity is inherently more salient than more neutral or pleasant stimuli is associated with defensive motivation in picture processing (Carretié, Albert, López-Martín, & Tapia, 2009; Norris, Gollan, Berntson, & Cacioppo, 2010). In the evaluative space model, it is proposed that neutral stimuli may appear more pleasant when positioned near a positive stimulus, leading to a positivity offset in which negative stimuli generally elicit higher levels of physiological arousal than positive stimuli (Norris et al., 2010). This dynamic could form the basis of protective and exploratory behaviours associated with defensive and appetitive motivation (Carretié et al., 2009; Norris et al., 2010). Supporting this, unpleasant images are sometimes found to elicit larger amounts of ERP activity for the N1, N2, P2 and select late positive components when shown alongside pleasant images (e.g., Carretié, Mercado, Tapia, & Hinojosa, 2001; Dai, Wei, Shu, & Feng, 2016; Dong, Zhou, Zhao, & Lu, 2011; Hilgard, Weinberg, Hajcak, Proudfit, & Bartholow, 2014; Huang & Luo, 2006). However, evidence for a negativity bias during picture processing is still mixed (e.g., Hajcak et al., 2012).

Evidence for the negativity bias in picture processing is mixed is due to a divergence between the emotional salience of unpleasant images compared to that of pleasant and neutral images, as some aspects of defensive motivation are not relevant for encounters with positive or neutral stimuli. The most aversive examples of unpleasant images often feature content that is potentially threatening, depicts mutilation of humans or animals, or elicits disgust (e.g., disease, unsanitary conditions, rotting food). Within the category of “unpleasant” the relative salience of negative stimuli could depend on how urgent a potential threat is to one’s safety. This differentiation between various aversive stimuli was observed by Schäfer, Scharmüller, Leutgeb, Köchel, and Schienle (2010), who presented scenes of medical surgery (e.g., operations, blood drawing) and found these images elicited the most positive P3 activity (340–500 ms), followed by images of human or animal threat, and then disgust images (e.g., maggots). These results align with those of Weinberg and Hajcak (2010), who reported that LPP amplitude (400–1000 ms) was most positive for images of injured or mutilated humans, followed by threat (e.g., animals with bared teeth, human assailants with weapons), and then disgust (e.g., dirty toilet, dead animals).

Rather than a straight negativity bias, specific stimuli may lead to a stronger aversion response than other types of negative content during

picture processing. Supporting this, scenes with mutilation (e.g., surgery, accidents), human threat, or animal threat content have been shown to evoke larger amounts of LPP or EPN activity than other unpleasant images (e.g., grief, contamination, disgust; Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010). However, the form this aversion divergence takes depends on the specific stimuli used to denote disgust, threat, or mutilation within an unpleasant image. For instance, Wheaton et al. (2013) found that disgust stimuli (e.g., vomit, infection) elicited larger amounts of EPN activity than images showing animal or human threat. Select EEG studies have also shown that images with disgust-eliciting or threat-related content lead to distinct patterns of P2, N2, and LPC activity when compared with neutral images (Carretié, Ruiz-Padial, López-Martín, & Albert, 2011; Krusemark & Li, 2011; Lu et al., 2016). The ERP modulation elicited by different types of unpleasant images is related to the arousal level of the negative content, however semantic differentiation could also contribute to these discrepancies (i.e., the assignment of meaning to different types of stimuli).

To summarise, there is evidence that the content of unpleasant images leads to ERP differentiation that could explain inconsistencies in the investigation of a negativity bias in picture processing. In terms of the evaluative space model, this means that the most aversive forms of negative stimuli lead to the strongest defensive response, a pattern which is observable in ERP indices of emotional salience. The challenge is how to disentangle the various factors that contribute to picture processing when unpleasant images are used as stimuli. Affective descriptors used to characterise emotional salience, even valence and arousal, are often constrained by language and cultural understanding. Some stimuli are universally considered negative or positive; however, this does not mean the brain discretely categorises stimuli as negative, positive, or neutral. Threat is an ideal candidate to investigate this type of semantic differentiation as even neutral or positive stimuli can take on threatening connotations, given the right circumstances. Rather than starting anew, prior research indicates that two conceptual dimensions of emotional salience will help to separate out the unique features of defensive motivation.

1.3. Characterising the aversion divergence in picture processing

Biological relevance has long been associated with emotional salience in picture processing. Recent ERP research has focused on snakes as a biologically relevant stimulus (e.g., van Strien et al., 2014; Grassini, Railo, Valli, Revonsuo, & Koivisto, 2019). Snakes are allegedly an archetypal threat with high levels of emotional salience (Isbell, 2009; van Strien & Isbell, 2017). However, high biological relevance extends to any stimulus with a strong phylogenetic association. Biologically relevant threats include mammals, insects, reptiles, and other creatures that are potentially dangerous to humans. Contaminative hazards, such as disease, injury and other disgust-eliciting content, are another type of stimuli which are high in biological relevance. Despite a strong theoretical basis, evidence for biological relevance in picture processing overlaps with social relevance. Humans are arguably high in biological relevance for other humans, but the magnitude of ERP activity during picture processing is also impacted by social cognition (for a review see Amodio, Bartholow, & Ito, 2014). Differentiating biological from social relevance, and vice versa, is difficult as both conceptual dimensions are important to an individual’s continued survival. For instance, in terms of evaluative space, biological relevance could serve as a cue for avoidance, whereas social relevance signals an opportunity for approach.

Another issue with conceptualising biological and social relevance in picture processing is that categorising images according to the affective dimensions of valence and arousal is generally the preferred method of defining the emotional salience of a picture, at least in

research utilising brain-based measures. Past research on biological or social relevance may instead signify semantic differentiation, rather than the processing of evolutionary significant or self-referential information. In the present context, we propose that semantic differentiation simply refers to distinguishing between the various types of stimuli often shown in images. Some negative stimuli are inherently more hazardous than others, suggesting that the negativity bias in picture processing resembles aversion divergence rather than clear-cut differentiation between unpleasant images and other pictorial stimuli in ERP modulation. In relation to defensive motivation, a common element shared between most images of threat and mutilation, but not disgust, is content related to the actual or implied execution of violence. The intent to attack is often associated with the depiction of threat, and yet, not all images used to denote threat show this type of implied aggression. Rather, threatening stimuli with high biological or social relevance are often featured in unpleasant images employed in picture processing research.

1.4. The present study

The primary aim of the present research was to examine whether biological and social relevance are better characterised as semantic differentiation for images showing threats during picture processing. In addition to valence and arousal, the emotional salience of images in the current study were classified according to the type of stimulus shown in the scene, as well as the potential for physical harm represented by the threat. Prior EEG research indicates that semantic differentiation occurs in ERP modulation evoked by threat, mutilation, and disgust images, however the types of stimuli depicted in these images are often intermixed and varied across different studies. In our study, images were restricted to three types of stimuli commonly featured in the most aversive unpleasant images. Snakes, as previously mentioned, are reptiles with high in biological relevance and low social relevance. In contrast, handguns are associated with threat, but are low in biological relevance due to these stimuli being human made. The operation of a weapon such as a handgun requires the presence of a human, indicating these stimuli are high in social relevance. Finally, scenes of human injury (i.e., mutilation) were shown alongside snake and handgun images.

The inclusion of injury images is an exploratory aspect of the present study, as affective judgements of these stimuli may not correspond to those typically found for threat images. However, scenes of injured humans, frequently employed as aversive stimuli in picture processing research, show the implied aftermath of attack behaviours and are high in both social and biological relevance for human participants. Injured humans are also high in emotional salience in terms of ERP activity (Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010), making these images a unique contrast to snake and handgun stimuli. The emotional salience of snakes and handguns is tied to the potential for attack and aggression implied by both stimuli, whereas the type of defensive motivation elicited by injured humans is not. Confining the presented images to three stimulus types with distinct biological relevance, social relevance and attack intent will also shed light on inconsistencies in the timing and location of ERP activity reported to index emotional salience. Multiple instances of late positivity spanning the 300–1000 ms range and beyond are linked to picture processing, while EPN modulation is reported to occur in both occipital and temporal occipital regions, and range between 150–300 ms (Hajcak et al., 2012; Olofsson et al., 2008; Schupp et al., 2006).

The unique approach to the investigation of defensive motivation in the present study means there is little evidence on which to base specific hypotheses about the direction of ERP modulation. However, broad predictions related to the primary study aim were generated based on the assumption that snakes and human injury images share the high levels of biological relevance often associated with images featuring organic matter (e.g., animals, contamination), while the implied

presence of a human perpetuating violence is a common element of social relevance in scenes showing injured humans or handguns. It was expected that ERP modulation indexing EPN and late positive activity would be observed. Based on the association of the EPN with biological relevance (e.g., Schupp et al., 2006; van Strien et al., 2014), it was hypothesised that snakes and human injury would elicit larger EPN activity than handgun images. The hazard of a handgun is dependent on an assailant wielding the inanimate weapon, while the danger of a snake relies upon the temperament of the reptile itself. Aggressive versions of snakes and handguns were expected to evoke greater amounts of late positivity in posterior regions (e.g., P3b, LPC) compared to non-attacking and neutral equivalents of the same stimulus types. These predictions were based on the association of the P3b/LPC with attention allocation and the integration of multiple types of incoming information. If attack intent is specifically indexed by the magnitude of the P3b/LPC, then aggressive forms of snakes and handguns were expected to evoke larger late positive activity than scenes of injured humans.

2. Method

2.1. Participants

Seventy-six individuals (21 male) were recruited through word-of-mouth or online advertising. Participants were screened for standard EEG exclusion criteria including psychiatric or neurological disorders, epilepsy, severe head trauma, giddiness, loss of consciousness, or concussions, as well as current or chronic use of psychoactive medication, cigarettes, illicit drugs, and alcohol (Keil et al., 2014; Picton et al., 2000). Individuals were also excluded if a history of phobia was reported (e.g., animals, small spaces, needles). Female participants were also asked to provide details about their menstrual cycle and current use of birth control medication; however, this information is not reported in the present study. The EEG recordings of two female participants were excluded prior to data processing. Excessive movement artefact was present in both EEG recordings, resulting in poor quality data for both women. The ages of the remaining 74 participants (21 male) ranged from 17 to 33 years old ($M = 23.61$, $SD = 4.56$). All reported normal or corrected-to-normal vision and a majority were right-handed (seven left-handed). All participants provided informed and written consent for the use of their data for research purposes. Ethics approval was granted by the Human Research Ethics Committee at the University of Newcastle, Australia (H-2012-0108).

2.2. Stimuli and materials

Valence, arousal, threat, and disgust ratings were collected using four visual six-point scales (see Supplemental Materials document). Ninety images¹ were selected from a larger pool of 260 full-colour stimuli sourced from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008) or downloaded from the Internet (Australian Copyright Council, 2016). All images were resized to 800 × 600 pixels and converted to .jpeg format. Thirty reptile, 30 firearm and 30 human images were selected, with ten images from each stimulus category being classified as either high threat, moderate threat, or neutral. Details regarding the collection and non-parametric analysis of valence, arousal and threat ratings upon which image selection was based are provided in the Supplementary Materials document. The probability of all differences reported in the following description of affective ratings was below the Bonferroni-corrected level of significance ($\alpha = .002$; all $ps < .002$). Aimed handguns were rated

¹ IAPS images used: 1050, 1051, 1052, 1070, 1114, 1120, 2102, 2359, 2381, 2382, 2383, 2390, 2593, 2594, 3016, 3017, 3120, 3130, 3140, 3181, 3213, 3261, 3400, 3130, 3140, 3213, 3261, 3400, 6230, 6260, 6263.

as the most unpleasant, arousing, and threatening firearm, followed by unarmed handguns, and then water pistols. Snakes in attack position were also judged as the most unpleasant, arousing and threatening reptile, followed by non-attacking snakes, and then turtles. High threat versions of injured humans consisted of particularly severe cases of injury (e.g., clearly dead or unconscious bodies with noticeable mutilation), while moderate threat scenes featured humans who were clearly injured but alert or awake. Unlike snakes and handguns, injured humans who are clearly incapacitated present a more immediate threat than a conscious injured person, as the latter is still responsive to an unseen danger while the former is not. Ratings of unpleasantness, arousal, and threat were similar for images of severely or moderately injured humans, but both types of images were rated as more unpleasant, arousing, and threatening than those showing non-injured humans engaged in everyday activities.

2.3. EEG recording and processing

EEG data were recorded via a 64-channel Quik-cap with sintered Ag/Ag Cl passive electrodes positioned according to the International 10–20 system of electrode placement (Jasper, 1958; Oostenveld & Praamstra, 2001). All data were collected with impedances below 10 k Ω and were continuously sampled at 1000 Hz with Neuroscan SynAmps2/RT amplifiers. Vertical and horizontal eye movements were assessed via four electrodes, located at the outer canthi of both eyes and above and below the left eye. EEG recordings were saved as continuous files and exported to BESA software (version 6) for offline processing. Standard BESA 6 procedures for manual selection and definition of eye-blinks (–100 to 400 μ V) were followed. This involves the use of principal component analysis to detect eye blinks, the generation of an eye blink model, and then the removal of eye blinks from each EEG recording with the BESA 6 adaptive method (Ille, Berg, & Scherg, 2002). On average, the eye blink model generated for each participant explained 98.94% of eye artifact variance. Following eye blink removal, artifact rejection was applied to EEG data using maximum amplitude thresholds of 100 and –100 μ V. Averaged ERP waveforms were generated from the remaining trials for each of the nine image conditions ($n \geq 40$). No less than 80% of trials were included per participant for each condition ($M = 95.64\%$). A high-pass filter of 0.16 Hz and a low-pass filter of 30 Hz were applied, and epochs were time-locked to image onset for a 1200 ms epoch (–200 ms to 1000 ms).

2.4. Procedure

The image rating task was programmed using Presentation 16 software. Each image was shown centrally on a dark grey background at eye-level on a 28-inch computer monitor positioned 70 cm away from the participant. The viewing angles for each image were approximately 17° (width) \times 13° (height). Instructions for the task were explained by the supervising researcher and shown on-screen. Participants were instructed to rate each image as honestly as possible when the six-point scale appeared, and that there were no right or wrong answers. All ratings were made with six buttons on a Presentation Cedrus RB-830 response pad. At the start of each trial a white fixation cross was shown for 1000 ms, and then an image for 1000 ms. The relevant six-point rating scale then appeared and remained onscreen until the participant responded, followed by an inter-trial interval of 500 ms. In the first block participants rated the valence (1 = pleasant, 6 = unpleasant), and then arousal (1 = stimulating, 6 = calming), of 90 randomly presented images. For the second and third blocks, the 90 images were randomly presented another four times each. Participants rated either the threat (1 = threatening, 6 = not threatening) or disgust (1 = disgusting, 6 = not disgusting) of the

image on each trial. The order of these rating types was randomised, and equal amounts of threat and disgust ratings were collected. Across the three blocks the 90 images were shown five times each, producing a total of 450 trials. The task took approximately 40 min to complete.

2.5. Design and data analysis

A 3(Stimulus type: firearm, reptile, human) \times 3(Threat level: high, moderate, neutral) design was followed for analyses. Within-subject factors for Coronal site and Sagittal location were added to analyses of ERP activity as needed. Data preparation, graphing, descriptive statistics and non-parametric analysis were conducted with Statistica 13 or GraphPad 7. Linear mixed effects (LME) analysis and assumption checks were performed with R 3.5.1 (R Core Team, 2018) through the RStudio (2016) interface. To ease interpretation of affective ratings, data for the arousal, threat, and disgust dimensions were reverse scored before analysis. Valence ratings were not modified as higher levels of this rating indicated greater unpleasantness. Assumptions of normality and equal variance were not met for affective ratings. The medians of these data were analysed with separate Friedman ANOVAs, with Bonferroni-corrected Wilcoxon matched-pairs tests ($\alpha = .002$) applied as necessary for post-hoc comparisons. Correlational analysis of affective ratings was performed using Spearman rank correlation coefficients.

2.5.1. ERP data

Average waveforms were computed from 64 channels and were used to score ERP modulation elicited by the image rating task. Before mean amplitude computation the 30 Hz low-pass filter was switched off to minimise extraneous voltage (Luck, 2014). Activity for a lateralised and midline EPN, a parietal occipital P3b, and a central parietal LPC were observed in the grand ERP waveform. Topography maps for the two types of EPN activity, P3b and LPC can be found in the Supplementary Materials document. Mean amplitudes for more than one EPN and late positivity time-frame were analysed as there have been inconsistencies in the timing and location of the EPN and late positivity during picture processing (e.g., Hajcak et al., 2012; Olofsson et al., 2008). Mean amplitudes for the P3b and the LPC were derived and analysed based on previous reports that affective images elicit more than one type of late positivity (e.g., Matsuda & Nittono, 2015). Many EEG studies which have examined EPN activity have employed rapid serial visual presentation (RSVP) to show images (Grassini et al., 2019; He, Kubo, & Kawai, 2014; van Strien et al., 2014), a format which contrasts to the slower image rating paradigm employed in the present study. For this reason, mean activity for a lateralised EPN in temporal occipital regions, and a midline EPN in occipital regions, were derived and analysed. Mean amplitudes for a frontal central N1 and a central medial N2 were also identified, computed and analysed. The results for the N1 are not included in the present study. N2 activity is reported, however, as N2 modulation has been linked to emotional salience in picture processing (Hajcak et al., 2012; Olofsson et al., 2008) and middle latency ERP activity, such as the N2, is associated with stimulus discrimination and response selection (Folstein & Van Petten, 2008; Olofsson et al., 2008).

2.5.2. LME analysis

Mean amplitudes were analysed with the linear mixed-effects model regression function (Bates, Mächler, Bolker, & Walker, 2015). The application of LME methods in psychological research is an area of active development (e.g., Boisgontier & Cheval, 2016), and additional detail on the procedures followed and R packages used for LME analysis can be found in the Supplementary Materials document. Each final model included a random Participant intercept and the fixed factors of Stimulus type and Threat level (Table 1). Sagittal location and Coronal site

Table 1

The final models estimated for the two EPNs (lateralised: 150–250 ms, midline: 200–300 ms), the N2, the P3b and the LPC. Abbreviations for factors are provided at the bottom of the table.

	R-notation
The lateralised EPN	Stim*Thr*Cor + Stim*Sag + (1 Participant)
The midline EPN	Stim*Thr + Stim*Cor + Thr*Cor + (1 Participant)
The N2	Stim*Thr + Stim*Cor + Stim*Sag + Sag*Cor + (1 Participant)
The P3b	Stim*Thr*Cor + Stim*Thr*Sag + Sag*Cor + (1 Participant)
The LPC	Stim*Thr + Stim*Cor + Stim*Sag + Thr*Sag + Sag*Cor + (1 Participant)

Note. Stim = Stimulus type, Thr = Threat level, Cor = Coronal site, Sag = Sagittal location.

Table 2

Fit values for the final models estimated for the EPNs (lateralised: 150–250 ms, midline: 200–300 ms), the N2, the P3b and the LPC. The ICC denotes variance due to the random participant intercept. Marginal and conditional R^2 index the variance explained by the fixed factors, and both the fixed factors and random intercept, respectively. Components for between- (τ_{00}) and within-subjects (σ^2) variance are also included.

	ICC _{participants}	Marginal R^2 / Conditional R^2	Variance components	
			Within (σ^2)	Between (τ_{00})
The lateralised EPN	.68	0.29/0.77	10.51	5.03
The midline EPN	.87	0.10/0.88	4.29	29.22
The N2	.79	0.29/0.85	1.74	6.50
The P3b	.51	0.26/0.64	4.70	4.88
The LPC	.54	0.20/0.63	1.96	2.29

factors were also added to the final models to denote electrode site where applicable. The fit values for the final models estimated² for the EPNs, N2, P3b and LPC mean amplitudes are shown in Table 2.

2.5.2.1. Individual differences. The motivation for using LME modelling was to ensure individual differences in the mean amplitude data were considered during analysis. Despite prior EEG research showing there are instances of consistent ERP modulation across people, there is still substantial variation across individual EEG recordings. As an example, there are known sex differences in brain area size and function (Grabowska, 2017; Ruigrok et al., 2014), individual variation that could influence the magnitude and location of brain-based measures. A Participant sex factor was not included in LME analyses due to there being substantially more female than male participants. However, the inclusion of a random Participant intercept during model estimation for each final model indirectly incorporated Participant sex (i.e., variation between males and females) into LME analyses. The inclusion of electrode clusters, rather than singular electrodes, was also motivated by the mixed sex sample. Selecting singular electrode sites for analysis is preferable for reducing type I error (Luck & Gaspelin, 2017). However, utilising single electrodes for analysis may inadvertently focus on ERP modulation inflated due to individual differences, such as sex-specific variation, rather than the shown image. Prior to data processing, the electrodes of interest were determined based on prior literature (e.g., Hajcak et al., 2012; Olofsson et al., 2008) and scoring of

² **Excluded data:** One female participant was excluded from model estimation for the 150–250ms EPN due to her data leading to a positive skew in the Participant random intercept during LME assumption checks. For the 200–300ms EPN, one data point for a female participant was deleted as this negative value was likely a recording error ($-14.94\mu\text{V}$). A Grubbs test indicated the data point was not a significant outlier ($G = 3.98, U = 1.00, p = .13$), however the value was more than 2SDs below the participant's average EPN activity prior to the deletion of the outlier ($M = 1.93\mu\text{V}, SD = 6.15$). The data of one male and one female were also excluded from model estimation for the P3b. At parietal occipital sites the percentage of P3b data over the upper 95% confidence interval limit was above 60% for both participants.

ERP components was focused on where activity was maximal, not the emergence of differences between image conditions.

2.5.2.2. The final model. Following model estimation, each final model was re-estimated with restricted maximum likelihood and Kenward-Rogers approximations were applied. Model fit within each final model was assessed with the intraclass correlation coefficient (ICC), marginal R^2 and conditional R^2 . The ICC denotes variance related to the random intercept in the model (Hox, Moerbeek, & van de Schoot, 2017), while conditional and marginal R^2 signals variance due to the fixed and random factors, and just the fixed factors, respectively (Nakagawa, Johnson, & Schielzeth, 2017). The results of the LME analyses will be reported using a combination of parameter information and estimated marginal means. For each ERP final model, the two-way relationship between Stimulus type and Threat level will be described. For brevity, parameter information will be restricted to the main relationships of Stimulus type and Threat level, as well as the relevant pair-wise comparisons for the two-way relationship between the two factors. The latter post-hoc analyses were calculated with the Kenward-Roger approximation and Bonferroni corrections were automatically applied to these values. The likelihood of a difference reaching significance was therefore reduced due to the application of these two conservative criteria.

3. Results

3.1. Affective ratings

The four separate Friedman ANOVAs performed on ratings of valence ($\chi^2(8) = 490.28, W = .83$), arousal ($\chi^2(8) = 270.01, W = .46$), threat ($\chi^2(8) = 481.57, W = .81$) and disgust ($\chi^2(8) = 495.53, W = .84$) each reached statistical significance (all $ps < .001$). High threat images were rated with the highest levels of unpleasantness, arousal, threat, and disgust within each stimulus category, followed by moderate threat images, and then neutral images (All $ps < .001$, Table 3). Images of human injury were rated with higher levels of unpleasantness, arousal, threat, and disgust than those showing snakes and handguns. The magnitude of the difference between ratings of severe and moderate injury images was also noticeably smaller compared to ratings for high and moderate threat images of reptiles and firearms (Table 3). Ratings of valence, arousal, threat and disgust were positively and significantly correlated (Spearman rank correlation coefficient, all $ps < .001$). Ratings for arousal were strongly associated with those for valence ($r = .66$), threat ($r = .66$) and disgust ($r = .65$). Correlations between threat, disgust and valence ratings were particularly strong (all $r > .86$).

3.1.1. Affective ratings summary

Severe injury, aimed handguns and attacking snakes were rated as more unpleasant, intense, threatening, and disgusting than moderate threat versions of these same stimuli. Images of injury, snakes or handguns were also differentiated from their neutral equivalents in unpleasant, arousal, threat and disgust ratings. Correlational analyses

Table 3

Median valence, arousal and threat ratings for images of reptiles, firearms and humans, categorised by threat level. Medians are shown with the relevant interquartile range.

	Valence	Arousal	Threat	Disgust
		<i>Reptile images</i>		
High threat	4.35 (4.90, 3.80)	4.05 (4.90, 3.40)	4.87 (5.20, 4.45)	4.48 (4.95, 3.95)
Moderate threat	3.65 (4.30, 3.00)	3.60 (4.10, 3.00)	3.80 (4.45, 2.85)	3.53 (4.30, 2.65)
Neutral	1.90 (2.50, 1.30)	2.95 (3.80, 1.90)	1.15 (1.60, 1.00)	1.20 (1.80, 1.00)
		<i>Firearm images</i>		
High threat	4.75 (5.20, 4.20)	4.35 (5.00, 3.70)	5.00 (5.75, 4.55)	4.70 (5.41, 4.25)
Moderate threat	4.00 (4.40, 3.40)	3.40 (4.00, 3.00)	4.00 (4.40, 3.45)	3.95 (4.20, 3.20)
Neutral	2.70 (3.10, 2.10)	3.05 (3.80, 2.10)	1.20 (2.00, 1.00)	1.33 (2.10, 1.00)
		<i>Human images</i>		
High threat	5.65 (5.90, 5.20)	4.95 (5.50, 4.10)	5.48 (5.80, 5.00)	5.65 (5.90, 5.25)
Moderate threat	5.20 (5.60, 4.90)	4.60 (5.10, 4.10)	5.08 (5.68, 4.55)	5.25 (5.55, 4.85)
Neutral	2.40 (2.70, 1.70)	2.40 (3.20, 1.70)	1.10 (1.60, 1.00)	1.23 (1.85, 1.00)

Note. Valence 1 = very pleasant, 6 = very unpleasant; Arousal 1 = not at all arousing, 6 = very arousing; Threat 1 = not at all threatening, 6 = very threatening; Disgust 1 = not at all disgusting, 6 = very disgusting.

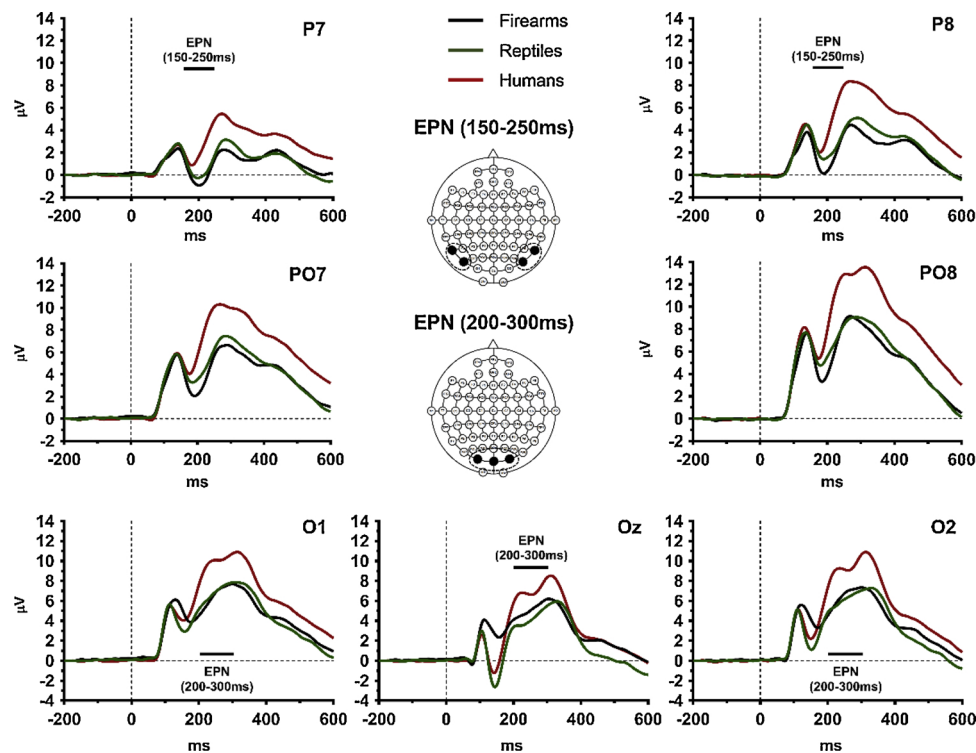


Fig. 1. Mean ERP waveforms for the lateralised (150–250 ms) and midline (200–300 ms) EPN, categorised by stimulus type. Electrode locations for the lateralised EPN are P7, PO7, P8, and PO8 and for the midline EPN are O1, Oz and O2 (see middle 2D electrode maps).

indicated that there was strong overlap between ratings for each affective dimension.

3.2. ERP data

3.2.1. The EPN

Amplitude modulation corresponding to the EPN previously reported for evolutionarily significant stimuli was observed in occipital regions between 200 and 350 ms (e.g., Grassini et al., 2019; He et al., 2014b; van Strien et al., 2014). However, visual inspection indicated this ERP activity was subject to overlapping positive and negative peaks in the observed modulation (Fig. 1). Activity for a lateralised EPN was also evident between 150 and 300 ms at electrodes corresponding to temporal occipital regions, which have previously been associated with EPN modulation (Fig. 1; e.g., Olofsson et al., 2008). Both types of EPN activity occurred primarily in the positive range, an effect noted in prior EEG studies (Hajcak et al., 2012; Schupp et al., 2006). Mean amplitudes

for lateralised and midline EPN activity were computed, from 150–200 ms and 200–300 ms post-stimulus respectively. Parameter information for the main relationships of Stimulus type and Threat level for the two types of EPN activity can be found in Table 4.

3.2.1.1. The lateralised EPN (150–250 ms)

Mean amplitudes for the lateralised EPN were derived from the left hemisphere electrodes P7 and PO7, and the right hemisphere electrodes P8 and PO8. Lateralised EPN activity was most negative for firearms, followed by reptiles, and then humans (Fig. 2A, all $ps < .001$). Images of handguns and snakes also elicited more negative EPN than images of human injury (all $ps < .001$). EPN amplitudes for images of non-injured humans were significantly reduced compared to those showing severe or moderate levels of injury (see Fig. 2A). In contrast, the magnitude of the EPN was similar for images of attacking snakes, non-attacking snakes and turtles. Images of unarmed handguns elicited significantly more negative EPN than those showing aimed handguns or water pistols.

Table 4
Parameter information (β [95% CI]) for the main relationships Stimulus type and Threat level in the EPN and N2 final models. Asterisks denote the level of significance between levels (* < .05, ** < .01, *** < .001).

Stimulus type	β [95% CI]
<i>The lateralised EPN (150–250 ms)</i>	
Firearms vs. Humans	2.07 [2.62, 1.51]***
Firearms vs. Reptiles	0.47 [1.03, -0.08]
Humans vs. Reptiles	3.00 [3.55, 2.44]***
<i>The midline EPN (200–300 ms)</i>	
Firearms vs. Humans	1.47 [1.97, 0.97]***
Firearms vs. Reptiles	-0.49 [0.01, -0.98]
Humans vs. Reptiles	-1.96 [2.45, 1.46]***
<i>The N2</i>	
Firearms vs. Humans	-2.48 [-2.23, -2.72]***
Firearms vs. Reptiles	-0.01 [0.23, -0.26]
Humans vs. Reptiles	-3.08 [-2.84, -3.33]***
Threat level	β [95% CI]
<i>The lateralised EPN (150–250 ms)</i>	
High vs. Moderate	-0.46 [0.06, -0.97]
High vs. Neutral	0.80 [1.31, 0.28]**
Moderate vs. Neutral	0.23 [0.75, -0.28]
<i>The midline EPN (200–300 ms)</i>	
High vs. Moderate	-0.57 [-0.07, -1.06]*
High vs. Neutral	-0.22 [0.27, -0.72]
Moderate vs. Neutral	1.51 [2.01, 1.01]***
<i>The N2</i>	
High vs. Moderate	0.57 [0.74, 0.39]***
High vs. Neutral	-0.36 [-0.18, -0.53]***
Moderate vs. Neutral	0.32 [0.50, 0.15]***

3.2.1.2. The EPN (200–300 ms). Mean amplitudes for the occipital EPN were derived from the occipital electrodes O1, Oz, and O2. The occipital EPN evoked by images of reptiles and firearms was significantly more negative than observed for human images (both $ps < .001$; Fig. 2B). EPN activity for reptile stimuli was also more negative compared to the EPN elicited by firearms ($p = .03$). Snake images evoked more negative EPN than human injury and aimed handgun images (all $ps < .001$), but levels of EPN activity were similar between unarmed handgun and snake stimuli (all $ps > .17$; Fig. 2B). Handguns also elicited more negative EPN than human injury images (all $ps < .01$). As for the lateralised EPN, images showing high threat and moderate threat human injury evoked significantly more

negative EPN than scenes of non-injured humans. The EPN for aimed handguns was also significantly reduced compared to water pistols ($p < .001$) and unarmed handguns ($p = .006$). Lastly, the EPN evoked by attacking and non-attacking snakes was significantly more negative than images of turtles.

3.2.1.3. EPN summary. Due to differences in the timing of maximal EPN activity in occipital and temporal occipital regions, mean amplitudes for the lateralised and midline EPN were analysed separately. Images of reptiles and firearms elicited more negative EPN than human images in both locations. Moreover, the EPNs for images of human injury was more negative than for non-injured humans in both temporal occipital and occipital regions. In contrast to predictions, handguns and snakes led to more negative lateralised EPN than images of human injury, while for midline EPN snake and unarmed handgun images evoked more negative activity than aimed handguns and human injury. Differences were also evident in the modulation of the lateralised and midline EPNs elicited by reptile and firearm stimuli. Reptiles evoked more negative midline EPN at occipital sites, whereas the reverse pattern of lateralised EPN modulation was observed at temporal occipital electrodes. However, the magnitude of this difference was larger in the temporal occipital region compared to the occipital location. Unarmed handguns were differentiated from other firearms in lateralised EPN, whereas the midline EPN for aimed handguns was reduced compared to other firearms. No modulation of threat level was observed for reptile stimuli in activity for the lateralised EPN, but for the midline EPN snakes elicited more negative activity than turtles.

3.2.2. The N2 (200–350 ms)

Modulation for a central medial N2 was evident at midline central and central parietal electrodes (Fig. 3), and N2 mean amplitudes were derived from 200 to 350 ms post-stimulus from electrodes C1, Cz, C2, CP1, CPz, and CP2. Parameter information for the Stimulus type and Threat level relationships in N2 activity can be found in Table 4.

Mean N2 activity was most negative for human stimuli, followed by reptiles, and then firearms (Fig. 3, all $ps < .001$). Images of human injury also elicited more negative EPN than snake or handgun images (all $ps < .001$). Non-injured humans evoked significantly more negative N2 activity than images showing severe or moderate levels of injury. Unlike human stimuli, differences between all three threat levels within the reptile and firearm stimulus categories were significant (Fig. 3). For

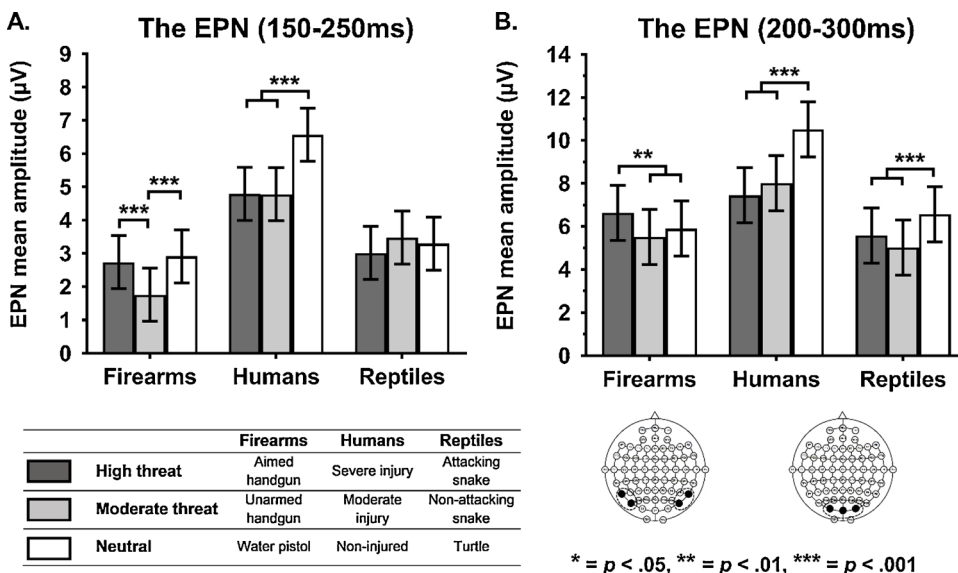


Fig. 2. Estimated marginal means for reptile, firearm and human stimuli, categorised by threat level (i.e., high threat, moderate threat, neutral) from the two EPN final models. The 2D electrode maps show the sites from which activity for the lateralised EPN and the midline EPN were derived. Vertical bars denote 95% confidence intervals.

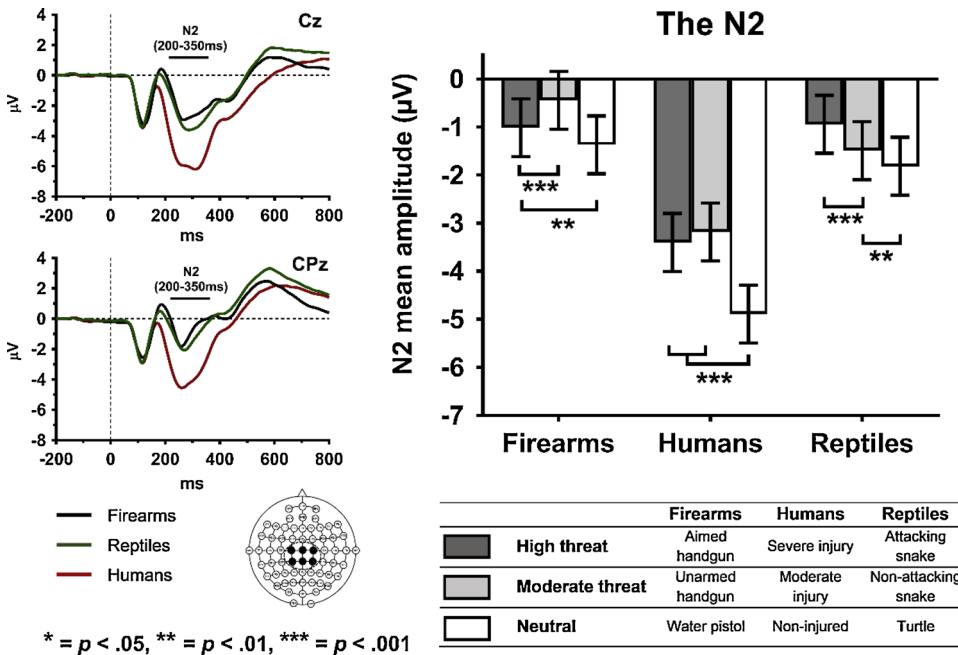


Fig. 3. Mean ERP waveforms for the N2 at the central and central parietal midline electrodes, categorised by stimulus type (left panel), and estimated marginal means from the N2 final model for reptile, firearm and human stimuli, categorised by threat level (i.e., high threat, moderate threat, neutral; right panel, vertical bars denote 95% confidence intervals). The 2D electrode map shows the sites from which activity for the N2 was derived.

reptile stimuli N2 amplitudes were most negative for turtle images, followed by images of non-attacking snakes, and then attacking snakes. In contrast, for firearm stimuli N2 activity was largest for water pistol images, followed by images of aimed handguns, and then unarmed handguns.

3.2.2.1. N2 summary. Hypotheses generated for the EPN were generalised to the N2 as the two components may index the same type of ERP activity due to the overlap in the timing of these negativities. The N2 was largest for images of humans, followed by reptiles, and then firearms. Similar to EPN modulation, images of human injury evoked larger amounts of N2 activity than snakes and handguns. N2 amplitudes were larger for non-injured humans compared to injured humans, a pattern of ERP activity that corresponds to the modulation of the two EPNs. N2 modulation also aligned with the threat level of reptile stimuli. In relation to firearms, the N2 was largest for water pistols, followed by aimed handguns, and then unarmed handguns.

3.2.3. Late positivity

Fig. 4 shows the averaged ERP waveforms for the midline electrodes CPz, Pz and POz. A posterior positive peak in parietal occipital regions was observed between 300–400 ms at midline electrodes for most participants; this ERP activity was designated the P3b. Between 450 and 700 ms, activity for a LPC was also evident at midline electrodes in central parietal and parietal regions. Mean amplitudes for the P3b were computed from 300 to 380 ms post-stimulus, while those for the LPC were derived from 500 to 650 ms post-stimulus. Parameter information for the Stimulus type and Threat level relationships for the P3b and the LPC are shown in Table 5.

3.2.3.1. The P3b (300–380 ms). In contrast to predictions, P3b activity was significantly more positive for aimed handguns and severe injury compared with scenes of attacking snakes (Fig. 5A, both $ps < .001$). The pattern of P3b modulation elicited by firearm and human stimuli also differed from that evoked by reptile stimuli. P3b activity was most positive for low threat turtle images, followed by images of attacking snakes, and then non-attacking snakes. In contrast, P3b amplitudes were most positive for high threat forms of firearm and human images, followed by moderate threat stimuli, and then neutral stimuli.

3.2.3.2. The LPC (500–650 ms). Confirming the hypotheses for late positive activity, images of attacking snakes evoked significantly more positive LPC activity than those showing severe injury or aimed handguns (Fig. 5B, both $ps < .001$). Unlike P3b modulation, patterns of LPC activity were similar between firearm and reptile stimuli. LPC mean amplitudes were significantly larger for images of aimed handguns compared with that elicited by unarmed handguns and water pistols. A similar pattern of mean activity was observed for reptile stimuli, as attacking snakes evoked significantly more positive LPC amplitudes than non-attacking snakes and turtles. In contrast, LPC activity for images showing severe or moderate levels of injury were significantly larger than those elicited in response to images of non-injured humans.

3.2.3.3. Late positivity summary. Two sources of late positivity were observed in averaged ERP waveforms, and mean amplitudes were derived and analysed for both late positivities as activity for each late positive component was maximal at different posterior locations. The late positivity in parietal occipital regions, designated as the P3b, was sensitive to the threat level of images with high social relevance. P3b amplitudes were larger for aimed handguns and severe injury compared to attacking snakes, whereas attacking snakes elicited more positive LPC activity than severe injury and aimed handguns. P3b became incrementally more positive as the threat level of firearm and human stimuli increased. For reptile stimuli, however, the P3b was largest for turtles, followed by attacking snakes, and then non-attacking snakes. This contrasted to LPC modulation, as aimed handguns and attacking snakes evoked larger amounts of LPC activity than moderate threat and neutral images within their respective stimulus categories. As with EPN and N2 activity, images of human injury were differentiated from non-injured humans in LPC activity.

4. Discussion

The present research investigated the role of biological and social relevance, via semantic differentiation, in ERP modulation elicited by the depiction of threats during picture processing. Predictions were made for the EPN and late positivity as activity for these types of ERP activity were expected to index the stimulus type and threat level of the presented images. Multiple sources of EPN and late positive activity were observed in ERP waveforms. Amplitude modulation for two types

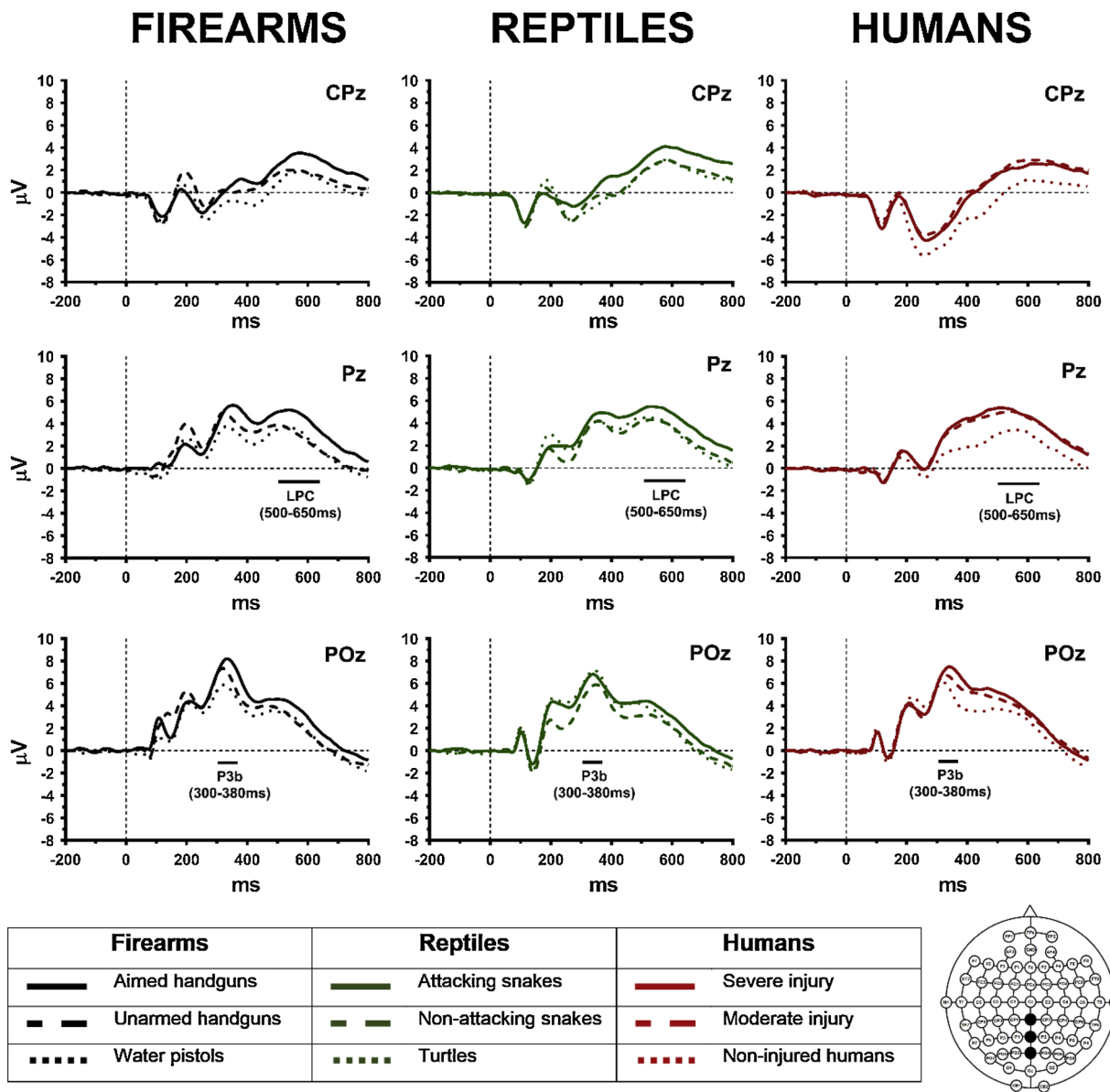


Fig. 4. Mean ERP waveforms showing modulation for the P3b (300–380 ms) and the LPC (500–650 ms) in response to reptile, firearm and human stimuli, categorised by threat level. Electrode locations are the midline sites CPz to POz (see 2D electrode map bottom right-hand corner).

of EPN, the N2, the P3b and the LPC were identified and analysed. Given the rationale of the present study is based on the deconstruction of threat in picture processing, the impact of EEG methodology on this question was also important to address. Hypotheses made in relation to the EPN were not supported, as snakes elicited more negative lateralised and midline EPN than human injury images in occipital or temporal occipital regions. However, predictions made regarding late positivity and the emotional salience of aggressive versions of reptile and firearm stimuli were confirmed via modulation of LPC activity. Overall, the current findings indicate that semantic differentiation contributes to the emotional salience of unpleasant images and that this relationship is indexed by ERP modulation during the picture processing stream.

The present findings suggest several avenues of investigation for future research. Some aspects of the reported ERP modulation will require further replication to determine if the observed effects generalise to paradigms other than the image rating task utilised, especially in the case of the EPN. However, one of the key strengths of the current research is the demonstration that the action disposition of a threat (e.g.,

attack intent) contributes to the emotional salience of unpleasant images. The perceptual characteristics that denote aggression and attack suggest the potential for physical harm to occur to the observer via imminent violence, while injury or mutilation represent a less urgent, though no less important, threat to one’s continued survival. Differentiation between negative stimuli in ERP modulation based on the degree of threat an unpleasant image represents also supports an aversion divergence form of negativity bias in picture processing. As discussed previously, prior EEG research has suggested the existence of an aversion divergence in ERP modulation for unpleasant images (e.g., Carretié et al., 2011; Krusemark & Li, 2011; Lu et al., 2016; Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010; Wheaton et al., 2013).

4.1. Biological relevance and early to middle latency negativity

Throughout the following sections brief summaries of the relevant ERP modulation are integrated into the discussion of the specific component. This approach has been taken as interim summaries of the

Table 5
Parameter information (β [95% CI]) for the main relationships Stimulus type and Threat level in the P3b and LPC final models. Asterisks denote the level of significance between levels (* < .05, ** < .01, *** < .001).

Stimulus type	β [95% CI]
<i>The P3b</i>	
Firearms vs. Humans	-0.71 [-0.27, -1.16]**
Firearms vs. Reptiles	4.57 [5.18, 3.97]***
Humans vs. Reptiles	-1.47 [-1.03, -1.92]***
<i>The LPC</i>	
Firearms vs. Humans	-0.46 [-0.20, -0.72]***
Firearms vs. Reptiles	0.43 [0.69, 0.17]**
Humans vs. Reptiles	-1.46 [-1.20, -1.72]***
Threat level	β [95% CI]
<i>The P3b</i>	
High vs. Moderate	-0.27 [0.18, -0.71]
High vs. Neutral	-0.67 [-0.23, -1.11]**
Moderate vs. Neutral	0.32 [0.76, -0.13]
<i>The LPC</i>	
High vs. Moderate	-1.36 [-1.15, -1.58]***
High vs. Neutral	-1.36 [-1.15, -1.57]***
Moderate vs. Neutral	0.27 [0.48, 0.05]*

main findings in the present study have been provided throughout the Results section. First, findings related to lateralised and midline EPN activity will be discussed. The present findings suggest that biological relevance is not the only determinant of EPN modulation. Prior EEG studies have reported that snake images elicit more negative EPN activity than a diverse range of organic stimuli (e.g., spiders, birds, butterflies, other reptiles; Grassini, Holm, Railo, & Koivisto, 2016, 2019; Langeslag & van Strien, 2018a, 2018b; van Strien et al., 2014; van Strien & Isbell, 2017). This pattern of activity was replicated in the present study in comparisons between images of snakes, turtles and humans in midline EPN amplitudes. However, the magnitude of the midline EPN was similar for snake, unarmed handgun, and water pistol images. Moreover, differentiation between snakes and turtles did not occur in modulation for the lateralised EPN. It is important to note, though, that the difference between reptile and firearm stimuli in occipital regions approached significance. The inclusion of reptile and firearm images with varying levels of threat in the present study indicates the action disposition of these stimuli may influence the magnitude of EPN modulation.

Recent research has focused on modulation of the EPN component

in occipital regions (e.g., Grassini et al., 2019; van Strien et al., 2014). Typically, EEG studies that analyse the EPN in occipital and temporal occipital regions combine these data into the same analysis (e.g., Weinberg & Hajcak, 2010; Schupp, Junghöfer, Weike, & Hamm, 2004; van Strien & Isbell, 2017). The present findings indicate the lateralised and midline EPN may be distinct types of ERP modulation. Unarmed handguns evoked larger amounts of lateralised and midline EPN than aimed handguns, but this same differentiation between water pistols and aimed handguns only occurred for the midline EPN in occipital regions. Despite differences in activity for the two EPNs in relation to reptile and firearm stimuli, lateralised and midline EPN modulation was consistently more negative for human injury compared to non-injured humans. Snake and handgun images also led to more negative lateralised and midline EPN than human injury, results which differ from EEG studies that have found no difference in EPN modulation evoked by images showing threat or mutilation (Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010). In addition to biological relevance, future research on the lateralised and midline EPN should consider the role of aversion divergence on the magnitude of activity for this ERP component.

The EPN activity observed in the present study may simply be due to the regions in which each type of ERP activity was maximal. Modulation of the EPN could originate from the visual cortex areas (Junghöfer et al., 2006), therefore lateralised and midline EPN modulation may reflect perceptual differences in the processing of reptile and firearm stimuli. As an example, Grassini et al. (2019) found that rope and snake images led to more negative occipital EPN than images of guns and birds, but when snakes were not included during RSVP the EPN for ropes, guns and spiders was of similar magnitude. The authors suggested that the absence of a threatening curvilinear stimuli (i.e., snakes) led to the lack of EPN modulation. Another reason for the discrepancy in lateralised and midline EPN modulation may be the timeframe chosen to derive mean amplitudes in the present study. He, Kubo, and Kawai (2014) analysed mean activity for the occipital EPN in 150–300 ms, 200–300 ms and 225–300 ms time windows, and found larger occipital EPN for snake compared to bird images for all three timings. However, like other EEG studies that have focused on the occipital EPN (e.g., Grassini et al., 2019; van Strien et al., 2014), He et al. (2014a) employed a RSVP to present their images.

ERP modulation for middle latency components, such as the N2 and the P2, have been linked with emotional salience in picture processing (Hajcak et al., 2012; Olofsson et al., 2008). However, it is difficult to tie ERP modulation traditionally linked with cognitive processing to

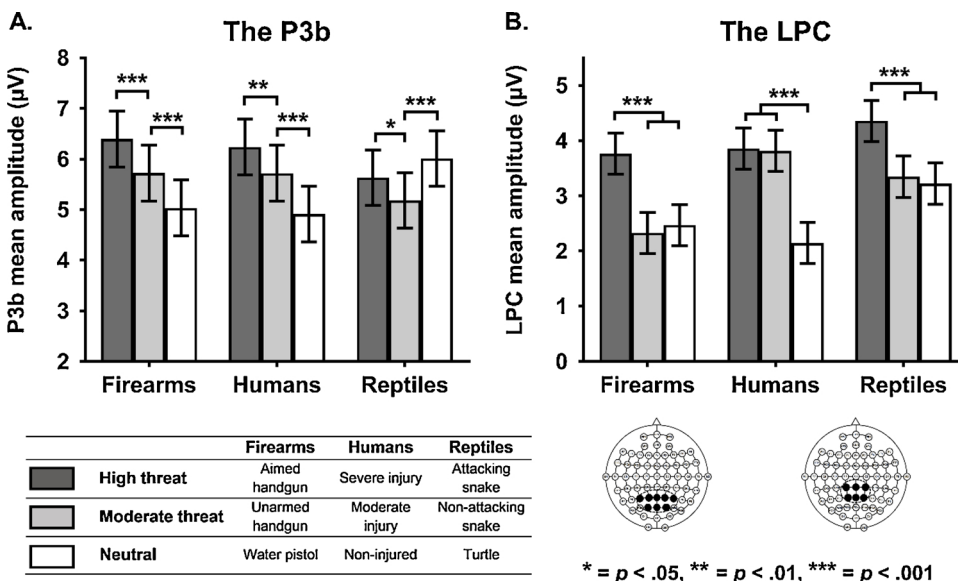


Fig. 5. Estimated marginal means for reptile, firearm and human stimuli, categorised by threat level (i.e., high threat, moderate threat, neutral) from the P3b and the LPC final models. The 2D scalp topographies show the electrodes from which P3b (parietal, parietal occipital) and LPC (central parietal, parietal) activity were derived. Vertical bars denote 95% confidence intervals.

emotional salience, such as the N2 (Folstein & Van Petten, 2008), as images are inherently more perceptually complex than the basic types of stimuli utilised in cognitive EEG research. The present findings for the N2 suggest semantic differentiation is one way to examine these basic ERP components in picture processing. In terms of stimulus type, the pattern of N2 amplitudes approximated a reversal of activity observed for the EPNs. The N2 was largest for images of humans, while lateralised and midline EPN activity was most reduced for these stimuli. The temporal occipital EPN allegedly occurs alongside a frontal central positivity and in the present study the observed pattern of N2 activity may have approximated this modulation, but in the negative range (Schupp et al., 2006). This relationship was further supported by the same pattern of differentiation occurring between the threat levels of firearm stimuli for the N2 and the lateralised EPN in temporal occipital regions, but in the opposite direction. Interestingly though, the N2 also indexed the threat level of reptile stimuli, as N2 activity was largest for turtles, followed by non-attacking snakes, and then attacking snakes.

4.2. The interplay between social and biological relevance in late positivity

The use of injured humans as a threat stimulus was novel in the present study, as these scenes show an aversive outcome of an external danger or hazard. Unlike snakes and handguns, the intensity of injury scenes did not modulate EPN, N2 or LPC activity. The emotional salience of human injury was still confirmed though, as images of human injury were differentiated from neutral images showing humans engaged in everyday activities in EPN, N2, and LPC activity (Schäfer et al., 2010; Weinberg & Hajcak, 2010). This lack of differentiation between high and moderate threat injury was consistent with the affective ratings upon which image selection was based, as the magnitude of the difference between ratings of severe and non-serious injury was smaller compared to that for high threat and moderate threat snakes and handguns. This indicates that the unpleasantness and intensity of injury images was not driven by whether the injured person was conscious or not, or the severity of the mutilation. Interestingly though, P3b modulation paralleled the threat level of both firearm and human stimuli, a finding which suggests this late positivity indexes the social relevance of threats. However, there was some evidence that biological relevance also impacts P3b modulation, as P3b activity for snake images was reduced compared to turtle images.

Bartholow (2016) suggests that aggression is inherently a social behaviour, a premise that may explain the P3b modulation observed in the present study in relation to socially relevant threat. Human and non-human animals both enact adaptive forms of aggression (e.g., hunting, self-defence, mating competition), which in turn facilitates continued survival. Thus, P3b modulation during picture processing may be tied to aggression and violence being forms of non-verbal communication as the P3b is thought to be a neural indicator of attentional and task engagement (Polich, 2007, 2012). The depiction of an aimed handgun or severely injured person could engage the most attentional resources due to these images being extreme examples of socially relevant threat. In terms of evaluative space, the actual or implied presence of another human may separately modify the tendency to approach or avoid a negative stimulus. A stimulus with high social relevance could also require a more nuanced behavioural response in which contextual information moderates the elicitation of defensive motivation in a top-down manner. In the case of the image rating task, the focus of the participants on the affective qualities of the presented images may have resulted in the differentiation between high threat, moderate threat and neutral images for human and firearm stimuli.

Perhaps the most theoretically meaningful finding from the present study was LPC modulation in response to the threat level of reptile and firearm images. Attacking snakes evoked larger LPC amplitudes than aimed handguns and human injury, suggesting biological relevance contributes to the magnitude of LPC activity. However, high threat

versions of snakes and handguns were both differentiated from moderate threat and neutral stimuli in LPC amplitudes. This raises the possibility that the depiction of attack or aggression may have driven the ERP modulation observed for late positive components in response to threat stimuli in prior research (Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010; Wheaton et al., 2013). The present findings also highlight the need to separate the different types of late positivity elicited by images. Matsuda and Nittono (2015) used temporal-spatial principal component analysis to examine ERP modulation evoked by unpleasant and neutral IAPS images. The authors found evidence for multiple late positive components, including two types of LPP activity and a P3 component in posterior regions. Modulation for an EPN peaking between 150–250 ms in occipital regions was also reported, although this activity also appears to have extended into temporal occipital regions.

Though not directly comparable, the semantic differentiation observed for unpleasant images in the present study corresponds to the results of two studies that employed brain-based measures to index the neural response to negative stimuli. Lu et al. (2016) found that images with fear content of moderate intensity (i.e., human and animal threat) evoked more negative frontal central N2 (190–290 ms) activity than high intensity fear images, a difference that was not found for disgust images. In contrast, high intensity disgust images elicited more positive LPC (400–700 ms) activity than those showing moderate intensity disgust content, a difference not found for fearful images. In another study, Kveraga et al. (2014) reported that BOLD activity corresponding to activation of the amygdala and the periaqueductal grey cortex, two brain regions associated with threat-related processing, was largest for images showing direct threat, followed by indirect threat, and then merely negative images. In this context, merely negative images included scenes of animals or humans who were dead, injured, or unconscious. Direct threat consisted of images depicting clear attack intent, such as animals with bared fangs and humans armed with weapons, while scenes of indirect threat showed attack intent from a third-person perspective (e.g., animal attacks, crime).

4.3. The emotional salience of threat: Implications and future directions

The present findings suggest several pathways for the future investigation of aversion divergence in picture processing. To recap, aversion divergence is a term to describe semantic differentiation between negative stimuli, a concept with clear implications for how defensive motivation and the negativity bias are characterised in picture processing research. The present study builds upon prior EEG research which indicates that threat, disgust, and mutilation images are distinguished from other types of unpleasant images (Schäfer et al., 2010; Schupp, Cuthbert et al., 2004; Weinberg & Hajcak, 2010) and may each elicit distinct patterns of ERP modulation (Carretié et al., 2011; Krusemark & Li, 2011; Lu et al., 2016). A promising avenue of investigation would be to address methodological inconsistencies between EEG studies to clarify what types of ERP modulation index aversion divergence. Comparison of the EPN and the late positivity elicited by RSVP, oddball tasks and other types of paradigms used to present images is one such instance. Further examination of the occurrence of multiple types of ERP activity that could denote the EPN or late positivity is also necessary. Due to the complex perceptual properties of many images, ERP component overlap may be unavoidable in some cases.

ERP measures are neural correlates of the time flow of processing in response to stimuli, visual or otherwise. Thus, any feature present in an image or a task demand experienced by a participant, may lead to its own unique pattern of ERP modulation. Thus, the investigation of emotional salience in picture processing must consider the contribution of perceptual elements to the magnitude of the EPN and late positivity in response to images. It is possible the image rating task led to the unique separation of P3b and LPC activity observed in the present

study. For instance, Everaert, Spruyt, Rossi, Pourtois, and De Houwer (2014) found the magnitude of difference waveforms indexing the frontal P3a (220–400 ms) in response to face stimuli during an oddball task was dependant on the type of instructions provided to participants. However, difference waveforms representing the central parietal P3b (400–800 ms) were not affected by the provided instructions. The P3b in the present study was named as such to differentiate this modulation from the LPC. However, it is possible our P3b was similar to the posterior P3a reported by Delplanque, Silvert, Hot, Rigoulot, and Sequeira (2006). In Delplanque et al.'s study, high-arousing unpleasant IAPS images led to larger P3a activity than neutral and high-arousing pleasant images at occipital and temporal occipital electrodes.

One aspect of the present research that has not been addressed up until this point is the active incorporation of individual differences into the study design via LME analysis. Brain-based measures such as EEG often produce data that are repeated measures on the same subject. In the case of the present study, at least 40 repeat measures were used to generate ERPs for each image condition, indicating these data are highly correlated. While the limits of this approach are generally understood by researchers who conduct EEG studies, there is still a need in psychological research to acknowledge the nested structure of our data and use appropriate statistical techniques to allow for this (Boisgontier & Cheval, 2016). Another advantage of LME analysis for EEG data is that a model design is not directly imposed onto a dataset. Rather, a model design must be built from the ground up, such that variables that do not explain variance in the dataset are dropped from the final model. While there is still a need to further develop the application of techniques such as LME analysis for EEG research, these methods offer the chance to advance our current understanding of what kinds of ERP modulation are similar, or different, between individuals.

The use of LME analysis may have contributed to the discrepancies between the findings in the present research and prior EEG studies. As suggested previously, however, images are complex visual stimuli, and it is not surprising that the range of ERP modulation elicited by images is also multifaceted. The key is to use the existing jigsaw pieces that prior researchers have provided to continue enhancing our understanding of picture processing. Examining whether the effects observed for attack intent generalise to other types of aversive stimuli in ERP modulation, especially for late positivity, is one avenue of potential investigation (e.g., other reptiles, animals, weapons). Other concerns for future research include exploring the relationship between lateralised and midline EPN modulation, clarifying whether the N2 elicited during picture processing is independent of EPN activity, and determining if there is late positivity which is uniquely responsive to attentional focus during picture processing (e.g., the P3b observed in the present study). Characterising these aspects of defensive motivation indexed by ERP modulation will also help define the relationship between perceptual processing and emotional salience in the neural response to an unpleasant image, especially those which denote threat.

To summarise, in the present study LPC activity indexed the attack intent of reptile and firearm images, while P3b modulation corresponded to the threat level of stimuli with high social relevance (i.e., firearms, humans). Lateralised and midline EPN modulation due to reptiles and firearms varied between occipital and temporal occipital regions and threat level appeared to play a role in these discrepancies. N2 modulation was observed in frontal central regions and this negativity aligned with the threat level of reptiles. Lastly, high and moderate threat human injury was differentiated from non-injured human images in EPN, N2 and LPC activity. The current findings support an aversion divergence view of picture processing and indicate that the emotional salience of negative stimuli is cumulative in nature. The presence of multiple perceptual cues associated with potential threat may enhance the relative salience of an unpleasant image. This perspective explains why images of human mutilation are often differentiated from other negative stimuli, as the lack of overt aggression is overruled by the presence of other emotionally salient features (e.g., blood, human,

dead/unconscious, ambiguous cause/assailant). Variation in ERP modulation across the picture processing stream could index the different stages at which these cues are perceived, assessed, and evaluated. Biological and social relevance may play an indirect role in this process via perceptual cues which are related to each conceptual dimension. Visual elements such as skin, texture, and other indicators of organic matter may denote biological relevance, whereas social relevance could be driven by perceptual cues associated with humans (e.g., spatial configuration of a face). Defensive motivation may depend upon the likelihood a stimulus represents a threat to an individual and in order to further clarify the emotional salience of potential threats, real or abstract, this aspect of the negativity bias in picture processing must continue to be addressed.

Funding

This research was supported by an Australian Postgraduate Award to Rosemarie K. Miller. This research was not supported by any other specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.biopsycho.2019.107788>.

References

- Amodio, D. M., Bartholow, B. D., & Ito, T. A. (2014). Tracking the dynamics of the social brain: ERP approaches for social cognitive and affective neuroscience. *Social Cognitive and Affective Neuroscience*, 9(3), 385–393. <https://doi.org/10.1093/scan/nst177>.
- Australian Copyright Council (2016). *Research or study*. July, Retrieved from http://www.copyright.org.au/acc_prod/ACC/Information_Sheets/Research_or_Study.aspx.
- Bartholow, B. D. (2016). The aggressive brain. In B. J. Bushman (Ed.), *Aggression and violence: A social psychological perspective* (pp. 47–60). New York: Routledge. <https://doi.org/10.4324/9781315524696-9>.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), <https://doi.org/10.18637/jss.v067.i01>.
- Boisgontier, M. P., & Cheval, B. (2016). The anova to mixed model transition. *Neuroscience and Biobehavioral Reviews*, 68, 1004–1005. <https://doi.org/10.1016/j.neubiorev.2016.05.034>.
- Bradley, M. M., Sabatinelli, D., & Lang, P. J. (2014). Emotion and motivation in the perceptual processing of natural scenes. In K. Kveraga, & M. Bar (Eds.), *Scene vision* (pp. 273–290). <https://doi.org/10.7551/mitpress/9780262027854.003.0013>.
- Carretié, L., Mercado, F., Tapia, M., & Hinojosa, J. A. (2001). Emotion, attention, and the 'negativity bias', studied through event-related potentials. *International Journal of Psychophysiology*, 41(1), 75–85. [https://doi.org/10.1016/S0167-8760\(00\)00195-1](https://doi.org/10.1016/S0167-8760(00)00195-1).
- Carretié, L., Albert, J., López-Martín, S., & Tapia, M. (2009). Negative brain: An integrative review on the neural processes activated by unpleasant stimuli. *International Journal of Psychophysiology*, 71(1), 57–63. <https://doi.org/10.1016/j.ijpsycho.2008.07.006>.
- Carretié, L., Ruiz-Padial, E., López-Martín, S., & Albert, J. (2011). Decomposing unpleasantness: Differential exogenous attention to disgusting and fearful stimuli. *Biological Psychology*, 86(3), 247–253. <https://doi.org/10.1016/j.biopsycho.2010.12.005>.
- Dai, Q., Wei, J., Shu, X., & Feng, Z. (2016). Negativity bias for sad faces in depression: An event-related potential study. *Clinical Neurophysiology*, 127(12), 3552–3560. <https://doi.org/10.1016/j.clinph.2016.10.003>.
- Delplanque, S., Silvert, L., Hot, P., Rigoulot, S., & Sequeira, H. (2006). Arousal and valence effects on event-related P3a and P3b during emotional categorization. *International Journal of Psychophysiology*, 60(3), 315–322. <https://doi.org/10.1016/j.ijpsycho.2005.06.006>.
- Dong, G., Zhou, H., Zhao, X., & Lu, Q. (2011). Early negativity bias occurring prior to experiencing of emotion: An ERP study. *Journal of Psychophysiology*, 25(1), 9–17. <https://doi.org/10.1027/0269-8803/a000027>.
- Everaert, T., Spruyt, A., Rossi, V., Pourtois, G., & De Houwer, J. (2014). Feature-specific attention allocation overrules the orienting response to emotional stimuli. *Social Cognitive and Affective Neuroscience*, 9(9), 1351–1359. <https://doi.org/10.1093/scan/nst121>.

- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, 45(1), 152–170. <https://doi.org/10.1111/j.1469-8986.2007.00602.x>.
- Grabowska, A. (2017). Sex on the brain: Are gender-dependent structural and functional differences associated with behavior? *Journal of Neuroscience Research*, 95(1–2), 200–212. <https://doi.org/10.1002/jnr.23953>.
- Grassini, S., Holm, S. K., Railo, H., & Koivisto, M. (2016). Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. *Biological Psychology*, 121, 53–61. <https://doi.org/10.1016/j.biopsycho.2016.10.007>.
- Grassini, S., Railo, H., Valli, K., Revonsuo, A., & Koivisto, M. (2019). Visual features and perceptual context modulate attention towards evolutionarily relevant threatening stimuli: Electrophysiological evidence. *Emotion*, 19(2), 348–364. <https://doi.org/10.1037/em0000434>.
- Hajcak, G., Weinberg, A., MacNamara, A., & Foti, D. (2012). ERPs and the study of emotion. In S. J. Luck, & E. S. Kappenman (Eds.). *Oxford handbook of event-related potential components* (pp. 441–472). United States: Oxford University Press.
- He, H., Kubo, K., & Kawai, N. (2014a). Spider is not special comparing with other animals in human early visual attention: Evidence from event-related potentials. *Japanese Cognitive Science Society*, 187–190. Retrieved from http://www.jcss.gr.jp/meetings/JCSS2014/proceedings/pdf/JCSS2014_05-4.pdf.
- He, H., Kubo, K., & Kawai, N. (2014b). Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. *NeuroReport*, 25(13), 1049–1053. <https://doi.org/10.1097/WNR.0000000000000227>.
- Hilgard, J., Weinberg, A., Hajcak Proudfit, G., & Bartholow, B. D. (2014). The negativity bias in affective picture processing depends on top-down and bottom-up motivational significance. *Emotion*, 14(5), 940–949. <https://doi.org/10.1037/a0036791>.
- Hox, J. J., Moerbeek, M., & van de Schoot, R. (2017). *Multilevel analysis: Techniques and applications* (3rd ed.). Routledge <https://doi.org/10.4324/9781315650982>.
- Huang, Y. X., & Luo, Y. J. (2006). Temporal course of emotional negativity bias: An ERP study. *Neuroscience Letters*, 398(1–2), 91–96. <https://doi.org/10.1016/j.neulet.2005.12.074>.
- Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology*, 19(2), 113–124. <https://doi.org/10.1097/00004691-200203000-00002>.
- Isbell, L. A. (2009). *The Fruit, the tree, and the serpent: Why we see so well*. Cambridge, Massachusetts: Harvard University Press.
- Jasper, H. H. (1958). Appendix to report to committee on clinical examination in EEG: The ten-twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology*, 10, 371–375.
- Junghöfer, M., Sabatinelli, D., Bradley, M. M., Schupp, H. T., Elbert, T. R., & Lang, P. J. (2006). Fleeting images: Rapid affect discrimination in the visual cortex. *Neuroreport*, 17(2), 225–229. <https://doi.org/10.1097/01.wnr.0000198437.59883.bb>.
- Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., ... Yee, C. M. (2014). Committee report: Publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, 51(1), 1–21. <https://doi.org/10.1111/psyp.12147>.
- Kok, A. (1997). Event-related-potential (ERP) reflections of mental resources: A review and synthesis. *Biological Psychology*, 45(1–3), 19–56. [https://doi.org/10.1016/S0310-0511\(96\)05221-0](https://doi.org/10.1016/S0310-0511(96)05221-0).
- Krusemark, E. A., & Li, W. (2011). Do all threats work the same way? Divergent effects of fear and disgust on sensory perception and attention. *Journal of Neuroscience*, 31(9), 3429–3434. <https://doi.org/10.1523/JNEUROSCI.4394-10.2011>.
- Kveraga, K., Boshyan, J., Adams, R. B., Mote, J., Betz, N., Ward, N., ... Barrett, L. F. (2014). If it bleeds, it leads: Separating threat from mere negativity. *Social Cognitive and Affective Neuroscience*, 10(1), 28–35. <https://doi.org/10.1093/scan/nsu007>.
- Lang, P. J., & Bradley, M. M. (2013). Appetitive and defensive motivation: Goal-directed or goal-determined? *Emotion Review*, 5(3), 230–234. <https://doi.org/10.1177/1754073913477511>.
- Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology*, 30(3), 261–273. <https://doi.org/10.1111/j.1469-8986.1993.tb03352.x>.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual*. Gainesville, Florida: University of Florida.
- Langeslag, S. J. E., & van Strien, J. W. (2018a). Cognitive reappraisal of snake and spider pictures: An event-related potentials study. *International Journal of Psychophysiology*, 130, 1–8. <https://doi.org/10.1016/j.ijpsycho.2018.05.010>.
- Langeslag, S. J. E., & van Strien, J. W. (2018b). Early visual processing of snakes and angry faces: An ERP study. *Brain Research*, 1678, 297–303. <https://doi.org/10.1016/j.brainres.2017.10.031>.
- LeDoux, J. E. (2012). Rethinking the emotional brain. *Neuron*, 73(4), 653–676. <https://doi.org/10.1016/j.neuron.2012.02.004>.
- LeDoux, J. E., Moscarello, J., Sears, R., & Campese, V. (2017). The birth, death and resurrection of avoidance: A reconceptualization of a troubled paradigm. *Molecular Psychiatry*, 22(1), 24–36. <https://doi.org/10.1038/mp.2016.166>.
- Lu, Y., Luo, Y., Lei, Y., Jaquess, K. J., Zhou, C., & Li, H. (2016). Decomposing valence intensity effects in disgusting and fearful stimuli: An event-related potential study. *Social Neuroscience*, 11(6), 618–626. <https://doi.org/10.1080/17470919.2015.1120238>.
- Luck, S. J. (2014). *An introduction to the event-related potential technique* (2nd ed.). Massachusetts, US: The MIT Press.
- Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't): How to get significant effects. *Psychophysiology*, 54(1), 146–157. <https://doi.org/10.1111/psyp.12639>.
- Matsuda, I., & Nittono, H. (2015). Motivational significance and cognitive effort elicit different late positive potentials. *Clinical Neurophysiology*, 126(2), 304–313. <https://doi.org/10.1016/j.clinph.2014.05.030>.
- Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society, Interface*, 14(134), 20170213. <https://doi.org/10.1098/rsif.2017.0213>.
- Norris, C. J., Gollan, J., Berntson, G. G., & Cacioppo, J. T. (2010). The current status of research on the structure of evaluative space. *Biological Psychology*, 84(3), 422–436. <https://doi.org/10.1016/j.biopsycho.2010.03.011>.
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, 77(3), 247–265. <https://doi.org/10.1016/j.biopsycho.2007.11.006>.
- Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology*, 112(4), 713–719. [https://doi.org/10.1016/S1388-2457\(00\)00527-7](https://doi.org/10.1016/S1388-2457(00)00527-7).
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., ... Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, 37(2), 127–152.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118(10), 2128–2148. <https://doi.org/10.1016/j.clinph.2007.04.019>.
- Polich, J. (2012). Neuropsychology of P300. In S. J. Luck, & E. S. Kappenman (Eds.). *The Oxford handbook of event-related potential components* (pp. 159–188). New York: Oxford University Press.
- R Core Team (2018). *R: A language and environment for statistical computing (Version 3.5.1)*. Retrieved from Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- RStudio (2016). *RStudio: Integrated development environment for R (Version 0.99.902)*. Boston, MA.
- Ruigrok, A. N. V., Salimi-Khorshidi, G., Lai, M.-C., Baron-Cohen, S., Lombardo, M. V., Tait, R. J., ... Suckling, J. (2014). A meta-analysis of sex differences in human brain structure. *Neuroscience and Biobehavioral Reviews*, 39, 34–50. <https://doi.org/10.1016/j.neubiorev.2013.12.004>.
- Schäfer, A., Scharmüller, W., Leutgeb, V., Köchel, A., & Schienle, A. (2010). Are blood-injection-injury stimuli different from other negative categories? An ERP study. *Neuroscience Letters*, 478(3), 171–174. <https://doi.org/10.1016/j.neulet.2010.05.010>.
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: Event-related brain potential studies. *Progress in Brain Research*, 156, 31–51. [https://doi.org/10.1016/S0079-6123\(06\)56002-9](https://doi.org/10.1016/S0079-6123(06)56002-9).
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Hillman, C., Hamm, A. O., & Lang, P. J. (2004). Brain processes in emotional perception: Motivated attention. *Cognition & Emotion*, 18(5), 593–611. <https://doi.org/10.1080/02699930341000239>.
- Schupp, H. T., Junghöfer, B. M., Weike, B. A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology*, 441–449. <https://doi.org/10.1111/j.1469-8986.2004.00174.x>.
- van Strien, J. W., & Isbell, L. A. (2017). Snake scales, partial exposure, and the Snake Detection Theory: A human event-related potentials study. *Scientific Reports*, 7, 46331. <https://doi.org/10.1038/srep46331>.
- van Strien, J. W., Franken, I. H. A., & Huijding, J. (2014). Testing the snake-detection hypothesis: Larger early posterior negativity in humans to pictures of snakes than to pictures of other reptiles, spiders and slugs. *Frontiers in Human Neuroscience*, 8. <https://doi.org/10.3389/fnhum.2014.00691>.
- 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. <https://doi.org/10.1037/a0020242>.
- Wheaton, M. G., Holman, A., Rabinak, C. A., MacNamara, A., Hajcak-Proudfit, G., & Phan, K. L. (2013). Danger and disease: Electroocortical responses to threat- and disgust-eliciting images. *International Journal of Psychophysiology*, 90(2), 235–239. <https://doi.org/10.1016/j.ijpsycho.2013.08.001>.