The electrophysiological correlates of processing expression intensities along emotion trajectories

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Abstract

In this thesis we utilise the Event Related Potential (ERP) technique to examine how expression intensities are processed along happy and angry emotion trajectories (defined as the continua of expression intensities between Neutral and Prototypical expressions). Emotion trajectories were formed by morphing the emotional faces to display expressions that were 20%, 40%, 60%, 80%, or 100% of the full expression. In both Experiments 1 and 2, we recorded Electroencephalography (EEG) while participants viewed faces that were either neutral in expression, or portrayed happy or angry expressions along an emotion trajectory. In Experiment 1, we examined the automaticity of expression intensity processing where participants were simply required to view the stimuli while performing an infrequent, unrelated task. In Experiment 2, we examined whether voluntary attention to emotion modulates expression intensity processing. In Experiment 1, we found that only high intensities of expression intensities were processed automatically, as shown by modulation of the Early Posterior Negativity (EPN). In Experiment 2, we found facilitatory effects of voluntary attention on expression intensity processing, reflected by graded modulation of the N170 based on expression intensity. Additionally, EPN amplitudes were more graded for angry expressions than happy expression intensities, suggesting that angry intensities were processed in more depth than happy ones. EPN amplitudes for each expression intensity were negatively correlated with the proportions of expressions rated ‘emotional’, suggesting that the EPN is involved in the perception of the emotion rather than the physical differences between expression intensities. In Experiment 3, we examined whether EPN modulation would reflect perceptual shifts in emotion intensity observed in behavioural adaptation/aftereffects experiments. We replicated EPN intensity effects for adaptor stimuli, but not the test stimuli. Furthermore, there were no systematic behavioural effects to assess whether the EPN might reflect perceptual shifts. Further refinement of the adaptation/aftereffects paradigm to utilise in EEG can help tease apart physical and perceptual shifts of emotion. Overall, this thesis provides evidence that expression intensity is coded in the brain, and that it is modulated by explicit attention to emotion. Furthermore, the data suggest that the EPN is associated with participants' evaluation of emotion rather than physical stimulus processing.

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Chapter 1: General Introduction

Emotional facial expressions are highly useful and complex visual stimuli. Visual recognition of different facial emotional expressions involves detecting morphological changes of the face that signify affective meaning. Perceiving others’ expressions provides a signal that we can use to respond suitably (Schupp et al., 2004). Therefore, the ability to detect and decipher expressions rapidly can be extremely beneficial. Research on the mechanisms underlying emotional facial expression processing have typically been grounded in the ‘categorical framework’ (e.g., Batty & Taylor, 2003; Calvo & Beltrán, 2013; Eimer & Holmes, 2007) and relatively little is known about how we process continua of emotional expressions. Recent work using Event Related Potentials (ERPs) as a technique has begun to fill this gap in understanding expression intensity processing; however, there is limited research and it is unclear whether there are systematic modulations of emotion related ERPs. This chapter summarises literature on categorical processing and continuous representation of emotional expressions, and discusses the utility of using ERPs to investigate continuous processing of expressions. The later part of this chapter then outlines the emotion-related ERPs implicated in expression intensity processing, the role of attention in emotional expression processing, and presents the thesis overview.

1.1. Categorical versus continuous frameworks

The categorical framework suggests that there are a small number of distinct emotion categories that expressions can be categorised into based on specific morphological changes in the face (Ekman & Friesen, 1971). Ekman (1992, 1994) suggests that these expressions can also be recognised universally because expressions are the result of the same changes in the muscles that help express the emotion on the face. This framework can help explain our ability to categorise characteristic changes in the morphology of the face into specific prototypical expressions (Ekman, 1992, 1994). Consistent with Ekman's original observations, most studies investigating emotion under this framework use six prototypical facial emotional expressions: joy, anger, fear, surprise, disgust, and sadness (e.g., Batty & Taylor, 2003; Calvo & Beltrán, 2013; Schupp et al., 2004).

In contrast to the categorical framework, continuous processing frameworks suggest that emotion perception is based on graded neural representations that vary along some critical dimensions. Unlike the categorical framework, where each emotion is distinct, the continuous framework suggests that emotions are related by the dimensions that underlie them. The modern two-dimensional continuous processing model, known as the circumplex model (Posner, Russell, & Peterson, 2005; Russell, 1980), suggests that emotional expressions are organised along two dimensions: hedonic valence, which is how pleasant or unpleasant the expression is; and arousal, which is defined by the intensity of activation that the expression evokes.

All continuous models share the idea that processing of emotional expressions should be graded along some critical dimensions, however different approaches emphasise different underlying variables. For instance, the multidimensional face space model (see Valentine, 2001) suggests that all faces can be represented as points in a multidimensional heuristic space where the relationship to each face is a unique point. The vectors in this space then represent select features that underlie face processing. Evidence for this theory comes from adaptation aftereffects studies where an adapting face that varies in a selected dimension (e.g., gender or identity) shifts the perception of the subsequent face in the opposite direction (see Webster & MacLeod, 2011, for a review). Studies using the adaptation/aftereffects paradigm also report shifts in the perception of neutral expressions that are preceded by 'anti-expressions' (faces with the opposite configurations of prototypical expression categories). The magnitude of the shift in perception is based on the intensity of the adapting stimulus (i.e., the more intense the adaptor, the greater the perceptual shift). These data suggest that expression intensity may be an underlying dimension that is coded in the brain (Cook, Matei, & Johnston, 2011; Skinner & Benton, 2010). However, these studies utilise only behavioural reports of perceived emotion to assess perceptual shifts. It is unclear whether these shifts are simply biases towards the prototypical emotional expression response, or whether they represent neural shifts in processing along the dimensions that the expressions vary in.

Categorical and continuous accounts are sometimes thought of as competing theories, but there is evidence for both types of coding (Harris, Young, & Andrews, 2012). The main lines of evidence supporting the categorical model are increased sensitivities to prototypical expressions (also referred to as the boundaries of expression categories), higher accuracies in categorising expressions into prototypical categories, and distinct neural substrates responsible for processing each prototypical expression. The following subsections discuss each of these lines of evidence and considers whether they provide evidence exclusively for categorical processing.

1.1.1. Sensitivity to boundaries of expression categories

In the broader object processing literature, a typical marker for categorical coding is an increased perceptual sensitivity to the boundaries of two categories (Hanard, 1987). For instance, Bornstein and Korda (1984) asked participants to indicate whether two colours were the 'same' or 'different' and showed participants colours of the same hue (e.g., two blues or two greens separated by 6 steps, each 2 nanometres apart) or two different hues that were separated by the same distance as the colours within the hue (e.g., a blue and green separated by 6 steps, each 2 nanometers). They found that the greater the physical difference between the hues was (i.e., more nanometers apart) the faster the participants' responses. Participants were faster at reporting 'different' when the colours differed between two different hues than for the same physical difference within the same hue. These data suggest that we are specialised for processing boundaries of categories (in this case wavelengths demarcating different hues).

Etcoff and Magee (1992) provided early behavioural evidence for enhanced perception of the boundaries of facial emotional expression categories. They asked participants to discriminate between pairs of drawings of facial expressions. The images were morphed so that they differed either within a prototypical emotion category, or differed by the same degree across different emotions. For example, a pair of faces within an expression might consist of two happy expressions that are morphed to different degrees along a trajectory between neutral and happy. In contrast, a pair of faces between expressions might consist of two happy faces that are morphed to different degrees between happy and sad expressions. Participants were asked to discriminate between three expressions that were presented in the sequence; A, B, X, where X was identical to either A or B, and A and B were always physically different. Similar to Bornstein and Korda's (1984) findings with colour, Etcoff and Magee's results showed that the same degree of difference is detected faster and more accurately between prototypical emotional expression categories than within the same emotional expression category. Calder, Young, Perrett, Etcoff, and Rowland (1996) replicated Etcoff and Magee's findings using photographic stimuli rather than drawings and more advanced face morphing techniques, suggesting that these results can be generalised to more ecologically valid stimuli.

Evidence for increased sensitivity for prototypical emotion categories also comes from studies that show that participants have higher accuracy and faster response times when they categorise expressions as basic prototypes when the morphed expression is closer to the prototype, compared with morphs that are closer to neutral expressions, or other prototypical expressions. For instance, Young et al. (1997) asked participants to categorise expressions that were morphed between two prototypical expressions. Participants had slower reaction times while categorising morphs between emotions when the morph was 50% of each emotion. Participants were generally faster and more accurate at identifying the dominant emotion when it accounted for 70% and 90% of the morph, but had difficulty identifying the other emotion that accounted for 30% and 10%, respectively, of the morph.

Taken together, these studies provide evidence that we are able to discriminate prototypical expressions quickly and accurately. Although these data provide evidence for the categorical model, these data do not provide evidence against continuous processing as participants were still able to discriminate between expressions in the same prototypical emotion categories, albeit slower and less accurately. This implies that there is processing of the continua of expressions in the morphs. However, the studies above rely on behavioural measures so we can make only limited inferences about the type of information that is processed to give rise to the behavioural outcomes. Using neural measures can provide further insight into the stimulus processing that takes place before the behavioural outcomes examined in the studies above.

1.1.2. Accuracy in categorising prototypical expressions

The categorical model suggest that faces can be recognised and categorised based on specific morphological changes (see Ekman, 1992). In behavioural studies, participants are typically shown pictures of prototypical emotional expressions that are posed by actors as per the basic emotions framework (Ekman & Friesen 1976). Participants are asked to categorise the expressions using predefined prototypical emotional expression labels (e.g., Calvo & Lundqvist, 2008; Tottenham et al., 2009). These studies show greater than chance accuracy in categorising prototypical expression categories. Participants are also able to categorise expressions morphed between prototypical expression categories (e.g., happy and sad), or between neutral and prototypical categories into prototypical expression categories (Etcoff & Magee, 1992). Furthermore, there is agreement in categories between independent raters, suggesting that the ability to recognise and categorise expressions into prototypical emotion categories is shared across individuals.

The ability to categorise prototypical expressions based on specific morphological changes provides evidence for the categorical framework, but it cannot be conflated with evidence against the continuous framework. As participants are typically provided with prototypical emotion labels in forced choice tasks, limited inferences can be made about the type of information that is being processed. When participants are provided with alternative continuous labels, they can also categorise expressions into the continuous labels. For instance, Adolphs and Alpers (2010) asked participants to rate the valence and arousal level of prototypical expressions from two different face stimulus sets. Participants were able to categorise the different prototypical emotional expressions into different valence and arousal levels, and there was agreement between participants in their valence and arousal ratings for different faces. These data show that it is possible to rate faces on continuous dimensions, not just into prototypical emotion categories. Results from these studies also need to be interpreted with caution, as the ability to categorise expressions according to labels provided by the experimenter does not necessarily reflect the way that the expression is coded. For example, if a face with 50% happy morphed with neural is categorised as happy, it may not be neurally represented in the same way as a prototypical (i.e., 100%) happy face.

Thomas, De Bellis, Graham, and LaBar (2007) used a signal detection approach and asked participants to indicate whether they saw a prototypical expression while participants viewed faces along continua ranging from angry-to-neutral, fear-to-neutral, and angry-to-fear. Instead of responses to two-alternative forced choices, they were able to examine the discriminability of the expression intensities. Thomas and colleagues found that participants were more likely to rate the expressions as the respective prototypical expression as the proportion of the expression in the morphed stimulus increased. These results imply that the continua (intensities) of expressions are coded in a graded manner. They also demonstrate that forced-choice labelling of prototypical expressions might mask processing of expression continua, that can be investigated using other experimental designs.

The evidence for higher accuracies for categorising prototypical expression is also limited because the results may not generalise to expressions that are not posed according to Ekman and Friesen's (1976) basic emotions framework. For instance, there is evidence that people are less accurate at categorising spontaneous prototypical expressions, compared with posed expressions (e.g., Motley & Camden, 1988). Additionally, people are less accurate at categorising dynamic expressions than pictures of static emotional expressions (e.g., Hess & Blairy, 2001; Wagner, 1990). Furthermore, there are systematic confusions between posed prototypical expressions. For instance, fear and surprise are more likely to be confused (e.g., Tottenham et al., 2009), and disgust is often confused for anger (e.g., Palermo & Coltheart, 2004). Therefore, accurate classification of prototypical expressions may not generalise to more ecologically valid stimuli.

1.1.3. Neutral substrates for categorical versus continuous processing

An assumption of the categorical processing model is that there are distinctive neural indices for each prototypical emotional expression. There is some evidence for greater activation in some regions for specific prototypical expressions. For instance, there is greater activity in the left putamen and left insula cortex when participants view disgusted expressions versus other prototypical expressions; greater activity in the right fusiform gyrus and left dorsolateral frontal cortex when participants view fearful faces; and greater activity in the posterior part of right cinguli and medial temporal gyrus of the left hemisphere when participants view angry expressions (Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998). However, while these regions may specialise in processing specific prototypical expression, they are also active for a range of different cognitive processes (e.g., see Uddin, Nomi, Hébert-Seropian, Ghaziri, & Boucher, 2017).

There are also regions that are active while processing all six prototypical basic emotional expressions (e.g., the amygdala, Whalen et al., 2013; the orbitofrontal region, Sprengelmeyer et al., 1998). Sprengelmeyer et al. suggest that expression coding can be considered in multiple stages with parallel non-overlapping processing for (presumably prototypical) expressions that output to a network of areas involved in expression recognition (see Adolphs, 2002). Therefore, neutral substrates for prototypical expressions may not be completely separable.

There is also evidence for neural substrates that process expression intensities independently of emotion type. Harris, Young, and Andrews (2012) used a similar procedure as Etcoff and Magee (1992) in a functional magnetic resonance imaging (fMRI) study to examine responses in face-sensitive regions of the brain. Participants viewed morphed faces that changed between versus within prototypical emotional expression categories. The fMRI data showed that the posterior superior temporal sulcus (pSTS) was sensitive to all changes in expression, whereas the amygdala was only active when processing expressions that were morphed between categories. The amygdala's response seems to reflect categorical processing. It is possible that activation of the pSTS might reflect changes in expression independent structural aspects of the face; however, they found that the pSTs was not active for changes in face identity, and therefore concluded that the pSTS is sensitive to within-emotion differences in emotional expressions (c.f. Sprengelmeyer & Jentzsch, 2006, who suggest that structural codes may also be used for expression intensity processing). These results converge with the neural model of face processing proposed by Haxby, Hoffman, and Gobbini (2000) which suggests that the pSTS is involved in processing changeable aspects of the face that are associated with expression.

The data discussed in this section suggest that there is limited evidence for distinct substrates for processing specific prototypical emotional expressions. Emotional expression processing seems to occur in a network of regions that are sensitive to expression intensities (i.e., to the continua of expressions) as well as prototypical emotional expressions.

1.1.4. Categorical versus continuous processing summary

The categorical framework has generated fruitful research into our ability to process discrete prototypical expression categories, as per the basic emotions' theory. The sections above reviewed the main lines of evidence for categorical processing and discussed why the data may not provide exclusive evidence for the categorical model. Studies showing increased sensitivity to the boundaries of expressions also show processing of differences in intensity within a prototypical expression, albeit slower than processing differences between two prototypical categories. A majority of these studies use behavioural paradigms that examine the behavioural responses to processing prototypical expressions, and they offer limited insight into how expression intensities are processed. Neuroimaging studies can provide a window into stimulus processing that is independent of response related processing.

Taken together, the evidence suggests that emotional facial expressions are processed both categorically and continuously. However, behavioural data and existing neuroimaging data are insufficient to deduce how expression intensities are processed. More recently, a few studies have utilised the ERP technique to explicitly investigate expression intensity processing. The following sections discusses the utility of the ERP technique for investigating emotional expression processing, and outlines the ERPs that may be implicated in expression intensity processing.

1.2. ERPs as a tool for investigating emotional expression processing

ERPs are used widely in the emotion processing literature, and have made significant contributions to our understanding of the processes that might underlie emotion processing (see Schupp, Junghöfer, Weike, & Hamm, 2003, for discussion). The ERP technique involves measuring voltage from the surface of the scalp and time-locking the measures to stimulus onset, or a response (e.g., a key press), and averaging the EEG signal over many trials. Each presentation of the stimulus/response involves a specific neural response that is embedded in on-going neural activity. As on-going neural activity should not be systematically related to the stimulus presentation, upon averaging several trials, the neural response that is systematically linked to the stimulus is ‘constructive’, whereas the rest of the on-going activity should be random and therefore ‘destructive’ (i.e., it should cancel out). Averaging the signal therefore allows us to obtain distinct components called ERPs that are labelled with respect to their polarity and latency (Luck, 2005; Woodman, 2010).

EEG signals travel at the speed of light, therefore they offer a temporal resolution with millisecond precision (Luck, 2005). This temporal precision is particularly useful for investigating the time course and sub-processes involved in stimulus processing. A historical example of this is the longstanding area of research on the time course of neural operations. Mental chronometry historically involved utilising reaction times to infer mental operations (see Jensen & Jensen, 2006; Posner 2005). However, these studies only had access to the input, in the form of the experimental manipulation, and the response, that was the outcome of decisions in the task. This limited the complexity of the experimental manipulations that could be utilised, as well as the inferences that could be made from the response measures. ERPs can provide a window into processing that occurs before the response is made, and it allows us to examine systematic modulations of the neural mechanisms that underlie both perceptual processing of stimuli and response-related processing (Luck et al., 2000). The subsections below summarise the specific ERP components associated with processing emotional expressions.

1.2.1. ERPs associated with expression intensity processing

1.2.1.1. P1

The P1 is an occipito-lateral component that peaks at about 100 ms after stimulus onset. There is evidence to show that P1 amplitude is greater for an attended versus unattended stimulus (see Hillyard, Vogel, & Luck, 1998). A few studies using the basic emotions framework report larger P1 amplitudes for prototypical emotional expressions versus neutral ones (Batty & Taylor, 2003; Holmes, Nielsen, Tipper, & Green, 2009). However, the differences in P1 amplitudes seem be driven by low level properties of the stimuli in at least some instances (see Joyce & Rossion, 2005; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005).

Most studies that have investigated emotion related ERPs have not found modulations of the P1 for expression intensity or emotion type (e.g., Duval, Moser, Huppert, & Simons, 2013; Leppänen, Kauppinen, Peltola, & Hietanen, 2007; Sprengelmeyer & Jentzsch, 2006). Utama, Takemoto, Koike, and Nakamura (2009) found that P1 amplitude was correlated with categorisation of emotion type but not intensity when participants were asked to rate both. It is unclear whether their results were due to systematic differences in the stimuli they used, explicit attention directed to emotion, or emotion processing per se.

1.2.1.2. N170

The N170 is an occipito-temporal component that peaks between 140-200 ms. The N170 is the first component that is considered to reflect face specific processing as it is characterised by larger, and earlier amplitudes for faces in comparison to other stimuli (see Eimer, 2012, for a review).

1.2.1.2.1. N170 may reflect expression independent structural coding

The N170 is thought to reflect expression independent structural coding of faces that helps us individuate faces (Bruce &Young, 1986). According to Bruce and Young, face identity and expression processing occur independently. However, there is some evidence to suggest that the N170 might also be sensitive to emotional expressions. Greater amplitudes of the N170 have been reported for emotional versus neutral faces (Ashley, Vullemier, & Swick, 2003;

Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007). Batty and Taylor (2003) examined modulation of N170 for all six basic expressions and found greater N170 amplitudes for fearful versus other stimuli. Surprisingly they found earlier responses to happy expressions. Batty and Taylor's findings demonstrate systematic differences in the N170 evoked by different emotions, and are contrary to the idea that the N170 reflects expression-independent structural coding. However, these effects have not been replicated in the literature (see Hinojosa, Mercado, & Carretié, 2015).

1.2.1.2.2. N170 emotion effects may be an artifact of the reference

Rellecke, Sommer, and Schacht (2013) suggest that previously reported N170 effects for emotion may be due to an overlap with the subsequent component, the Early Posterior Negativity (EPN), which varies as a function of emotion. They suggest that the divergent findings in the literature may be due to an artifact of the different referencing scheme used in each study. As EEG measures a voltage difference between each electrode and a reference, the closer the recording electrode is to the reference, the smaller the signal. The N170 is thought to be generated by regions in the occipital face area and the fusiform face area (Eimer, 2012) whereas EPN is thought to be generated by temporo-parieto-occipital regions (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Hajcak, Macnamara, & Olvet., 2010; Olofsson, Nordin, Sequeira, & Polich., 2008; Schupp et al., 2006). As the source of the EPN seems to be closer to the mastoid reference, Rellecke et al. suggested that using the mastoid reference would reduce the chances of finding emotion effects on the amplitude of the N170. Nevertheless, emotion effects on the N170 have been reported where the linked mastoid reference is used (e.g., Zhang & Zhou, 2014).

Wronka and Walentowska (2011) suggest that attention to the emotion might explain N170 sensitivity to emotional expressions. They found that the N170 was sensitive to emotion when participants were asked to categorise prototypical emotion category, but not when they were asked to categorise gender. However, a meta-analysis of N170 effects suggests that there are sometimes stronger emotion effects on the amplitude of the N170 when there is no task (Hinojosa et al., 2015). Therefore, the conditions under which the N170 is sensitive to emotion type effects remain unclear.

1.2.1.2.3. N170 may reflect expression intensity processing

Larger N170 amplitudes have been also reported for higher versus lower intensities of emotion (Müller-Bardorff et al., 2016; Sprengelmeyer & Jentzsch, 2006; Utama et al., 2009). Sprengelmeyer and Jentzch (2006) found larger N170 amplitudes for greater intensities of angry, fearful, and disgusted expressions versus lower intensities. These effects preceded main effects, and were independent, of emotion type. They suggest that the N170 might reflect monitoring of expression salience that occurs before prototypical categories of emotional expressions are processed.

Larger N170 amplitudes have also been reported for higher intensities of expressions in tasks that have manipulated perceptual load. Müller-Bardorff et al. (2016) presented participants with pairs of horizontal bars and asked them to indicate the location of the shorter or longer bar. Each pair of bars was superimposed onto a face that had either high or low intensities of angry or happy expressions, or a face that was neutral in expression. Müller-Bardorff et al. manipulated perceptual load by arranging large and small differences in the lengths of the two bars. They found that modulations of the N170 component occurred irrespective of task;

however, perceptual load affected the valence effects (positive versus negative) for N170. This suggests that emotion type processing might differ from intensity processing.

1.2.2. The Early Posterior Negativity (EPN)

The EPN is a broadly distributed tempro-parietal negativity that starts between 150-200 ms, and is maximal between 250-300 ms. Although the EPN rests on an overall positivity, it is referred to as a ‘negativity’ for emotion, rather than a ‘positivity’ for neutral faces. This is due to source analysis work that shows that the EPN amplitude may be generated by temporo-parieto-occipital regions (Cuthbert, et al., 2000; Hajcak et al., 2010; Olofsson et al., 2008; Schupp et al., 2003). Effects that mirror the EPN are sometimes reported over the anterior sites as the Early anterior positivity (EAP), or the Frontocentral-emotion positivity (FcEP; Eimer & Holmes, 2007). Both of these are thought to reflect the dipolar reflections of the EPN (Oloffson et al., 2008).

1.2.2.1. EPN may reflect ‘natural selective attention’

The EPN is thought to reflect ‘natural selective attention’, or the automatic recruitment of attentional neural resources to process emotional stimuli (see Schupp et al., 2004, 2003). This suggests that explicit attention not required for EPN modulation, and it may also be immune to the effects of explicit attention. The EPN has been investigated extensively for emotion laden stimuli (see Cuthbert et al., 2000; Hajcak et al., 2010; Olofsson et al., 2008; Schupp, Flaisch, Stockburger, & Junghöfer, 2003). Greater EPN negativities have been reported for positive and negative facial expressions (Calvo & Beltran, 2013; Rellecke et al., 2013) and non-facial emotional stimuli, in comparison with neutral facial expressions or neutral stimuli (Schupp et al., 2004, 2003). These data are in line with the theory that the EPN might reflect ‘natural selective attention’ to emotion, however, others report greater EPN amplitudes for threatening expressions (e.g., fearful) versus friendly (i.e., happy) or neutral expressions (Schupp et al., 2004). These data suggest that the EPN might reflect natural selective attention to threatening expressions, and not friendly ones (Adolphs, 2002; Bradley, 2000; Bradley & Lang 2007; Lang et al., 1997; LeDoux, 1996; Öhman, 2002). These studies have used a variety of different tasks and expressions; therefore, it is difficult to form a cohesive interpretation of the significance of EPN modulations.

1.2.2.2. EPN for prototypical expressions may be modulated by task

Rellecke et al., (2012) presented participants with neutral, prototypical happy, and prototypical angry faces in four different conditions. The first condition was a 'true passive task', where participants were simply asked to view the expressions. The other three conditions consisted of a gender discrimination task, a face versus word task, and an emotion categorisation task, where participants made a forced choice response about the emotional expression that the face displayed. Each of these tasks directed different levels of voluntary attention towards emotion. They found that the EPN for happy expressions was more negative for tasks that required deeper processing (i.e., the gender discrimination and emotion categorisation task) than for tasks that required superficial processing (i.e., passive viewing and face word processing). Rellecke et al.'s data suggest that the EPN is under attentional control as task difficulty increases. Crucially, the effects were only significant for happy expressions, suggesting that the EPN effects might not be equivalent for all emotion types.

1.2.2.3. EPN may reflect automaticity of expression intensity processing

There is evidence to suggest that the EPN might reflect automaticity of processing expression intensities. Sprengelmeyer and Jentzsch (2006) conducted a gender discrimination task while they recorded ERPs for angry, fearful, and disgusted expression intensities. They found a linear relationship between EPN amplitude and intensity, suggesting that the EPN may be an electrophysiological index of intensity. However, Sprengelmeyer and Jentzsch only examined responses to negative expressions so it is unclear whether this modulation reflects threat-specific processing or natural selective attention. Leppänen et al. (2007) extended this work by examining the EPN responses to happy expressions and fearful expressions. They found that fearful expression intensities modulated the EPN, but happy expression intensities did not. This suggests that expression intensities might only be processed for threatening expressions.

The two studies above investigated EPN modulation along negative emotional expression trajectories (Sprengelmeyer & Jentzsch, 2006), or in tasks that required explicit emotional expression recognition (Leppänen et al., 2007). Therefore, it is unclear whether the EPN reflects ‘natural selective attention’ to both positive and negative expression intensities.

1.2.3. The Late Positive Potential (LPP)

The LPP is a broadly distributed centro-parietal positivity, that starts at between 300-400 ms. The time course and spatial distribution of the LPP overlap with the P3, which has been divided into the P3a and P3b. The P3a typically has a posterior central distribution and is evoked for novel stimuli. The LPP may be associated with the P3b which occurs later than the P3a, and has a fronto-central distribution (see Kok, 2001). There are multiple generators of the LPP signal, giving rise to discrepant LPP effects and competing hypotheses regarding its functional significance (Foti, Hajcak, & Dien, 2009).

1.2.3.1. LPP may reflect extrinsic task related processing

The LPP is thought to reflect sustained attention allocated towards processing 'task relevant' stimuli (Cuthbert et al., 2000; Hajcak, Dunning, & Foti, 2007; Hajcak et al., 2010). When participants are asked to label prototypical emotional expressions via button press, happy and angry emotional expressions evoke larger LPPs than neutral expressions, and the amplitudes evoked for angry expressions are larger than those evoked by happy expressions (Duval, et al., 2013; Schupp et al., 2000, 2003).

Rellecke et al. (2012) examined the effect of task demands on the amplitude of the LPP. They found that, irrespective of emotion type, LPP amplitude was systematically higher as more explicit attention was drawn towards emotion (i.e., graded from passive viewing < face-word task < gender discrimination < expression discrimination). This is consistent with the idea that the LPP might reflect elaborate task related processing of emotional stimuli (Cuthbert, et al., 2000; Hajcak, et al., 2007, 2010).

1.2.3.2. LPP may reflect intrinsic motivation

As emotional expressions are extremely useful social stimuli, they may be intrinsically relevant and thereby modulate the amplitude of the LPP (Cuthbert, et al., 2000; Hajcak et al., 2007; Hajcak, et al., 2010; Schupp et al., 2000). Supporting this idea, Schupp et al. (2004) found higher amplitudes of LPPs for threatening (angry) expressions versus friendly (happy) and neutral expressions. Furthermore, in the emotion regulation literature, neutral interpretations of unpleasant emotional pictures were related to lower amplitudes of LPP than negative interpretations. Lower LPP amplitudes have also been associated with reduced anxious-depressed symptoms (Dennis & Hajcak, 2009). Taken together, these findings suggest that the LPP is associated with individuals' perception of affect.

The LPP has mainly been investigated when voluntary attention is directed at expression intensities. Therefore, it is unclear whether the LPP reflects the intrinsic motivational significance of expressions or the experimental task related processing of expression intensities. Investing the LPPs evoked for expression intensities under passive and active conditions can help shed light on the issue.

1.3. Attention and ERPs associated with expression intensity processing

The evidence for facilitatory processing of prototypical emotional expressions and expression intensities is similar to voluntary attention effects observed in the broader attention literature (Hilliyard, Vogel, & Luck, 1998). The ERP modulations observed in these studies may be implicated in expression-independent explicit attention processes. However, it has been suggested that emotions 'capture attention', which might mean that they do not *require* explicit attention to be processed (Bradley, Keil, & Lang, 2012; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1997; Öhman & Mineka 2001; Öhman & Weins, 2003). Furthermore, ERPs evoked for expression intensities may not be modulated when explicit attention is directed to emotion. An alternative hypothesis suggests that only threat-specific emotions are processed without voluntary attention. This would suggest that only threatening expressions are processed automatically, and they are immune to explicit attention effects. These two perspectives are summarised below.

1.3.1. Emotion processing is ‘automatic’

Attention is generally thought to gate visual perception. However, emotions are thought to belong to a class of stimuli that ‘capture’ or orient attention automatically because of their motivational and evolutionary significance (Bradley, Keil, & Lang, 2012; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1997; Öhman & Mineka 2001; Öhman & Weins, 2003). Automatic capture of attention implies that emotional stimuli may not *need* voluntary attention for to be processed (Öhman, 2002). In the broader attention literature, voluntary attention generally increases the responses associated with processing stimuli (e.g., boosts in fMRI and ERP signals; see Palermo & Rhodes, 2007; Pessoa, Kastner, & Ungerleider, 2008, for discussions).

If emotions do ‘capture’ attention, then there should not be any additive effects of voluntary attention on ERPs. There is evidence that emotion processing and voluntary attention have different underlying neural bases. Specifically, voluntary attention is mediated by a frontoparietal network (Corbetta & Shulman, 2002), whereas the amygdala mediates processing of emotional stimuli in the sensory areas (Pourtois et al., 2013). This has led some researchers to suggest that the effects of voluntary attention should be additive, and should therefore enhance responses to emotional stimuli (see Pessoa, Kastner, & Ungerleider, 2008).

1.3.2. Threat-specific processing is ‘automatic’

An alternative hypothesis suggests that only threat-specific stimuli (including facial expressions) are processed automatically. This occurs through a ‘fast’ subcortical route which involves a subcortical (thalamo-amygdala) pathway that can act quickly and coarsely analyse threat related information, possibly without attention (Adolphs, 2002; LeDoux, 1996; Öhman, 2002). In contrast, non-threatening expressions might be processed via a ‘slow’ route that may require voluntary attention. The ‘slow’ route involves a thalamo-cortico-amygdala pathway that allows slower, more fine-grain analysis of the stimulus.

There is converging evidence to suggest that threatening expressions may be prioritised in processing. Positron-emission tomography (PET) studies show greater amygdala activation to fearful versus happy faces (Morris et al., 1996, 1998). This suggests that the amygdala activity might reflect monitoring of salience to determine threat (Morris et al., 1996). fMRI studies also show increased responses in fusiform face area which is thought to be modulated by the amydgala for fearful expressions in comparison to neutral or happy expressions (Vuilleumier & Pourtois, 2007). Furthermore, people with damage or lesions to the amygdala do not show increased responses to fearful versus neutral stimuli (Adolphs, Tranel, Damasio & Damasio, 1994; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

In ERP studies, Rellecke et al. (2012) found significantly greater amplitudes of the P1, N170, and EPN for angry versus neutral faces irrespective of task. These results are suggestive that the early components reflect the automaticity of threat-related emotion processing. A number of studies report larger amplitudes of LPP evoked for threatening versus non-threatening expressions (e.g., Leppänen et al., 2007; Schupp et al. 2004). However, Sabatinelli, Keil, Frank, and Lang (2013) suggest that the LPP has both subcortical and cortical sources, which might mean that it is sensitive to all emotional expressions, not only threatening ones.

1.4. Thesis outlook

The literatures summarised highlight the paucity of systematic investigation into emotional expression intensity processing. The ERPs associated with intensity processing have mainly been investigated in paradigms that have required explicit attention to emotion. Therefore, it is unclear whether the effects can be replicated in paradigms where explicit attention is not required for processing. Furthermore, the extent to which emotion-related ERPs are driven and modulated by explicit attention also needs to be investigated systematically. This thesis aims to address these gaps by examining the ERP correlates of continuous processing of emotional expression intensities when explicit attention is, and is not, directed towards emotion.

In Experiment 1 (Chapter 2), we examine the automaticity of processing emotion type and expression intensities. Specifically, we examine whether intensities of both happy and angry faces modulate the EPN, and whether the LPP reflects automaticity of expression intensity processing when emotion is task irrelevant. Furthermore, we examine whether there are interactions between expression intensity and emotion type processing. Given the threat prioritisation hypothesis, it seems likely that threatening (angry) expressions should be discriminated at lower intensities (i.e., that threatening information would be more salient) than non-threatening (happy) stimuli.

In Experiment 2 (Chapter 3), we examine the effects of voluntary attention on emotion expression processing. Participants in this experiment were asked to indicate via button press whether the expression they viewed was ‘Emotional’ or ‘Neutral’ in expression. We used similar parameters as in Experiment 1 to allow direct comparisons between ERPs across an active and a passive task. In particular, although the EPN is thought to reflect ‘natural selective attention’, it is unclear whether it is immune to the facilitatory effects of voluntary attention. In contrast, the LPP is thought to reflect allocation of voluntary attentional resources. Therefore, EPN modulations should be similar between Experiments 1 and 2, whereas LPP amplitudes may be larger in Experiment 2 for the stimuli relevant to the explicit task.

In Chapter 4, we examine how the ERP modulations observed in Experiment 2 are associated with behavioural measures; specifically, the proportion of faces rated emotional and the reaction times. Examining the correlation between emotion-related ERPs and behavioural measures will assess the relationship between stimulus processing and response-related activity, shedding light on the functional significance of the ERPs. The functional significance of the EPN in expression processing has yet to be investigated. Previous research suggests that the LPP is involved in elaborate task related processing, like emotion categorisation (e.g., Calvo & Beltrán, 2013), and therefore should be associated with response times. If the level of intensity changes how task-related the expression is, then we would expect that proportion of faces rated as emotion might be positively correlated with the amplitude of the LPP.

In Chapters 2-4 we examine responses to physical morphological changes in the face stimuli. However, perception of intensity can also vary without physical change. One way to examine perceptual shifts is through adaptation/aftereffects paradigms. These are typically investigated with behavioural measures. However, correlating the perceptual behavioural shifts with ERPs may provide further insight into perceptual processing of expression intensities which may be independent of the response. In Chapter 5, we used an adaptation/aftereffect task to examine whether EPN and LPP amplitudes correlate with perceptual shifts in emotion intensity perception.

Chapter 2: Automaticity of expression intensity processing along emotion trajectories

2.1. Introduction

Emotional expressions convey extremely useful social signals that can help guide our social interactions. Given their evolutionary and motivational significance, it has been proposed that expressions are processed 'automatically' (i.e., without voluntary attention; Bradley, Keil, & Lang, 2012; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1997; Öhman, 2002; Öhman & Mineka, 2001; Vuilleumier et al., 2001). Furthermore, converging evidence from behavioural, neuroimaging, and facial electromyographic (EMG) studies suggest that emotional expressions are detected and deciphered 'automatically' (i.e., without intention to process them, or awareness; see Palermo & Rhodes, 2007, for a review). In particular, expressions that signal threat, such as fear and anger, evoke faster and larger responses than neutral, friendly, or other negative emotional expressions that do not signal threat (e.g., sad expressions; Schupp et al., 2004). This is taken as evidence that threatening expressions may be processed via neural circuitry in the human fear system that prioritises processing of stimuli that signal threat (Le Doux, 1996; Morris, Öhman, & Dolan, 1999).

Empirical work that provides evidence for the automaticity of emotional expression processing are typically based on the 'basic emotions' framework, which suggests that there are innate neural substrates associated with a small number of universal expressions (as described in Ekman & Friesen, 1976). These studies examine differences between responses for prototypical 'emotional' (happy, angry, fear, surprise, disgust, and sad) and 'neutral' expressions. However, emotional expressions are processed both categorically and continuously (i.e., at different intensities; Harris, Young, & Andrews, 2012). Evidence for continuous processing comes from studies that have utilised morphing techniques, which have enabled researchers to vary the intensity of emotional expressions systematically along an ‘emotion trajectory’, defined as the continuum of an expression as it changes from neutral to prototypical emotion.

A small number of studies have explored the electrophysiology of the emotion trajectory. These studies report main effects of emotion intensity on the amplitudes of the P1 (Utama et al., 2009), N170 (Müller-Bardorff et al., 2016; Sprengelmeyer & Jentzsch, 2006; Utama et al., 2009; Wang et al., 2013), EPN (Leppänen, 2007; Müller-Bardorff et al., 2016; Sprengelmeyer & Jentzsch, 2006) and the LPP (Duval et al., 2013; Müller-Bardorff et al., 2016). There are inconsistent findings within this literature and, because there is limited research, many effects have not been replicated. In order to investigate this systematically the existing findings and limitations are outlined below.

2.1.1. P1

Utama, et al., (2009) examined the P1 amplitudes for morphed expressions while participants rated emotion type and expression intensity level. They found that the intensity of the P1 amplitude was correlated with ‘correct’ categorisation of emotion type. However, P1 amplitudes were not reported in other studies that have examined ERPs associated with expression intensity (e.g., Müller-Bardorff et al., 2016; Sprengelmeyer & Jentzsch, 2006). Furthermore, a large number of studies have not found differences in P1 amplitudes for prototypical versus neutral emotional expressions (e.g. Eimer and Holmes, 2006). Low-level stimulus differences between faces/expressions have been shown to drive P1 differences at least in some instances (e.g., Rossion & Caharel, 2011), and could be responsible for the observed emotion effects on P1. Therefore, it is important to control for luminance and spatial frequency to examine the effects of emotion type and expression intensity on the amplitudes of the P1.

2.1.2. N170

Sprengelmeyer and Jentzsch (2006) reported modulation of the N170 as a function of expression intensity irrespective of emotion type. Based on these findings they suggest that we might process the ‘salience’ (intensity) prior to coding emotion type. As the N170 is typically a marker for structural coding of faces that is thought to be independent of emotion processing (see Bruce & Young, 1986), Sprengelmeyer and Jentzsch suggest that intensity coding may also involve processing ‘structural codes’. However, Sprengelmeyer and Jentzsch examined only negative expressions and a limited range of emotion intensities (50%, 100%, and 150% expression intensities). Furthermore, several studies do not report N170 modulation as a function of expression intensity (Duval et al., 2013; Leppänen et al., 2007). Therefore, the experimental parameters that produce these results are unclear. In this experiment, we aim to examine amplitudes of the N170 for larger range of expression intensities in the absence of task constraints.

2.1.3. EPN

Sprengelmeyer and Jentzsch (2006) found more negative EPNs for greater intensities of expressions when participants viewed 50%, 100% and 150% expression intensities. As they did not investigate positive expressions, it was unclear whether EPN reflected intensity processing of threatening information only, or whether it reflects intensity for emotions in general. Leppänen et al. (2007) extended Sprengelmeyer and Jentzsch’s study by including angry and happy expressions of the same intensities. They found a main effect of intensity on the EPN for fearful but not happy faces. Therefore, they suggest that the EPN might reflect threat specificity, not automaticity in processing expression intensity.

Sprengelmeyer and Jentzsch (2006) used a gender discrimination task which may require less attention to the stimuli than the emotion categorisation task used and Leppänen et al.'s (2007) study. Therefore, it is unclear whether happy expressions would also modulate the EPN when explicit attention is not directed towards emotion. In this experiment, we aim to examine the extent to which the EPN is 'automatically' modulated by both positive (happy) and negative (angry) expression intensities.

2.1.4. LPP

Duval et al. (2013) demonstrated that the LPP is sensitive to expression intensity when participants are required to categorise emotional expressions. They found higher amplitudes of the LPP for higher intensities of both happy and angry expressions, compared with neutral or lower intensities. Higher amplitudes for angry faces were sustained over a longer period than for happy expressions, suggesting that the LPP might reflect the motivational relevance of stimuli. Leppänen et al. (2007) also found larger LPP for angry versus happy faces, but no main effect of intensity, in an emotion categorisation task. However, their analysis was limited to comparing only 100% and 150% expression intensities, as 50% intensities were excluded from analysis due to a larger proportion of 'incorrect' responses.

Most studies investigating emotion expression intensity have examined the LPP in instances that required explicit emotion recognition, and the LPP is differentially modulated by the explicit experimental task relevance of stimuli (Hajcak, et al., 2009; Hajcak et al., 2010; Moser, Hajcak, Bukay, & Simons, 2006; Rellecke, Palazova, Sommer, & Schacht, 2011). Therefore, higher LPP amplitudes might reflect the experimental task relevance of expression intensities rather their intrinsic relevance. To examine the effects of intrinsic relevance of emotional stimuli, we examine whether the LPP can be modulated as a function of emotion intensity when explicit attention is not drawn to emotion. Additionally, as LPPs are thought to reflect threat-selective processes, it is possible that there would be an interaction between emotion type and emotion intensity. In particular, prioritisation of threat might be reflected by increased sensitivity to lower intensities of angry expressions that signal threat, versus happy expressions that do not signal threat.

2.1.5. Rationale and aims of this study

The findings thus far are insufficient to elucidate whether expression intensities along emotion trajectories are processed automatically. Studies that have examined ERPs modulated by emotion trajectories have used a variety of experimental tasks that require varying levels of explicit and implicit processing. For example, some experiments involve the explicit evaluation of positive, negative, or neutral valence (Duval et al., 2013), or require participants to categorise emotion (Leppänen et al., 2007), or rate the intensity level of the image (Utama et al., 2009). In contrast, other studies include a task that is unrelated the emotion expressed, like responding to face gender (Sprengelmeyer & Jentzsch, 2006). Previous studies also differ in morph intensities, with some comparing 50%, 100% (prototypical), and 150% (caricaturized) intensities (Leppänen et al., 2007; Sprengelmeyer & Jentzsch, 2006), whereas others compare smaller, systematic increments along the emotion trajectory (Duval et al., 2013; Müller-Bardorff et al., 2016; Utama et al., 2009). The different parameters used in the experiments make it difficult to compare results directly, and discern whether there are any ERP effects for emotion intensity processing that occur independently of task. We aim to address this gap by systematically exploring the modulation of emotion-related ERPs along emotion trajectories when attention is not directed to emotion.

We recorded EEG while participants viewed faces that were either neutral in expression or portrayed happy or angry expressions along an emotion trajectory. Emotional trajectories were formed by morphing the emotional faces to display expressions that were 20%, 40%, 60%, 80%, or 100% of the full expression. We examined whether there were systematic modulations of the P1, N170, EPN, or LPP as a function of expression intensity, and emotion type. Extending previous research, the results will help elucidate how emotions are processed along emotion trajectories. In particular, they will inform us about whether emotion intensities are processed ‘automatically’ and if they interact with emotion type.

2.2. Method

2.2.1. Participants

Participants in this study were 24 volunteers (18 female) from the University of Auckland. The mean age was 22.5 (*SD* = 3.91, *range* = 18-31). One participant was left-handed. Two participants were unable to complete the experiment as the experimental computer screen flickered unpredictably during the experiment. Participants’ data were included if at least 60% of trials (60 trials) were left per condition after artifact rejection (Luck, n.d.). Data from one participant were not included, as too many trials (66%) were rejected.

Volunteers with conditions that impaired their ability to recognise facial expressions or with a history of epilepsy or migraines did not meet the criteria to participate in the study. All participants reported normal or corrected-to-normal vision. Participants provided written, informed consent prior to their participation. All participants received a $20 supermarket voucher as koha for their participation in the study. Research protocols were approved by The University of Auckland Human Participants Ethics Committee.

2.2.2. Stimuli

Images of happy, angry, and neutral faces from the Karolinska Directed Emotional Faces (KDEF) database (Lundqvist, Flykt, & Öhman, 1998) were chosen for this study to represent the span of emotion valence and arousal. The KDEF contains images of actors who made the expressions according to Ekman and Friesen (1976). An oval mask was overlaid on each image to remove outer facial features (e.g., hair and ears). Faces were then loaded onto Fantamorph (http://www.fantamorph.com) to create morphed emotional expressions in 20% increments along the neutral-happy, and neutral-angry emotion trajectories. An in-built face model was used to set the control points on the face. There were a total of 106 control points on the face (28 points around the face, 16 around the eye brows, 26 around the eyes, 16 around the nose, and 20 points around the lips) on all faces. These were manually adjusted so that the emotional and neutral face were properly aligned to create morphs. Images were then equalised for contrast and luminance by using the SHINE toolbox (Willenbockel et al., 2010) in MATLAB (The Mathworks, Inc.).

There were a total of 50 images per expression intensity, and they were repeated twice throughout the experiment. Images subtended 5.26° x 6.53° of visual angle. A different face from the NimStim set (Tottenham et al., 2009) was presented in about 10% of the trials. Participants were asked to press the spacebar whenever they saw the NimStim face. EEG data from these trials were not analysed. The NimStim face was included to provide an accuracy measure to assess whether participants were viewing the stimuli on screen. Participants were required to respond accurately for at least 80% of the trials for their EEG data to be included in the analysis.

2.2.3. Procedure

Participants were seated in a dimly lit faraday cage. The monitor was positioned 57 cm in front of the participant. Experimental stimuli were presented on a 21-inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh; Schneider, Eschman, & Zuccolotto, 2002a, 2002b).

We recorded EEG while participants viewed faces that were either neutral in expression or morphed faces that were 20%, 40%, 60%, 80%, or full-intensity angry or happy faces (see Figure 2.1b and c). Before the experiment started, participants were asked to familiarise themselves with the NimStim face, and they were instructed to ‘Press the space bar’ when they viewed the face. They then performed a practice block in which they viewed 10 examples of the morphed stimuli on happy and angry emotion trajectories (these stimuli were not included in the main experiment), and four instances of the NimStim face. If participants could detect the NimStim face at least three out of four times, they were able to continue with the experiment, otherwise they repeated the practice block.

The experiment was split up into 10 blocks. Each block contained 132 trials (20 trials of each emotion intensity, and 12 instances of the NimStim face which required a response). Each trial began with a fixation cross that was presented for 200-400 ms, then a face was presented for 500 ms, and then a blank slide was presented for 1000-1200 ms (see Figure 2.1a). After each block, a “break” slide appeared for 30 seconds, followed by a slide with the NimStim face and a reminder to ‘Press the space bar’ when participants viewed that face. Once this slide appeared, participants were able to press the spacebar to continue when they were ready to continue the experiment.

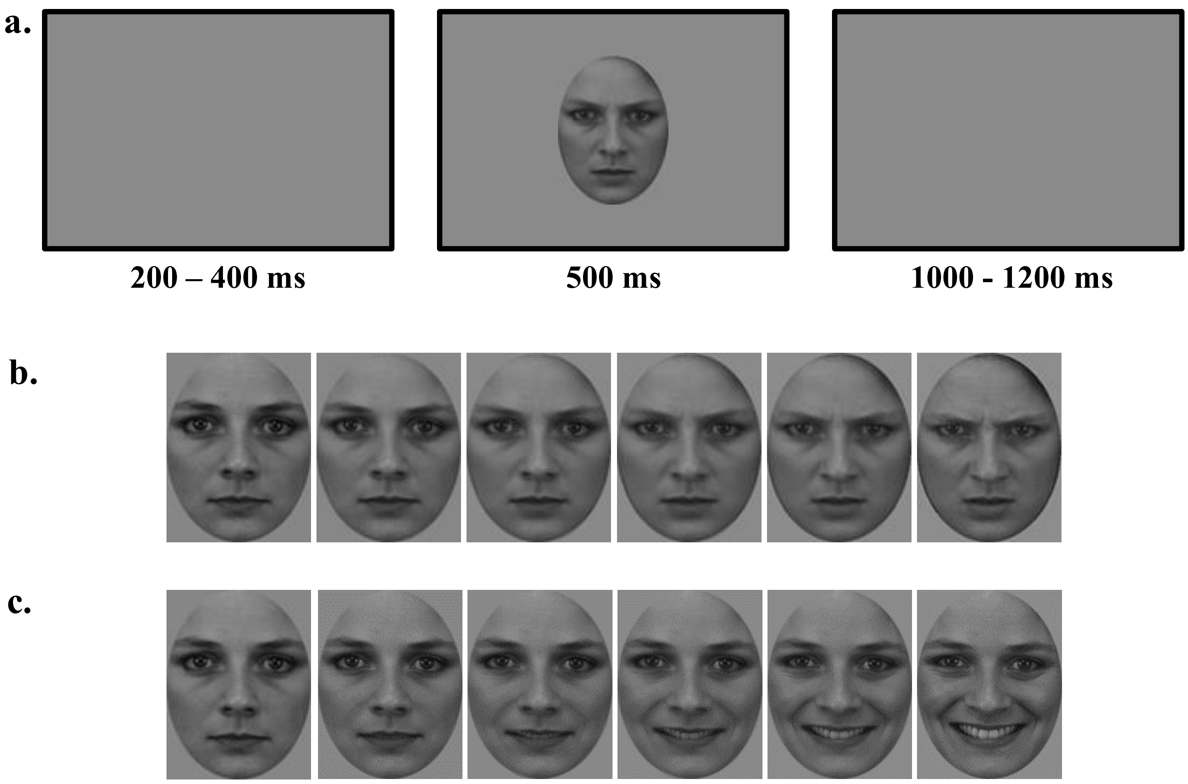


Figure 2.1. a. The sequence of events during each trial. Each trial began with a fixation cross that was presented for 200-400 ms, a face was then presented for 500 ms, and then a blank slide was presented for 1000-1200 ms. b. An example of an angry emotion trajectory. c. An example of a happy emotion trajectory (from left to right: neutral, 20%, 40%, 60%, 80%, and 100%).

2.2.4. EEG acquisition and pre-processing

Prior to data collection, a photocell was used to measure the time difference between the display of trigger values that code conditions on Net Station, and the image display on the experimental computer. We recorded an average lag of 16 ms between trigger and stimulus display. All time points were shifted by 24 ms while analysing the RAW EEG data (16 ms to account for the lag in the timing test, and 8 ms to account for the default lag in the 300-amplifier system).

EEG data were recorded using a 128-sensor Geodesic Sensor Net and Net Amps 300 amplifiers (Electrical Geodesics Inc., EGI, Eugene, Oregon, USA). Data were digitised at 1000 Hz and acquired using Cz as the reference electrode. Individual electrode impedance was kept below 40 kΩ and measured both before the beginning and half way through the experiment. EEG data were pre-processed using the EEGLab toolbox (Delorme & Makeig, 2004). Data were processed using custom written scripts for MATLAB (The Mathworks, Inc.).

RAW files were imported to EEGLab (Delorme & Makeig, 2004), and 24 ms were added to all time points in the data. This accounts for the 16 ms lag recorded using the photocell, and the default 8 ms lag that the EGI 300 amplifier has between trigger value display on the EEG acquisition computer and image display on the experimental computer. Data were then down-sampled to 250 Hz due to memory constraints on the analysis computer. The binary trigger values (that represent a numerical code for each stimulus presented on screen) were combined to show a single trigger value for each condition. Channel location coordinates were added for each electrode site. The fiducials were taken out of the data matrix and Cz was marked as the recording reference electrode. Data were then filtered using the Butterworth filter in ERP lab (0.1 Hz high-pass filter; Lopez-Calderon & Luck, 2014). Bad channels were identified and rejected using spectra rejections with the threshold of 5 and 15 *SD* as well as the automatic channel rejection in EEGlab (Delorme & Makeig, 2004). Rejected channels were interpolated after Independent Components Analysis (ICA) with a spherical-spline interpolation in EEGlab (Delorme & Makeig, 2004). Data were re-referenced to the average of all scalp electrodes and the Cz channel was added back into the analysis. The EEGlab plug-in CleanLine (Mullen, 2012) was used to remove sinusoidal power line noise from the data. ICA was then implemented in EEGlab (Delorme & Makeig, 2004). Data were then segmented into epochs that were 1.2 seconds long (200 ms before stimulus presentation, and 1 s after). Epochs which contained horizontal eye movements were rejected if the differences between electrodes at the outer canthi of each eye were greater than 52 microvolts (16 µV/1° visual angle that the image was subtended; Lins, Picton, Berg, & Scherg, 1993). Then the ADJUST toolbox (Mognon, Jovicich, Bruzzone, & Buiatti, 2011) was used to identify artifactual components, which were removed from the data. Then epochs with activity that deviated by more than +/- 100 mv were rejected. One participant's data were excluded at this point, as ~66% of trials were rejected from the dataset.

2.2.5. ERP analysis

Grand averages of the trials were computed for each condition per participant, and for each condition collapsed across participants. A baseline correction (based on the average of the 200-ms baseline period) was subtracted from each time point in the epoch.

Electrodes for analysis were chosen on the basis of previous literature, as well as the scalp maxima of the current dataset when all the conditions were collapsed together. Conditions were collapsed to avoid a biased selection of electrodes based on maximal differences between conditions. The P1 was measured at two homologous electrodes clusters around O1 in the left hemisphere (electrodes 70, 66, and 71), and around O2 in the right hemisphere (electrodes 83, 76, and 84). N1 was measured at two homologous electrode clusters which included P7 and P9 in the left hemisphere (electrodes 58, 64, and 63) and P8 and P10 in the right hemisphere (electrodes 99, 95, and 90). The EPN was measured at electrodes 66, 67, and 60 in the left hemisphere and 77, 84, and 85 in the right hemisphere. The LPP was measured at the midline electrodes Pz, CPz, and Cz. We chose to analyse the posterior rather than anterior components as they appear to be dipolar reflections of the same component (see Joyce & Rossion, 2005; Olofsson et al., 2008).

To quantify the early ERP components (P1 and N170) we identified the peak based on the grand-averaged waveform of all the conditions and participants collapsed. We then computed the mean amplitude in a 20-ms window around the peak of each component. A 20-ms time window was chosen to maintain consistency with Sprengelmeyer and Jentzsch (2006). Furthermore, mean amplitudes have been demonstrated to be more robust than peak amplitudes (see Luck, 2014, for discussion).

The EPN and LPP have been reported over a wide range of time periods in the literature. We chose our analysis windows based on previous literature that examined expression intensity processing. To quantify the EPN, we took the same approach as Sprengelmeyer and Jentzsch (2006), and analysed EPN amplitudes in four 50-ms blocks from 202-408 ms (202-252 ms; 252-304 ms; 304-356 ms, 356-408 ms) and a 200-ms time window between 408-608 ms. The LPP is reported to be maximal between 400-600 ms so we chose this window for analysis (Leppänen et al., 2007; Rellecke et al., 2012).

2.2.6. Statistical analyses

A series of 2 (Emotional expression: happy, angry) x 2 (Hemisphere: left, right) x 6 (Emotion intensity: Neutral, 20%, 40%, 60%, 80%, and 100%) repeated measures analyses of variance (rANOVAs) was performed to analyse intensity effects on the amplitudes of P1, N170, and EPN. As the LPP is calculated from the midline electrodes, hemisphere was not included as a factor for analysis. Therefore, 2 (Emotional expression) x 6 (Emotion intensity) rANOVAs were performed to analyse LPP amplitudes. We conducted planned simple contrasts between each emotion intensity level and neutral in order to examine which intensity levels drive intensity effects.

When analysing intensity effects, we included ‘Neutral’ in our analysis to compare each intensity level with neutral, as is conventional in studies in the basic emotion framework (e.g., Ashley, Vuilleumier, & Swick, 2004; Batty & Taylor, 2003; Eimer & Holmes, 2002). To compare our results with the other studies examining emotion trajectories (Duval et al., 2013; Leppänen et al., 2007; Sprengelmeyer & Jentzsch, 2006), we also conducted rANOVAs without neutral as a level in the ‘intensity’ factor. A series of 2 (Emotional expression: happy, angry) x 2 (Hemisphere: left, right) x 5 (Emotion intensity: 20%, 40%, 60%, 80% and 100%) rANOVAs were used to analyse emotion valence effects on the amplitudes of P1, N170, and EPN in the absence of neutral. Likewise, 2 (Emotional expression) x 5 (Emotion intensity) rANOVAs was performed to analyse LPP amplitudes.

We used an alpha level of .05 for all statistical tests, and applied Greenhouse-Geisser corrections to degrees of freedom where appropriate.

2.3. Results

We calculated the response accuracy for the behavioural task to ensure participants were viewing the stimuli. All participants had 100% accuracy and were included in the ERP analysis.

2.3.1. P1 (90-110 ms)

There were no main effects of emotion, hemisphere, or intensity, or interactions between these variables on the amplitudes of the P1 (all *p*s > .05).

2.3.2. N170 (144-164 ms)

There were no main effects of emotion, hemisphere, or intensity or interactions between these variables on the amplitudes of the N170 (all *p*s > .05).

2.3.3. EPN (202-608 ms)

We analysed the EPN in five time windows (202-252 ms, 252-304 ms, 304-356 ms, 356-408 ms, and 408-608 ms) as in Sprengelmeyer and Jentzsch (2006).

We first examined whether the EPN is modulated by the emotion type. Our 2 (Emotion type) x 2 (Hemisphere) x 6 (Emotion intensity) rANOVA revealed main effects of emotion type between 202-408 ms (see Figure 2.2.; **200-252 ms:** $F(1, 20) = 7.624$, $p = .012$, ${\eta_p}^2 = 0.276$**;** **252-304 ms:** $F(1, 20) = 8.159$, $p = .010$, ${\eta_p}^2 = 0.290$; **304-356 ms:** $F(1, 20) = 13.043$, $p = .002$, ${\eta_p}^2 = 0.395$; **356-408 ms:** $F(1, 20) = 4.698$, $p = .042$, ${\eta_p}^2 = 0.190$**).**

Bonferroni-adjusted post-hoc analyses show that the angry expressions evoked slightly greater EPN negativities than happy expressions between 202-408 ms (**202-252 ms:** Angry $M = 3.303$ µv, $SD = 0.460$, Happy $M = 3.552$ µv, $SD = 0.523$; **252-304 ms:** Angry $M = 2.890$ µv, $SD = 0.356$, Happy $M = 3.192$ µv, $SD = 0.419$; **304-356 ms:** Angry $M = 2.841$ µv, $SD = 0.311$, Happy $M = 3.158$ µv, $SD = 0.376$**; 356-408 ms:** Angry $M = 2.219$ µv, $SD = 0.290$, Happy $M = 2.445$ µv, $SD = 0.318$).

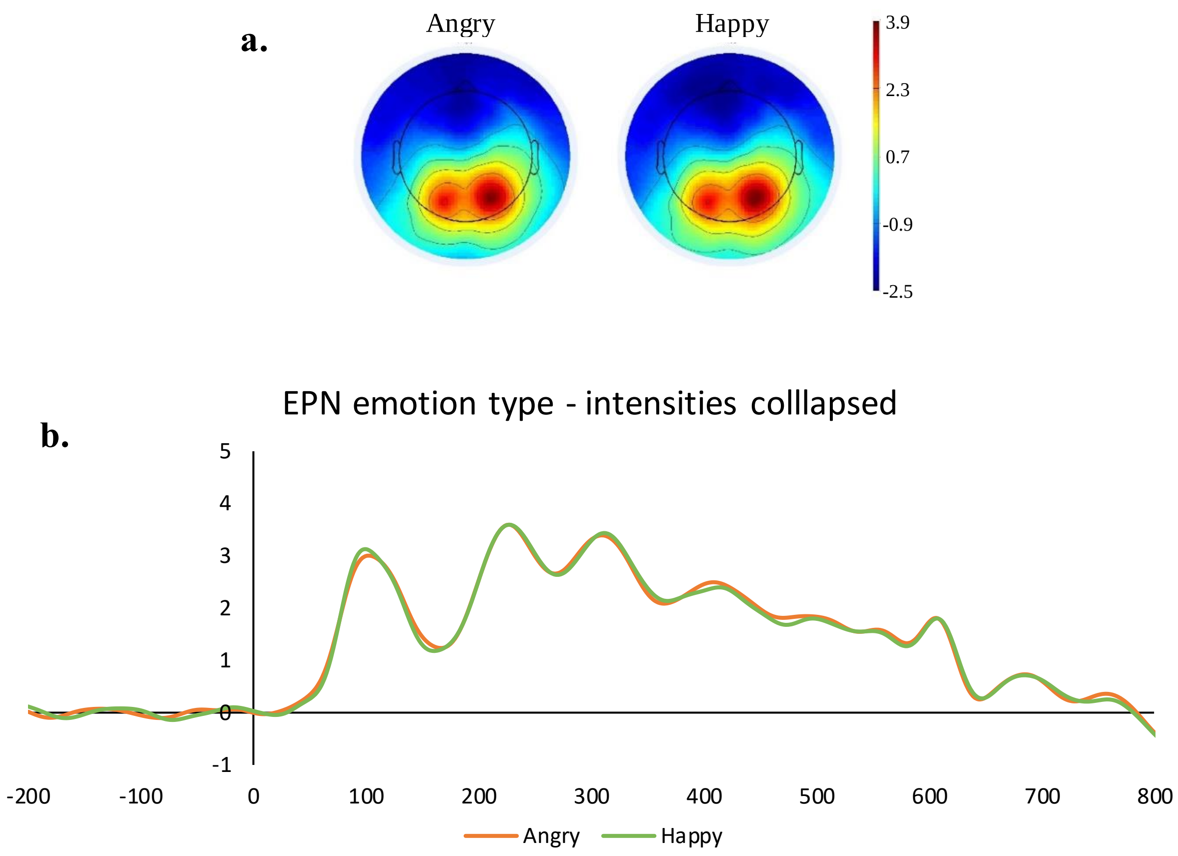
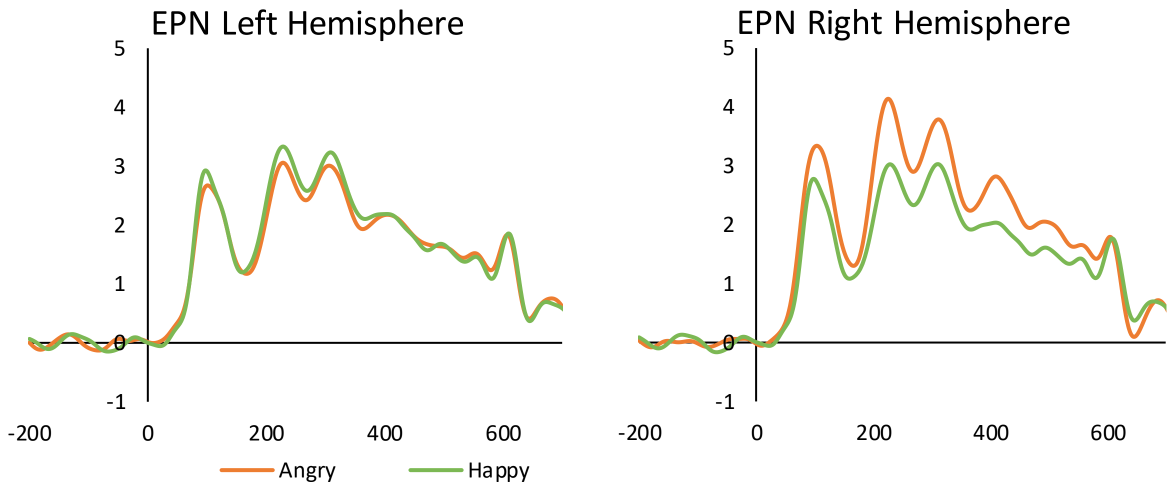


Figure 2.2. a. The topographies showing the spatial distribution of activity for the EPN evoked by angry expressions (left) and happy expressions (right). b. The ERPs for each emotion type when intensity was collapsed.

EPN negativities were greater in the left hemisphere than in the right hemisphere electrodes in all the time windows analysed (**202-252 ms:** *F*(1, 20) = 14.456, *p* = .001, $\eta_p{}^2$ = 0.419, left hemisphere *M* = 2.936 µv, *SD* = 0.492, right hemisphere *M* = 3.919 µv, *SD* = 0.522 ; **252-304 ms:** *F*(1, 20) = 5.361, *p* = .031, $\eta_p{}^2$ = 0.211, left hemisphere *M* = 2.706 µv, *SD* = 0.399, right hemisphere *M* = 3.303 µv, *SD* =0.416; **304-356 ms:** *F*(1, 20) = 8.067, *p* = .010, $\eta_p{}^2$ = 0.287, left hemisphere *M* = 2.672 µv, *SD* = 0.345 right hemisphere *M* = 3.327 µv, *SD* = 0.379; **356-408 ms:** *F*(1, 20) = 4.376, *p* = .049, $\eta_p{}^2$ = 0.180, left hemisphere *M* = 2.078 µv, *SD* = 0.326, right hemisphere *M* = 2.541 µv, *SD* = 0.311).

The significant main effects of Emotion and Hemisphere were modulated by a significant interaction between these variables in the 202-408 ms windows (**202- 252 ms:** $F(1, 20) = 5.124$, $p = .035$, $\eta_p^2 = 0.204$; **252-304 ms:** $F(1, 20) = 8.855$, $p = .007$, $\eta_p^2 = 0.307$), and the 356-608 ms windows (**356-408 ms:** $F(1, 20) = 8.353$, $p = .009$, $\eta_p^2 = 0.295$; **408-608 ms**: $F(1, 20) = 10.954$, $p = .003$, $\eta_p^2 = 0.354$).

Angry expressions had a slightly more negative EPN than happy expressions in the left hemisphere, whereas happy expressions had significantly more negative EPNs in the right hemisphere than angry expressions (See Figure 2.3).


EPN Left Hemisphere

EPN Right Hemisphere

Figure 2.3. EPN for angry and happy expressions from electrodes 66, 67, and 60 in the left hemisphere (left), and electrodes 77, 84, and 85 in the right hemisphere (right).

We then examined whether the EPN is modulated as a function of expression intensity, irrespective of emotion type. Our rANOVA showed main effects of emotional expression intensity between 252-408 ms (**252-304 ms:** $F(5, 16) = 8.323$, $p < .000$, $\eta_p^2 = 0.722$; **304-356:** $F(5, 16) = 5.218$, $p = .005$, $\eta_p^2 = 0.722$; **356-408 ms:** $F(5, 16) = 3.254$, $p = .032$, $\eta_p^2 = 0.504$).

Simple contrasts comparing neutral expression with each intensity level show that the effects were driven by differences between neutral and 80% expressions, and between neutral and 100% expressions (**252-304 ms:** neutral versus 80% $F(5, 16) = 16.412$, $p = .001$, $\eta_p{}^2 = 0.451$ and 100% $F(5, 16) = 19.581$, $p < .000$, $\eta_p{}^2 = 0.495$; **304-356 ms:** neutral versus 80% $F(5, 16) = 7.875$, $p = .011$, $\eta_p{}^2 = 0.283$ and 100% $F(5, 16) = 29.657$, $p < .000$, $\eta_p{}^2 = 0.597$; **356-408 ms:** neutral versus 80% $F(5, 16) = 11.929$, $p = .003$, $\eta_p{}^2 = 0.374$ and 100% $F(5, 16) = 12.818$, $p = .002$, $\eta_p{}^2 = 0.319$. All intensity effects remained significant when neutral was removed from the analysis.

There were no other main effect of intensity and no other significant effects or interactions involving emotion or intensity (all *p*s > .05).

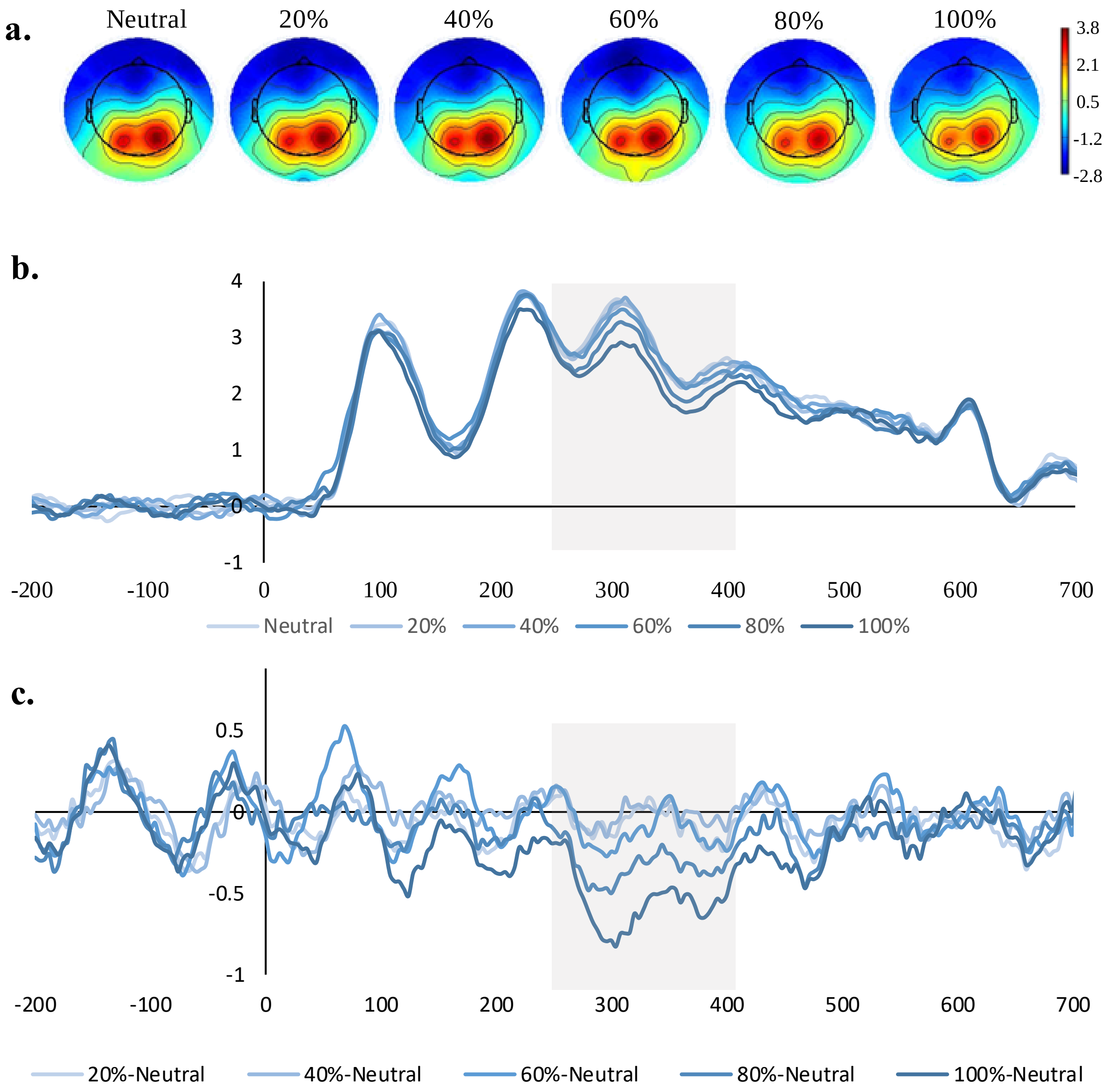


Figure 2.4. a. The topographies showing the spatial distribution of activity for each intensity between 252-408 ms. b. The ERPs evoked by each intensity when emotion type was collapsed, plotted from electrodes 66, 67, and 60 over the left hemisphere, and electrodes 77, 84, and 85 over the right hemisphere c. To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the EPN evoked for an expression intensity and neutral. The shaded grey boxes represent significant effects in the window analysed.

2.3.4. LPP (400 – 600)

There were no main effects of emotion type at electrode Cz, $F(1, 20) =$, $p = .811$, $\eta_p{}^2 = 0.003$, or main interactions involving emotion type (all *p*s > .05).

There was a main effect of intensity between 400-600 ms at electrode Cz**,** $F(5, 16) = 3.315$, $p = .023$, $\eta_p{}^2 = 0.644$. This effect was driven by a significant difference between neutral faces and 60% emotional expressions, $F(5, 16) = 7.089$, $p = .015$, $\eta_p{}^2 = 0.262$. There were no other main effects, or interaction involving emotion or intensity (all *p*s > .05).

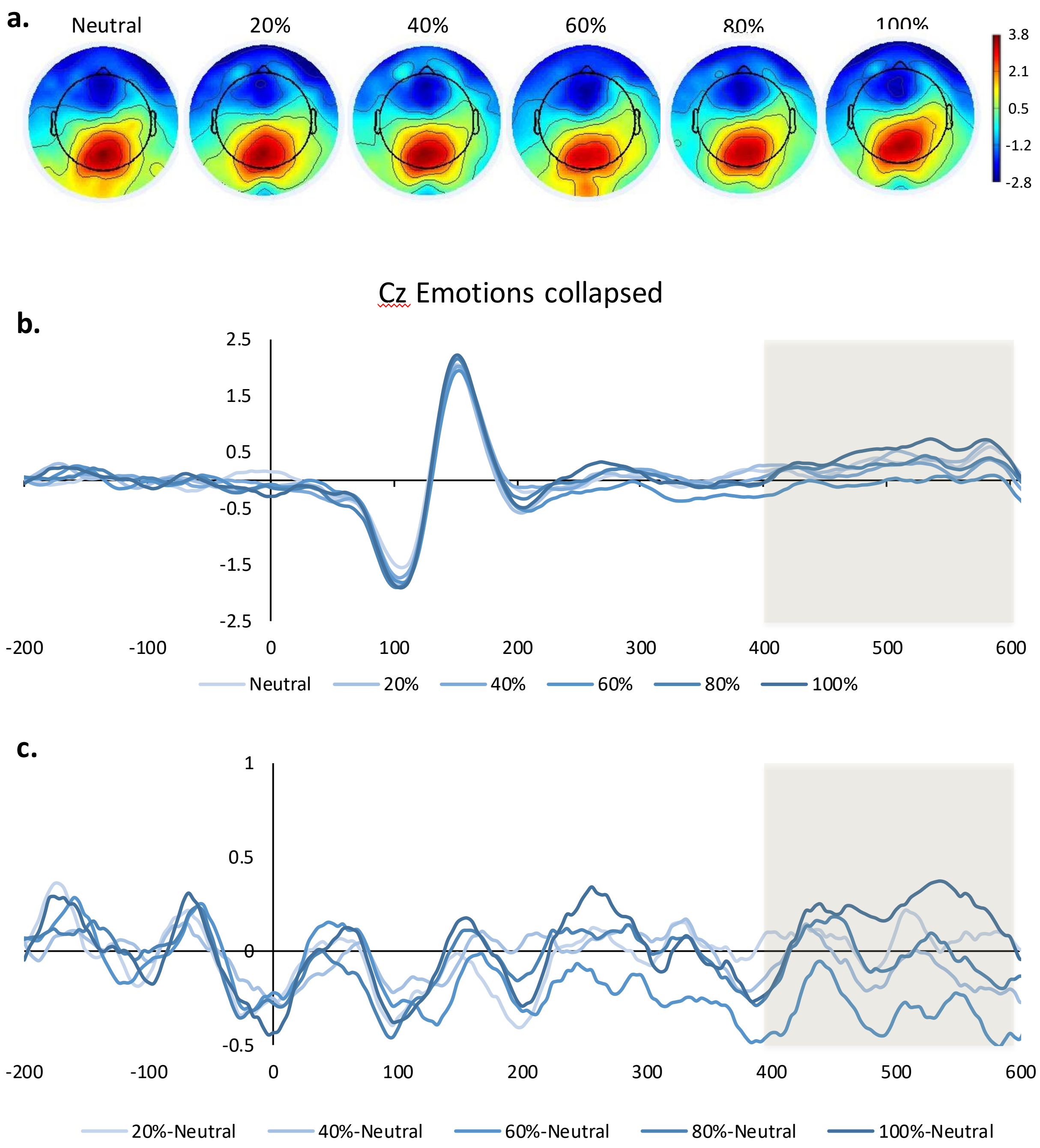


Figure 2.5. a. The topographies showing the spatial distribution of activity for each intensity between 400-600 ms. b. The ERPs evoked by each expression intensity when emotion type was collapsed, plotted from Cz. c. To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the LPP evoked for an expression intensity and neutral. The shaded grey boxes represent significant effects in the window analysed.

2.4. Discussion

We examined the automaticity of processing facial emotional expression intensity, and the interaction between expression intensity and emotion type, by analysing modulations of emotion-related ERPs along happy and angry emotion trajectories. Participants were simply required to view the expressions presented on screen, and respond to the identity of one particular face from a different stimulus set. We found main effects of emotion type on the EPN, and main effects of intensity on the EPN and the LPP. Our main finding for each component and their significance is discussed below.

2.4.1. P1

We found no main effects of emotion type, or intensity on the amplitude of the P1. If the P1 does reflect processing of low-level image properties (see Rossion & Caharel, 2011), the lack of P1 effects in our experiment might be explained by the fact that we equalised for luminance and spatial frequency between the images in our experiment. Based on this, we assume that other significant results in our experiment do not reflect differences in low-level image properties. Alternatively, P1 effects may also reflect explicit attention to emotion in the face. Therefore, it is also possible that the lack of P1 modulation was due to the lack of explicit attention drawn to emotion or intensity in the expressions.

2.4.2. N170

We did not observe main effects of emotion type or expression intensity on the amplitude of the N170. The lack of effects is consistent with the body of the work that suggests that the N170 might reflect expression-independent structural coding of faces, as described in Bruce and Young (1986). These results are inconsistent with Sprengelmeyer and Jentzsch's (2006) results which show that the N170 is systematically modulated for expression intensity. One difference between our task and theirs that might account for this discrepancy is that their task required participants to assess the gender of each face whereas ours required participants to detect the identity of a single face in a small percentage of trials. Although neither task draws attention to emotion in the face, it is possible that Sprengelmeyer and Jentzch's task may require more voluntary attention overall as participants needs to evaluate each face as male or female. There is some evidence to suggest that voluntary attention to emotion might mediate N170 sensitivity to emotion (see Wronka & Walentowska, 2011; c.f. Hinojosa et al., 2015). The effects of voluntary attention have not been investigated for expression intensity processing. Future studies could direct attention to the emotion in the face in order to examine the N170 sensitivity to expression intensity (see Experiment 2, Chapter 3).

2.4.3. EPN

Overall, angry expressions evoked slightly greater EPN negativities than happy expressions. Our analyses also reveal emotion type interactions with hemisphere; angry expressions evoke greater EPNs in the left hemisphere than happy ones, whereas happy expressions evoke greater negativities in the right hemisphere than angry ones. EPN amplitudes that are collapsed across hemisphere seem to support the hypothesis that the EPN reflects threat prioritisation (Cuthbert et al., 2000; Schupp et al., 2000; Schupp et al., 2006); however, the interaction between hemisphere and emotion type complicates this interpretation. Our interaction effects are inconsistent with laterality of emotion theories which suggest that the right hemisphere is specialised for processing emotional expressions (Gainotti, 2012; Lindell, 2018; Prete, Laeng, Fabri, Foschi, & Tommasi, 2015; Sato & Aoki, 2006), or that the right hemisphere might be specialised in processing negative emotions, whereas the left might prioritise positive emotions (see Silberman & Weingartner, 1986).

The interaction effect on the EPN bears some resemblance to Morris et al.'s (1996) findings using PET measures. They reported greater activation to fearful versus happy faces in the left amygdala suggesting that this area is involved in threat specific processing of emotion. While it is possible that the emotion type-hemisphere interaction observed in this experiment is related to increased activation in the left amygdala, such a relation would be speculative as deep brain structures like the amygdala are not tractable to EEG.

We also found main effects of expression intensity on the EPN, irrespective of emotion type. Extending on Sprenglemeyer and Jentzsch's (2006) findings of intensity effects on negative expressions, we also observed that intensity effects of EPN occur for positive (happy) expressions as well. This suggests that intensity is not coded specifically for expressions that signal threat (c.f. Leppänen et al., 2007).

Sprengelmeyer and Jentzsch's (2006) findings suggest that the EPN is systematically modulated as a function of emotion intensity. Whereas, our planned contrasts show that the main effect of intensity on the EPN was driven by difference between neutral and high emotion intensities (80% and prototypical emotional expressions). There are two critical differences between our study and Sprengelmeyer and Jentzsch's that could explain this discrepancy. The task in Sprengelmeyer and Jentzsch's study involved gender discrimination of each face. Although the facial expression was irrelevant to the behavioural task, it is possible that attention is allocated differently when participants must make judgements about every face versus only 10% of faces displayed, as in our study. Therefore, it is possible that the EPN modulation for intensity reflects processes that are mediated by attention, rather than completely 'automatic' processes. This is consistent with the observation by others in the literature that the EPN generators overlap with areas typically associated with selective attentional processes (see Pessoa et al., 2008). Further investigation of EPN modulation in tasks that require participants to pay more attention to emotional expressions can help examine the ways in which attention interacts with EPN effects (see Chapter 3).

A second crucial difference between Sprengelmeyer and Jentzsch's (2006) experiment and ours is that they compared 50%, prototypical emotions, and 150% emotion intensities. In contrast, we investigated emotion trajectories within the bounds of the prototypical emotion categories (i.e., 0-100%). Although the ranges we examined overlap, they are quantitatively and perhaps qualitatively different. EPNs for 20%-60% intensities did not differ significantly from the EPN evoked for neutral expressions in our experiment. Therefore, if we discard EPN responses to 0%-40% expression intensities, to examine a similar window to Sprengelmeyer and Jentzch, we would also see systematically graded negative EPN amplitudes for increasing expression intensities, thus changing the interpretation of our results. However, we cannot conclude that all intensities are coded 'automatically' when we examine a wider range of expression intensities (i.e., 0%-100%).

Neither our N170 nor EPN results provide evidence for the two-phase model discussed in Sprenglemeyer and Jentzch (2006). According the two-phase model, the first phase of processing involves processing the salience of information (here emotion intensity), and the second involves more in-depth analysis of affective information, including processing of emotion type. Instead, we found that information about emotion type was processed in an earlier time window than intensity (see Figure 2.2 for emotion type effects on the EPN and Figure 2.4 for intensity effects on the EPN).

As emotion type and only high intensities of expression seem to be processed automatically, we might hypothesise that expression recognition is based on categorical processing, where people match visual representations of emotion types with existing representations (i.e., template matching; Edelman & Bülthoff, 1992). This would suggest that prototypical expression categories might make up 'view-centered descriptions' that are involved in expression coding from the Bruce and Young (1986) framework. However, it is also possible that our emotion type effects are driven by coarse coding of emotion valence (positive and negative) as per the circumplex model of affect (see Posner & Russell, 2005; Russel, 1980). As the two emotion types we used also differ in emotion valence, we are unable to distinguish between these alternatives. However, Sprengelmeyer and Jentzch (2006) examined the EPN for three different negative valence emotion types and found main effects of emotion type. This suggests that the EPN might reflect coding of specific emotion types rather than their valence. Future experiments can examine a wider range of emotion types using the same parameters as our experiment to directly test this hypothesis.

2.4.4. LPP

We found no main effect of emotion type on the LPP. Angry expressions did not evoke larger LPPs than happy faces, contrary to other findings in studies that used prototypical emotional expressions at stimuli (e.g., Schupp et al., 2004). These results contradict the idea that the LPP reflects intrinsic task relevance of emotional expressions. Our results were obtained in a task that did not require explicit attention to be directed to emotion. Therefore, further understanding of the processes underlying LPP effects can be gained from tasks that manipulate the explicit task relevance of emotional expressions.

We found main effects of intensity on LPP which were driven by a lower amplitude for 60% emotional expression than all other intensities (see Figure 2.5). This finding contradicts the hypothesis that the LPP reflects the intrinsic motivational value of emotional expression processing, or threatening expressions. It is unclear why this might occur based on the literature. However, we could speculate that these results align with a recently proposed hypothesis that the LPP might reflect stimulus ambiguity. Sun, Ren, and He (2017) suggest that non-ambiguous expressions evoke larger LPPs than ambiguous ones. It is plausible that 60% expression intensity might reflect the point of subjective equality. The other stimuli, occupying the extremes of expression intensities, might be unambiguously categorised as a prototypical or neutral expression and therefore evoke larger LPPs. However, behavioural data is required in order to test whether the point of subjective equality lies at or around 60%.

There is also the possibility that the LPP might overlap with the P300. The P300 is larger for stimuli that are presented infrequently on screen, compared with stimuli that are presented frequently (Donchin, 1979, Johnson, 1988). Therefore, it is possible that our effects reflect the subjective probability of seeing emotional expressions presented on screen. If we hypothesise that the point of subjective equality lies at or around 60% emotional expression, the neutral, 20%, and 40% may be perceptually categorised as ‘neutral’, and 80% expression and prototypes may be categorised as ‘emotional’. This would result in 60% emotional expressions being ‘oddballs’ or ‘rare’ in the stimulus set. However, this line of argument leads to the prediction that 60% expression should evoke larger LPPs than for the other intensities, whereas our data suggest the reverse pattern (Figure 2.5).

2.4.5. Conclusion

The main aim of our study was to examine the automaticity of processing expression intensities along happy and angry emotion trajectories. Our results suggest that only high intensities of both positive and negative emotional expressions are processed automatically, as reflected by modulation of the EPN. EPN negativities were greater for negative versus positive emotions, which is consistent with the theory that expressions that signal threat are prioritised in processing. We did not find evidence for the hypothesis that the LPP might reflect the intrinsic motivational value of emotional expressions when attention is not directed to emotion.

Chapter 3: Explicit processing of emotional facial expressions along emotion trajectories

3.1. Introduction

A large corpus of research suggests that directed voluntary attention can facilitate stimulus processing (Hillyard et al., 1998). However, it has been suggested that emotion-laden stimuli can be processed ‘automatically’, implying that emotion processing might occur without explicit attention (Öhman, 2002; Vuilleumier & Schwartz, 2001). This may be because emotional expressions maximally engage attention resources as they are highly significant stimuli, or it may be that they are fully processed independently of attention.

In Experiment 1 (Chapter 2), we examined the automaticity of expression intensity processing while participants viewed emotional expressions that varied along happy and angry emotion trajectories, and performed an infrequent face identification task. We found modulations of the EPN that appear to reflect the ‘automatic’ processing of high intensities of happy and angry expressions, as well as an unexpected attenuation of the LPP for 60% expression intensity, in comparison with the other intensities examined. In non-face emotion laden stimuli, the effects of attention and emotion are additive (Sabatinelli, Keil, Frank, & Lang, 2013). If the underlying neural mechanisms of emotional expression processes overlap with selective attentional processes, explicitly paying attention to emotional expressions might enhance neural responses to emotional expression intensities more so than simply viewing while performing an unrelated task (Olofsson et al., 2008). Rellecke et al. (2012) systematically explored tasks that require explicit expression processing (e.g., emotion judgement task), as well as passive viewing, from the basic emotions framework. Their data suggest that both the EPN and LPP are modulated by intention to evaluate emotional expressions.

There is a paucity of research comparing ‘automatic’ (or ‘implicit’) and ‘explicit’ processing of emotional expressions along emotion trajectories. Existing studies that examine explicit emotion intensity processing use a variety of explicit tasks that may not be equivalent, or directly comparable (see Rellecke et al., 2013). Furthermore, these studies often examine only a subset of the data which is subsampled based on participants’ ‘correct’ responses to the expression presented (e.g., Leppänen et al., 2007; Utama et al., 2009; cf. Duval et al.'s, 2013, analysis of the LPP). While this approach allows researchers to explore the possible functional consequences of the ERPs, it does not produce results that can be directly compared with results from experiments that do not require a judgement on the expressive face; because data cannot be subsampled on the basis of responses in the latter case (e.g., Sprengelmeyer & Jentzsch, 2006). Therefore, Experiment 2 examines explicit emotion intensity processing along emotion trajectories using identical parameters to Experiment 1. Instead of asking participants to simply view the expressions (as in Experiment 1), we drew attention to the emotion in expressions by asking participants to indicate whether the expression they viewed was ‘Neutral’ or ‘Emotional’ in expression. This experiment will allow a direct comparison of the modulation of emotion related ERPs (i.e., the P1, N170, EPN, and LPP).

3.1.1. P1

Emotion type and expression intensity did not modulate the amplitudes of P1 in Experiment 1. We suggested that the lack of effects might be explained by the fact that we controlled low level stimulus properties (see Rossion & Caharel, 2011). However, the P1 can also be considered as an index of attention to emotion (Luck, Woodman, & Vogel., 2000; Woodman, 2010). Therefore, in this experiment we examine whether the P1 is modulated by expression intensity or emotion type when participants are explicitly instructed to pay attention to emotion.

3.1.2. N170

In Experiment 1, we also found no modulation of the amplitude of the N170 as a function of emotion type, or expression intensity. The N170 is thought to be immune to the facilitatory effects of selective attention (Cauquil, Edmonds, & Taylor, 2000). However, studies that examine N170 emotion effects have used a variety of different tasks that require different amounts of directed attention. Therefore, the parametric space in which the N170 is sensitive to emotion effects remains elusive. In this experiment we examine whether drawing attention to the emotion in expressions produces greater (i.e., more negative) N170 amplitudes for high intensities of expressions versus low intensities, and for 100% (prototypical) happy and angry expressions in comparison with neutral ones.

3.1.3. EPN

In Experiment 1 (Chapter 2), we found greater EPN negativities for angry versus happy expressions, and for high (80% and 100%) expression intensities in comparison with lower intensities (<80%). These results support the idea that the EPN might reflect automatically recruited neural resources to process emotional stimuli (see Olofsson et al., 2008); but they contradict the idea that the EPN is systematically modulated for expression intensity (Sprengelmeyer & Jentzsch, 2006). We suggested that the difference between our results and Sprengelmeyer and Jentzch's may be due to the different expression intensities examined (50%, 100%, and 150% in their experiment versus Neutral, 20%, 40%, 60%, 80%, and 100% in our experiment). The differences in results could also be because more attention was drawn to the stimuli in Sprengelmeyer and Jentzsch's task than in ours. Such an interpretation is inconsistent with the idea that the EPN might reflect 'natural selective attention' towards emotional stimuli (Schupp et al., 2006). It is unclear whether the EPN is susceptible to attentional control, and if so, how it interacts with attention. For instance, if the EPN reflects emotional stimuli which maximally 'capture' attentional resources, then we would expect similar results when attention is directed towards emotion versus when emotion is implicitly perceived (as in Experiment 1). However, if 'natural selective attention' of emotion and explicit attention shift the EPN in the same direction, paying attention to emotion should produce greater EPN negativities in this experiment than in Experiment 1, where the EPN was modulated by only the mechanisms that drive emotion processing (Olofsson et al., 2008; Vuilleumier & Pourtois, 2007).

3.1.4. LPP

In Experiment 1, we did not find evidence for the hypothesis that the LPP reflects intrinsic task relevance of emotion type, or expression intensities. Instead we found that 60% expression intensities had lower LPP amplitudes than the other intensities. We suggested that this might reflect the ambiguity of 60% expressions (see Sun et al., 2017). However, there are a number of disparate LPP results in the literature that complicate this interpretation. The LPP amplitude is greater for 100% (prototypical) angry expressions than neutral ones in tasks that require explicit emotion categorisation (i.e., evaluating whether the face is happy, angry, or neutral), but not in tasks that require less evaluation of the stimulus (e.g., discrimination between faces and words; Rellecke et al., 2013). Modulations of LPP for expression processing along emotion trajectories have been examined using a variety of tasks. In a valence judgment task, the LPP amplitude increased as the emotion intensity increased along an emotion trajectory (Duval et al., 2013). In one prototypical emotion judgement task, the LPP was greater for fearful versus happy faces (Leppänen et al., 2007).

Given the disparate findings in the literature, as well as differences between previous studies and Experiment 1, Experiment 2 will use the same parameters as Experiment 1 and systematically examine modulation of LPP when an explicit emotion judgement is required. This will improve our understanding of how the LPP is modulated when attention is directed to emotion intensities along emotion trajectories. Furthermore, direct comparisons with data from Experiment 1 may reveal how these modulations differ from passive viewing.

3.1.5. Rationale and aims of this study

There are a number of differences between previous studies and the procedure of Experiment 1, which makes it difficult to compare results directly to examine differences between passive viewing and overt attention to emotion for processing expressions along emotion trajectories. In this experiment, we recorded EEG while participants viewed and evaluated the emotion expressed in faces that were either neutral in expression or portrayed expressions of happiness or anger along an emotion trajectory. Consistent with Experiment 1, the emotional faces were morphed to display expressions that were 20%, 40%, 60%, 80%, or 100% of the full expression to form emotional trajectories. We examined whether intention to process the emotion lead to systematic modulations of the P1, N1, EPN, and LPP as a function of emotion intensity and emotion type. These results can help extend our understanding of how emotional expressions are processed along expression trajectories when attention is drawn to the emotion in the face. Furthermore, this experiment will provide a direct comparison with the results from Experiment 1, which assessed processing of emotional expressions in a passive task. These comparisons will help distangle directed attentional versus ‘automatic’ process involved in intensity processing, and explicate the differences between automatic and explicit processing of emotional expressions.

3.2. Methods

3.2.1. Participants

Participants in this study were 23 volunteers (13 female) from the University of Auckland. The mean age was 23.86 (*SD* = 5.36, *range* = 18-35). One participant was left-handed. Participants' data were included if at least 60% of trials (60 trials) were left per condition after artifact rejection (Luck, n.d.). This resulted in exclusion of three participants' data. On average, 89% (*range* = 88-90%) of trials were retained for the remaining participants.

Volunteers with conditions that impaired their ability to recognise facial expressions or with a history of epilepsy or migraines did not meet the criteria to participate in the study. All participants reported normal or corrected-to-normal vision. Participants provided written, informed consent prior to their participation. All participants received a $20 supermarket voucher as koha for their participation in the study. Research protocols were approved by The University of Auckland Human Participants Ethics Committee.

3.2.2. Stimuli

We used the same stimuli for the experiment as in Experiment 1 (see Chapter 2, Section 2.2.2) with one exception; the face from the NimStim stimulus set (Tottenham et al., 2002, 2009) was not included as it was not required for the behavioural task in this experiment.

3.2.3. Procedure and design

Participants were seated in a dimly lit faraday cage. The monitor was positioned 57 cm in front of the participant. Experimental stimuli were presented on a 21- inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh).

We recorded EEG while participants viewed faces that were either neutral in expression or morphed faces that were 20%, 40%, 60%, 80%, or full-intensity happy or angry faces (see Chapter 2, Figure 2.1b and c). Before the experiment started, participants performed a practice block in which they viewed, and responded via button press to 10 examples of the morphed stimuli on happy and angry emotion trajectories (these stimuli were not included in the main experiment). Participants were not provided with feedback on their performance in the task.

The experiment was split up into 10 blocks. Each block contained 120 trials (20 trials of each emotion intensity). Each trial began with a fixation cross that was presented for 200-400 ms, then a face was presented for 500 ms, and then a blank slide was presented for 1000–1200 ms (see Chapter 2, Figure 2.1a). Participants were asked to press one of two keys (labelled 'E' and 'N' on the keyboard) to indicate whether the face they saw was expressing an 'emotion', or whether it was 'neutral'. Participants kept their left and right index fingers on the 'E' and 'N' keys throughout the experiment. The hands that they responded 'E' and 'N' with were counterbalanced between participants. Participants were asked to judge facial expressions they saw as 'Emotional' if they could identify what the expression was, or 'Neutral' if they did not know what expression it displayed, or if they thought the face was unemotional. After each block, a "break" slide appeared for 30 seconds. Another slide then appeared with a reminder to 'Press the 'E' if they thought the face expressed an emotion, or 'N' if it was neutral in expression. The slide also contained instructions to 'Please press the space bar to continue the experiment'. Before the experiment started, participants were also verbally informed that they could take a break for as long as they want, and press the spacebar to continue when they were ready to continue the experiment.

3.2.4. EEG acquisition and pre-processing

Data were acquired and pre-processed in the same way as in Experiment 1 (see Chapter 2, Section 2.2.4) to allow for direct comparisons between viewing and active evaluation of the emotional facial expressions.

3.2.5. ERP analysis

Grand averages of the trials were computed for each condition per participant, and for each condition collapsed across participants. A baseline correction (based on the average of the 200-ms baseline period) was subtracted from each time point in the epoch.

Electrodes for analysis were chosen on the basis of previous literature, as well as the scalp maxima of the current dataset when all the conditions were collapsed together. Conditions were collapsed to avoid a biased selection of electrodes based on maximal differences between conditions. Consistent with Experiment 1, the P1 was measured at two homologous electrodes clusters around O1 in the left hemisphere (electrodes 70, 66, and 75) and right hemisphere (electrodes 83, 90, and 84). The N170 was measured at two homologous electrode clusters which included P7 and P9 in the left hemisphere (electrodes 58, 64, and 63), and P8 and P10 in the right hemisphere (electrodes 90, 95, and 99). The VPP was measured at Cz and CPz. The EPN was measured at electrodes 60, 61, and 53 in the left hemisphere and electrodes 85, 86, and 78 in the right hemisphere. The LPP was measured at the midline electrodes Pz, CPz, and Cz.

3.2.6. Statistical analyses

After artifact rejection, we checked if there were differences in the number of trials retained per condition by conducting a 2 (Emotional expression: happy, angry) x 6 (Emotion intensity: Neutral, 20%, 40%, 60%, 80%, and 100%) repeated measures ANOVA (rANOVA).

A series of 2 (Emotional expression: happy, angry) x 2 (Hemisphere: left, right) x 6 (Emotion intensity: Neutral, 20%, 40%, 60%, 80%, and 100%) repeated measures analyses of variance (rANOVAs) was performed to analyse intensity effects on the amplitudes of P1, N170, and EPN. As the LPP is calculated from the midline electrodes, hemisphere was not included as a factor for analysis. Therefore, 2 (Emotional expression) x 6 (Emotion intensity) rANOVAs were performed to analyse LPP amplitudes. We conducted planned simple contrasts between each emotion intensity level and neutral in order to examine which intensity levels drive intensity effects.

When analysing intensity effects, we included ‘Neutral’ in our analysis to compare each intensity level with neutral, as is conventional in studies in the basic emotion framework (e.g., Ashley et al., 2004; Batty & Taylor, 2003; Eimer & Holmes, 2002). To compare our results with the other studies examining emotion trajectories (Duval et al., 2013; Leppänen et al., 2007; Sprengelmeyer & Jentzsch, 2006), we also conducted rANOVAs without neutral as a level in the ‘intensity’ factor. A series of 2 (Emotional expression: happy, angry) x 2 (Hemisphere: left, right) x 5 (Emotion intensity: 20%, 40%, 60%, 80% and 100%) rANOVAs were used to analyse emotion type effects on the amplitudes of P1, N170, and EPN in the absence of neutral. Likewise, 2 (Emotional expression) x 5 (Emotion intensity) rANOVAs were performed to analyse VPP and LPP amplitudes.

We used an alpha level of .05 for all statistical tests, and applied Greenhouse-Geisser corrections to degrees of freedom where appropriate.

3.3. Results

At least 94 trials per condition per participant were retained for analysis after artifact rejection. Our 2 (Emotional expression) x 6 (Emotion intensity) rANOVA showed that there were no differences in the number of trials retained for each condition (all *p*s > .05).

3.3.1. P1 (92 - 112 ms)

We examined whether the P1 was modulated as a function of emotion type or as a function of expression intensities. As in Experiment 1, we analysed a time window of 20 ms around the peak of the grand average of the P1. Consistent with Experiment 1, there were no significant differences between P1 amplitude for angry versus happy expressions, or as a function of expression intensities along happy and angry emotion trajectories (all *p*s > .05).

3.3.2. N170/VPP (138 - 158 ms)

As in Experiment 1, we analysed a 20-ms window around the peak of the grand averaged waveform of the N170 (See Figure 3.1b). Consistent with Experiment 1, there were no differences in N170 amplitude for angry versus happy faces ($p > .05$). However, in contrast with Experiment 1, we found a main effect of intensity on the amplitude of the N170, $F(5, 15) = 4.502$, $p = .010$, ${\eta_p}^2 = 0.600$ (see Figure 3.1). This effect was present even when neutral expressions were removed from analysis, $F(4, 16) = 5.871$, $p = .004$, ${\eta_p}^2 = .595$.

We then conducted simple contrasts to examine which expression intensities drive intensity effects on the amplitude of the N170. These tests revealed that intensity effects on the N170 were driven by a significant difference between neutral and 100% (prototypical) expressions, *F*(5, 15) = 7.868, *p* = .011, $\eta_p{}^2$= 0.293. However, results were also significant when neutral was removed from the analysis, so there were differences between the other intensity conditions that did not reach statistical significance.

To enable better visualisations of these differences, we computed difference waves by subtracting the N170 evoked by neutral from the N170 evoked by each expression intensity (Figure 3.1c.). We then examined modulation of the VPP, which is considered to be a dipolar reflection of the N170 (Joyce & Rossion, 2005). Contrary to what we expected, we did not find significant modulation of the VPP amplitude as a function of emotion expression intensity (*p* > .05). Difference waves also showed that a broadly distributed positivity seemed to be overlapping our N170 effects. Therefore, we conducted a follow up analysis in which we re-referenced our data to the mastoid reference and re-examined whether the amplitude of the N170 was still modulated systematically by emotion intensity. As the paired mastoid references are closer to the topographical distribution typically seen from the EPN, Rellecke et al. (2012) suggest that re-referencing to the mastoid reduces the broadly distributed positivities, which in turn diminishes the N170 effects for emotion. However, our follow up analysis using the dual mastoid reference also revealed a significant main effect of intensity on the N170, *F*(5, 15) = 4.329, *p* = .005, $\eta_p{}^2$ = 0.591. Again, this effect remained significant when neutral was removed from the data, F(4, 16) = 5.700, p = .005, $\eta_p{}^2$ = 0.588.

There were no other significant main effects or interactions involving emotion or intensity for the N170 (all *p*s > .05).

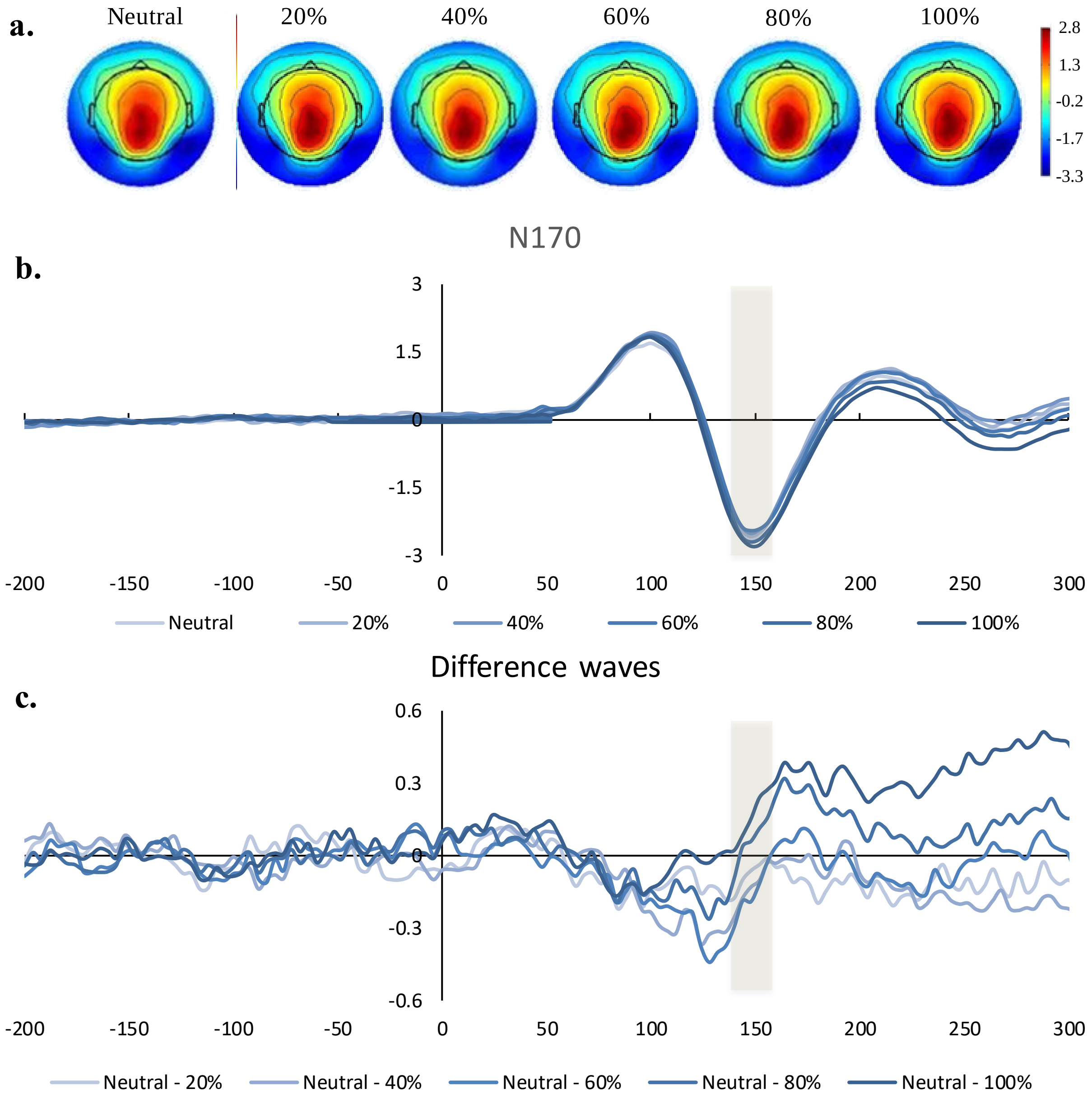


Figure 3.1. a. The topographies showing the spatial distribution of activity for each intensity between 138-158 ms. b. The ERPs evoked by each intensity when emotion type was collapsed, plotted from electrodes 58, 64, and 63 over the left hemisphere, and electrodes 90, 95, and 99 over the right hemisphere. c. To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the N170 evoked for an expression intensity and neutral. The shaded grey boxes represent significant effects in the window analysed.

3.3.3. EPN (202 – 408 ms)

We chose analysis windows for the EPN that were consistent with those from Sprengelmeyer and Jentzsch (2006) with one exception; 408 – 608 ms was omitted as we did not find EPN effects in Experiment 1, and other overt expression tasks suggest that effects in this time period are driven by the LPP (see Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Duval et al., 2013; Leppänen, Hietanen, & Koskinen, 2008; Leppänen et al., 2007; Schupp et al., 2000).

We examined whether the EPN was modulated as a function of emotion type. There was a main effect of emotion on the amplitude of the EPN, however this significant effect started around 150 ms after the EPN differences for emotion type found in Experiment 1 (these earlier effects were found between 202-408 ms; See Chapter 2, Figure 2.2). In this experiment, the effect was distributed from 356-408 ms, $F(1, 19) = 8.168$, $p = .010$, ${\eta_p}^2 = 0.301$ (Figure 3.2b).

The main effect of emotion in this experiment was driven by larger negativities of EPN for happy expressions in comparison with angry expressions, 356-408 ms: happy $M = 2.702$, $SD = 0.368$, angry $M = 2.883$, $SD = 0.062$. We computed a difference wave to enable better visualisation of the difference between the EPN for happy versus angry (see grey line in Figure 3.2b). In Experiment 1, angry expressions had lower EPN amplitudes than happy ones (see Figure 2.2).

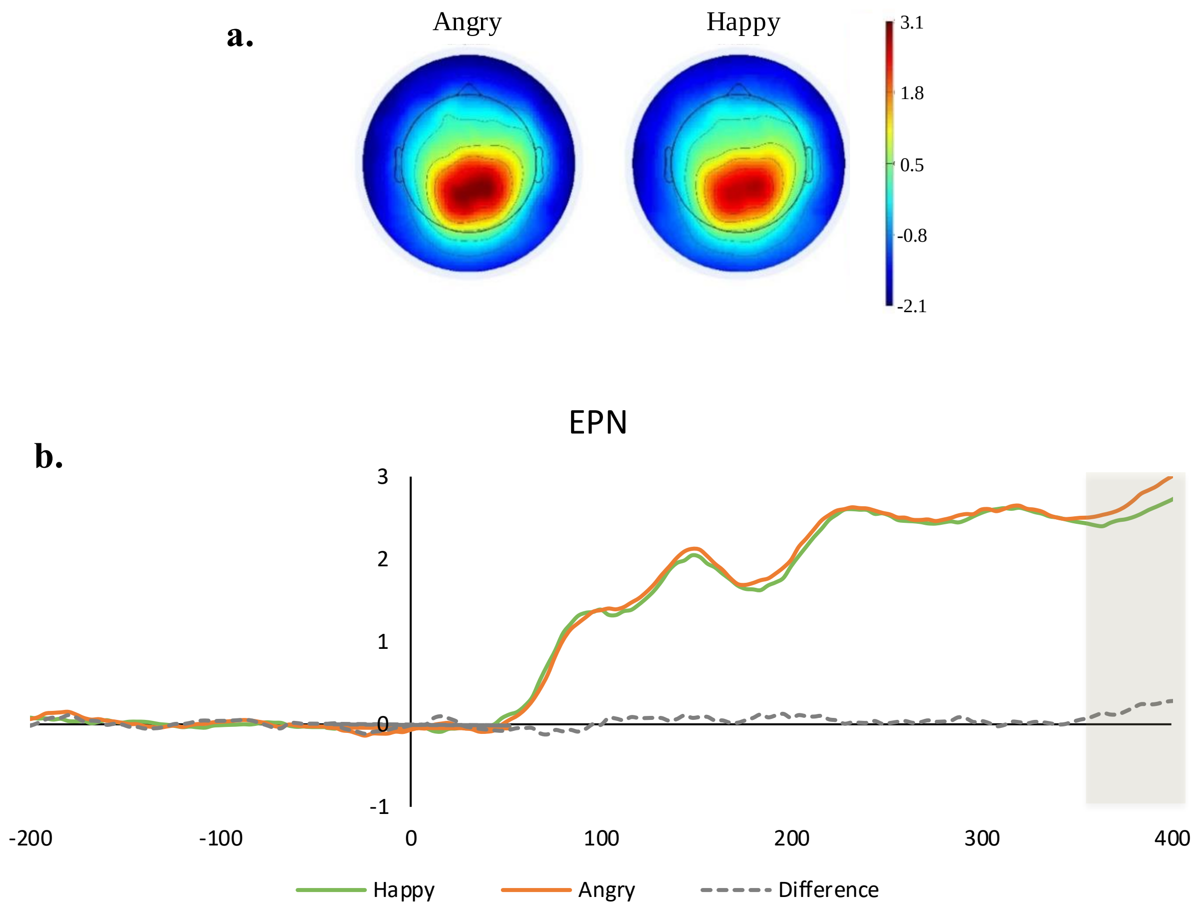


Figure 3.2. a. The topographies showing the spatial distribution of activity for the EPN evoked by angry expressions (left) and happy expressions (right). b. The ERPs for each emotion type when intensity was collapsed. c. To allow better visualisation of the difference, the grey line represents the difference waveform when the amplitude evoked by happy expressions is subtracted from the EPN evoked by angry expressions. The shaded grey boxes represent significant effects in the window analysed.

We examined whether the EPN was modulated as a function of expression intensity. We found modulations of the EPN as a function of emotion intensity between 252-356 ms (see Figure 3.3b; **252-304 ms:** $F(5, 15) = 3.700$, $p = .022$, $\eta_p{}^2 = 0.552$; **304-356 ms:** $F(5, 15) = 4.811$, $p = .008$, $\eta_p{}^2 = 0.616$). When neutral face were removed from the analysis, the effects were significant between 252-304 ms: $F(4, 16) = 4.912$ $p = .009$, $\eta_p{}^2 = 0.551$.

We then conducted simple contrasts to examine which expression intensities drive intensity effects on the amplitude of the EPN. These revealed that intensity effects were mainly driven by larger negativities for 100% (prototypical) expressions versus neutral ones (**252-304 ms:** $F(5, 15) = 9.027$, $p = .007$, ${\eta_p}^2 = 0.332$; **304-356 ms:** $F(5, 15) = 13.753$, $p = .011$, ${\eta_p}^2 = 0.293$).

To enable better visualisation of these differences, we computed difference waves by subtracting the EPN evoked by each expression intensity from the EPN evoked by neutral (see Figure 3.3c.).

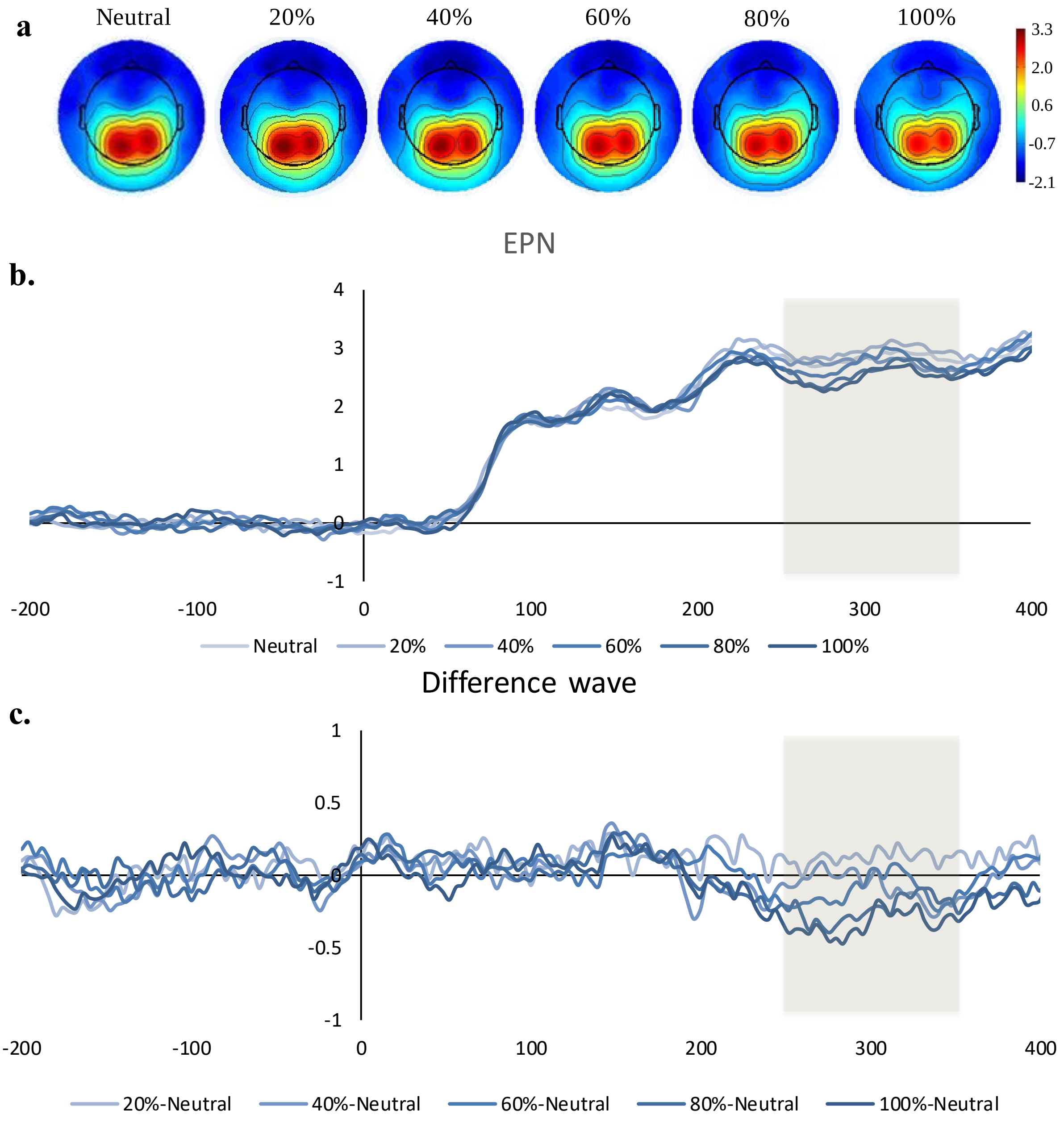
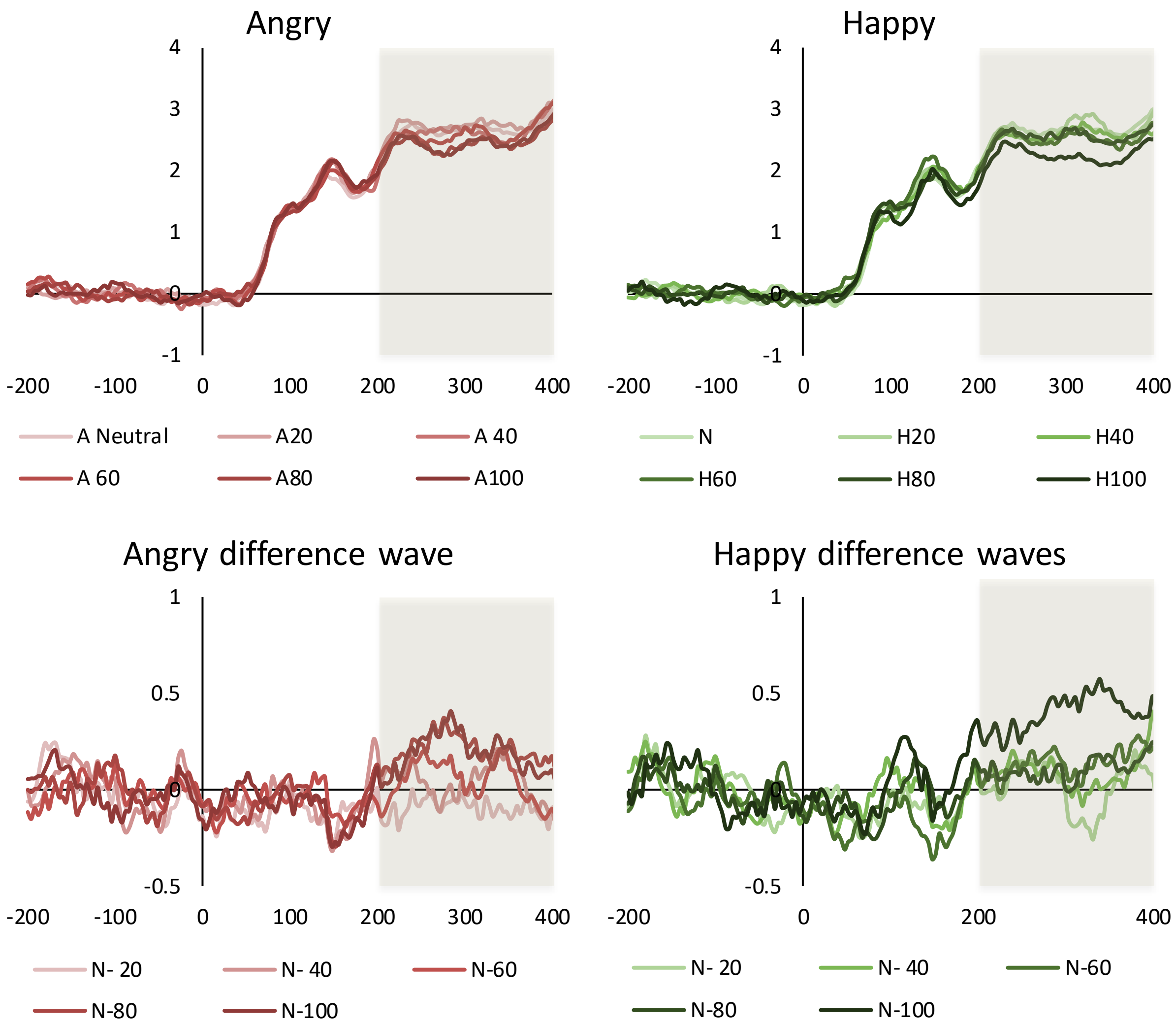


Figure 3.3. a. The topographies showing the spatial distribution of activity for each intensity between 252-356 ms. b. The ERPs evoked by each intensity when emotion type was collapsed, plotted from electrodes 60, 61, and 53 over the left hemisphere and electrodes 85, 86, and 78 over the right hemisphere. c. To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the EPN evoked for an expression intensity and neutral. The shaded grey boxes represent significant effects in the window analysed.

The significant main effects of emotion type and intensity were also modulated by a significant interaction between the two variables between 202-408 ms (**202-252 ms:** $F(4, 16) = 4.379$, $p = .014$, $\eta_p{}^2 = 0.523$; **252-304 ms:** $F(4, 16) = 4.828$, $p = .010$, $\eta_p{}^2 = 0.547$; **304-356 ms:** $F(4, 16) = 5.367$, $p = .006$, $\eta_p{}^2 = 0.573$; **356-–408 ms:** $F(4, 16) = 3.323$, $p = .037$, $\eta_p{}^2 = 0.454$).

The interactions reveal that happy expressions evoked larger EPN negativities for 100% expression intensities (i.e., prototypical happy expressions) in comparison with all other expression intensities. The interaction effects started earlier than emotion type effects (356 ms) and emotion intensity effects (252-356 ms) and lasted throughout the analysis window. The EPN for angry expressions was graded for emotion intensity, whereas for happy expressions the difference was mainly between 100% intensity (prototypical expression) and neutral (see Figure 3.4).

There were no other significant main effects or interactions involving emotion or intensity (all *p*s > .05).


Angry

Happy

Angry difference wave

Happy difference waves

Figure 3.4. ERPs evoked for all intensities for angry expressions (top right) and happy expressions (top left). To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the EPN evoked for an angry (bottom left) or happy (bottom right) expression intensity and neutral. The shaded grey boxes represent significant interaction effects in the window analysed.

3.3.4. LPP (400 – 600 ms)

The effects were the largest at Cz so we report these here for brevity. We chose an analysis window between 408-608 ms based on Leppänen et al. (2007), as well as reports of maximal LPP effects in the face and non-face literatures (see Olofsson et al., 2008; Schupp et al., 2006).

In this experiment, we found a main effect of emotion type on the amplitude of the LPP, $F(1, 19) = 16.711$, $p = .001$, $\eta_p{}^2 = 0.468$. This was driven by larger amplitudes of LPPs evoked by angry expressions, ($M = 2.771$, $SD = 0.412$) than those evoked by happy expressions ($M = 2.673$, $SD = 0.330$).

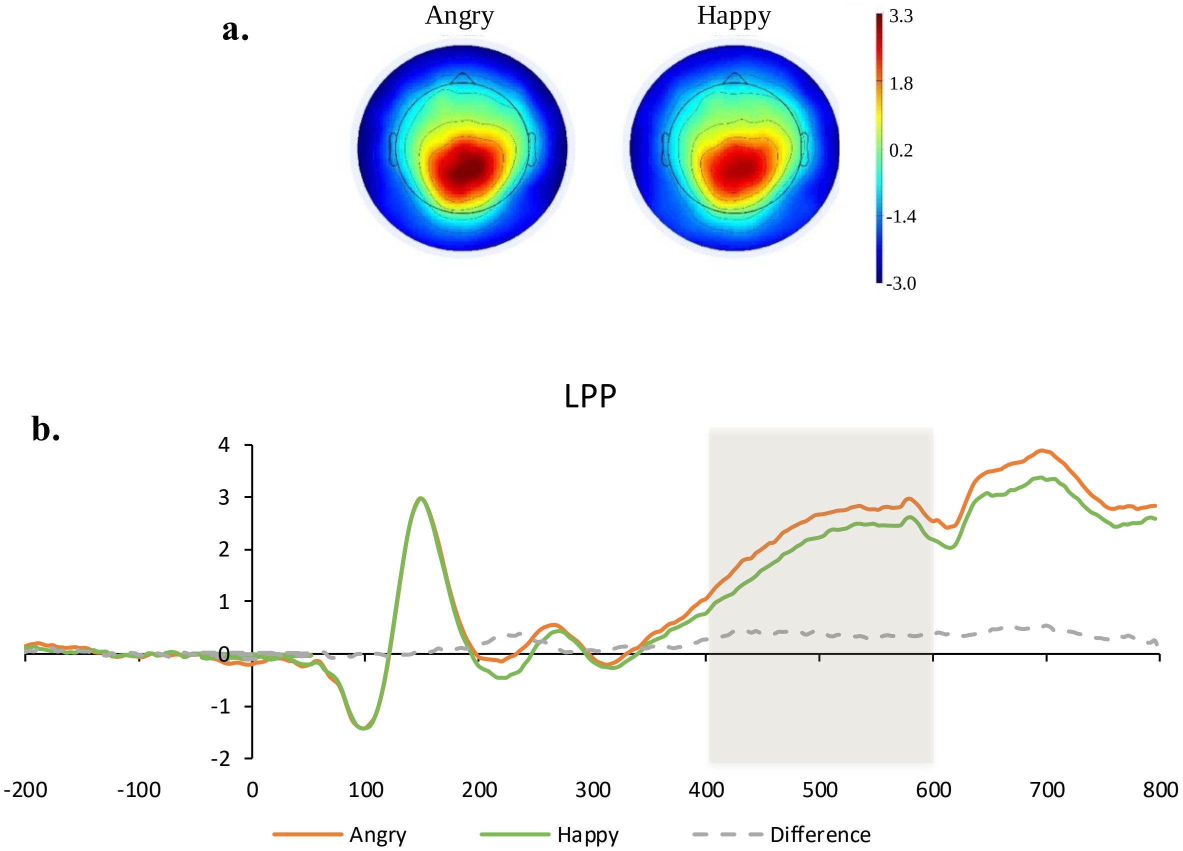


Figure 3.5. a. The topographies showing the spatial distribution of activity for the LPP evoked by angry expressions (left) and happy expressions (right). b. The ERPs for each emotion type when intensity was collapsed. To allow better visualisation of the difference, the grey line represents the difference waveform when the amplitude evoked by happy expressions is subtracted from the LPP evoked by angry expressions. The shaded grey box represent a significant effect in the window analysed.

The LPP was also modulated by intensity, $F(5, 15) = 9.314$, $p < .000$, $\eta_p{}^2 = 0.329$, ε = 0.703. This was driven by differences between neutral expressions and 60% $F(5, 15) = 14.356$, $p = .001$, $\eta_p{}^2 = 0.430$, differences between neutral expressions and 80% $F(5, 15) = 11.016$, $p = .004$, $\eta_p{}^2 = 0.367$, and differences between neutral expressions and 100% $F(5, 15) = 8.477$, $p = .009$, $\eta_p{}^2 = 0.309$ intensity. Therefore, the main effect of intensity remained significant when neutral expressions were removed from the analysis, suggesting that there were also differences between the other expression intensities, $F(4, 16) = 9.314$, $p < .000$, $\eta_p{}^2 = 0.349$, ε = 0.630.

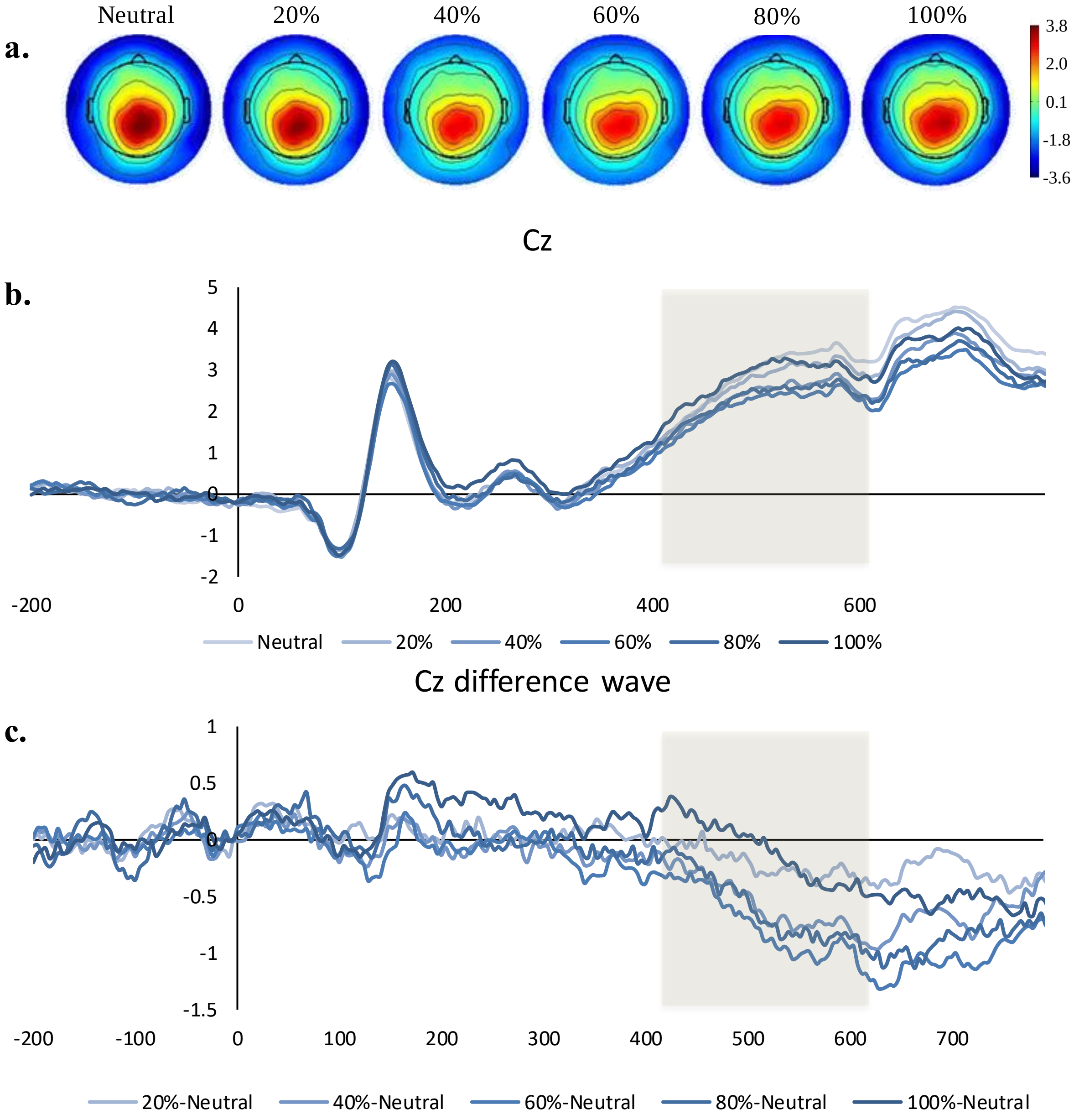


Figure 3.6. a. The topographies showing the spatial distribution of activity for each intensity between 408-608 ms. b. The ERPs evoked by each intensity when emotion type was collapsed, plotted from Cz. c. To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the LPP evoked for an expression intensity and neutral. The shaded grey boxes represent significant effects in the window analysed.

In contrast to Experiment 1, there were main effects of both emotion type and intensity on the amplitude of the LPP, and these effects were also modulated by an interaction between emotion type and intensity, $F(5, 15) = 4.885$, $p = .012$, $\eta_p{}^2 = 0.205$, $\varepsilon = 0.413$. This interaction effect remained significant when neutral was removed from the analysis $F(4, 16) = 3.539$, $p = .036$, $\eta_p{}^2 = 0.157$, $\varepsilon = 0.528$.

The interaction effect between emotion type and intensity (see Figure 3.7) shows that Neutral, 20%, and 100% (prototypical) angry expressions evoked larger LPP amplitudes than 40%, 60%, and 80% angry expressions. In contrast, neutral and 20% happy expressions evoked larger amplitudes than all the other happy expression intensities (i.e., 40%, 60%, 80%, and 100%). These results differ from Experiment 1, in which only 60% expression intensity evoked larger responses than all other expression intensities, irrespective of emotion type.

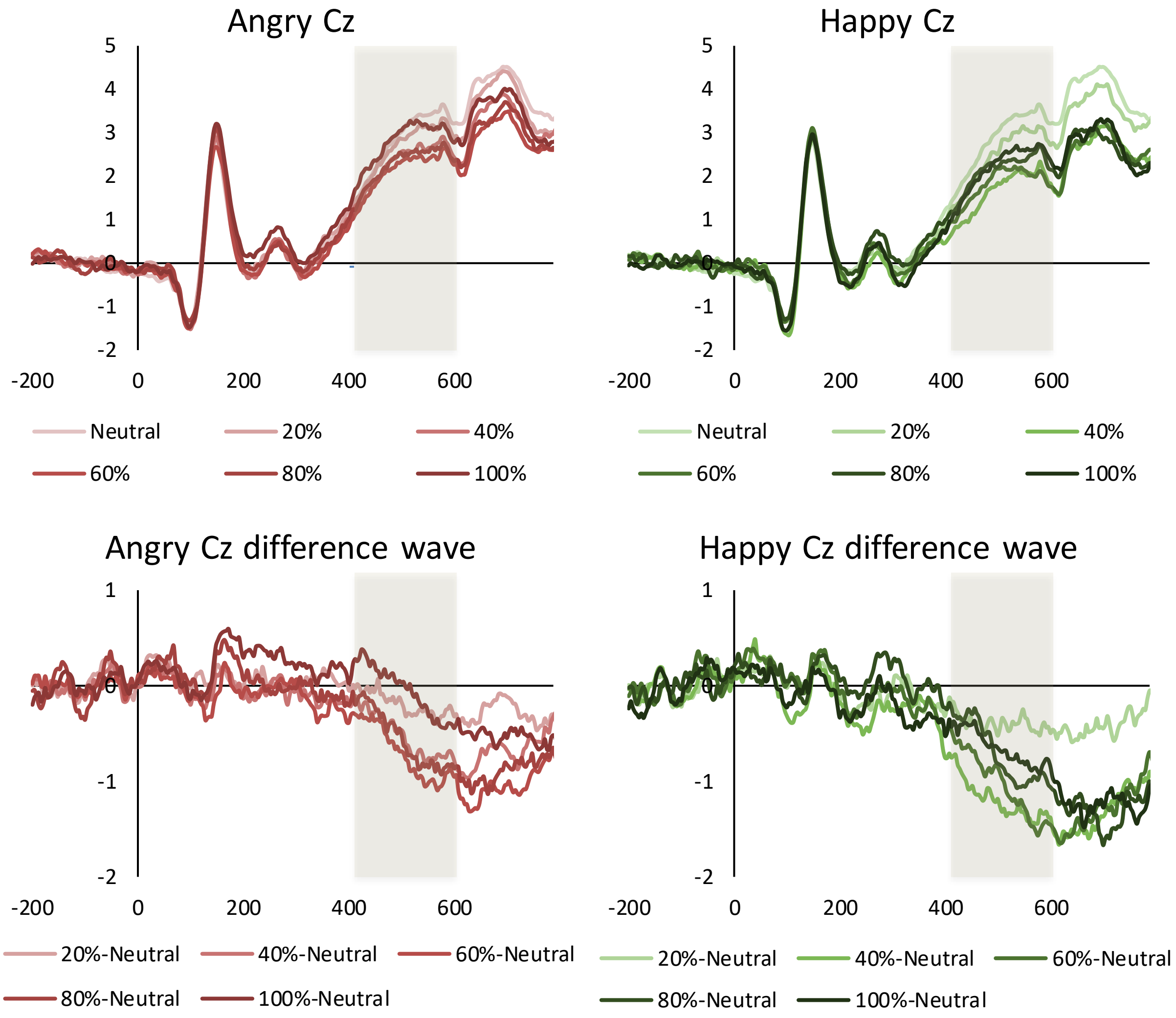


Figure 3.7. ERPs evoked for all intensities for angry expressions (top right) and happy expressions (top left). To allow better visualisation of the difference, we computed difference waves; each line represents the difference between the LPP evoked for an angry (bottom left) or happy (bottom right) expression intensity and neutral. The shaded grey boxes represent significant interaction effects in the window analysed.

3.4. Discussion

We examined expression intensity processing when attention was drawn to the emotion in faces. Participants were required to view different intensities of expressions along happy and angry emotion trajectories and evaluate whether the faces were ‘emotional’ or ‘neutral’ in expression. We found main effects of emotion type on the EPN and LPP, and main effects of intensity on the amplitudes of the N170, EPN, and LPP.

3.4.1. P1

Consistent with Experiment 1, we found no modulation of the P1 amplitude in Experiment 2. Past literature suggests that stimulus based properties modulate the P1 (see Rossion & Caharel, 2011). Taken together, results from Experiments 1 and 2 suggest that there are no systematic differences between basic stimulus properties across emotion type and intensity conditions in our experiment.

3.4.2. N170

Our results show that the N170 is modulated by expression intensity. This difference was mainly driven by the difference between the N170 evoked for 100% (prototypical) emotion intensity and 0% neutral; however, the effects remained significant when neutral expressions were removed from our analysis. Therefore, there were likely differences between the other conditions as well. There are a number of possible interpretations for this data. Taken together with our results from Experiment 1, which show no systematic modulation of the N170 during passive viewing, these results suggest that the sensitivity of the N170 to expression intensities is gated by voluntary attention (see Wronka & Walentowska, 2011; cf. Blau et al., 2007). Alternatively, the data may be driven by overlapping EPN modulations that are gated by attention. Lastly, it is also possible that both attention and the EPN overlap jointly determine N170 modulation for emotion intensity.

Although attention-gated modulation of N170 is the simplest interpretation, it may not be the most parsimonious. We did not find corresponding modulation of the VPP, despite a large corpus of research suggesting that the VPP is a dipolar reflection of the N170 (see Eimer, 2012, for a discussion). The absence of this modulation can either be taken as evidence against a unitary generator of the N170 and VPP, or suggest that our effects were driven by a different generator. Consistent with previously reported data, our waveforms (Figure 3.1) show that the N170 peak overlaps with a more widely distributed positivity which is likely to be the EPN (see Rellecke et al., 2013; Vuilleumier & Pourtois, 2007). As the mastoid electrodes are closer to the generators of the EPN, Rellecke et al. (2013) suggest that using the mastoid reference can dampen the contribution of the EPN. We conducted a follow up analysis using the mastoid reference to assess the N170, in an attempt to reduce EPN effects. The N170 effects were still present when using the mastoid reference, suggesting that the N170 could be modulated independently of the overlapping EPN. However, both EPN and N170 seem to be generated by a network of posterior regions in the extra-striate cortex (see Chapter 1). Therefore, it is possible that their generators at least partially overlap. In sum, despite the results of our follow-up analyses, we cannot rule out completely the possibility of the EPN contributing to the observed N170 modulation. Disentangling the EPN and N170 may be possible with the use of simultaneous EEG-fMRI recordings, as the EPN is thought to overlap with areas associated with selective attention that are affected by modulatory influences from the amygdala (see Pessoa et al., 2008), whereas the N170 is thought to be generated by regions in the occipital face area and the fusiform face area (see Eimer, 2012). Disentangling the generators of these components would help assess the contributions of selective attention versus expression dependent structural processing on the modulation of the N170.

3.4.3. EPN

Our results show greater EPN negativities for 100% (prototypical) expressions than neutral ones (Figure 3.3b and c). In contrast to Experiment 1, we also found an emotion type and expression intensity interaction starting at an earlier time-window than the main effects for emotion type or expression intensity. This interaction effect was sustained throughout the time window analysed. The EPN evoked for angry expression was graded with respect to expression intensity (i.e., more negative for greater intensities of angry expressions; see Sprengelmeyer & Jentzsch, 2006, for similar findings in a passive task). In contrast, happy expressions evoked greater EPN negativities for prototypical expressions in comparison with neutral ones.

These results differ from those in Experiment 1, where only high expression intensities (80% and 100%) evoked larger EPNs, irrespective of emotion type (see Chapter 2, Figure 2.4). The discrepant results between the Experiment 1 and 2 suggest that expression intensity processing is susceptible to attentional influences. Although our results do not contradict the idea that expressions and intensities ‘automatically’ attract attention (Öhman, 2002), they do suggest that emotion type and expression intensities do not engage attentional resources to the extent that they are not susceptible to top-down attentional control.

Furthermore, the interaction between emotion type and intensity suggests that the EPN reflects sustained processing of intrinsically relevant and task related stimuli. Intensities along angry emotion trajectories evoked graded EPN responses, whereas intensities along happy emotion trajectories evoked greater negativities for only 100% intensity (prototypical) happy versus neutral expressions. As threat-related information is prioritised for processing, directing top-down attention towards the emotional content of the face might facilitate recruitment of more resources for processing angry expressions in more depth. In contrast, as happy expressions are not threatening, directing top-down attention towards happy expressions might only facilitate processing of the intensity that is required for the task (i.e., the prototypical expression). This explanation can be tested empirically by drawing attention specifically to the intensity of happy expressions, and assessing whether they evoke EPNs that are graded for different intensities of happy.

3.4.4. LPP

Angry expressions evoked larger LPPs than happy ones, suggesting that the LPP reflects sustained threat prioritisation. We found no modulation of the LPP based on emotion type in Experiment 1, which suggests that this effect is mediated by overt attention to threat-related information. These results appear to be consistent with the hypothesis that the LPP reflects enhanced activity, or pooling of resources, to process ‘motivationally relevant’ stimuli (Schupp et al., 2000). However, the systematic modulations of the LPP as a function of emotion intensity suggest that the LPP is also involved in elaborate task related processes (see Hajcak, Dunning, & Foti, 2009; Olofsson et al., 2008).

Overall, the intensity effects on the LPP were driven by larger amplitudes for 20%, neutral, and 100% (prototypical) expression intensities. This contrasts with results from previous studies which suggest that the LPP is larger in amplitude for 100% (prototypical) expressions versus neutral ones (e.g., Schupp et al., 2000). Modulation of the LPP in Experiment 2 seems congruent with results from Experiment 1, and suggests that the smaller LPP amplitudes might reflect processing of ambiguous stimuli (Sun et al., 2017). We refer to stimuli as ‘ambiguous’ versus ‘task relevant’ based on the results from Experiment 1, where there was no explicit emotion related task. In Experiment 2, the conditions that evoked the largest amplitudes were Neutral (0%), 20%, and 100% emotion, which are possibly the most unambiguous intensities. It is possible that additional processing is required to categorise any intensities between the two extremes. If the LPP is systematically modulated as a function of ‘ambiguity’, then changing task requirements to manipulate what is ‘ambiguous’ could be a fruitful approach for future experiments. For instance, if we ask people to categorise ‘happy’ versus ‘angry’ we might find larger responses to these two prototypes (i.e. 100% intensities) versus all other expression intensities.

While the ambiguity interpretation is consistent with the interaction effects observed for angry expressions and intensity, it is less consistent with the interactions between happy expressions and intensity. Greater LPP amplitudes were observed for neutral and 20%, but not 100% happy expressions in comparison with all other intensities. We would assume, based on our interpretation about ambiguity, that both 100% (prototypical) happy and neutral expressions would evoke larger LPPs. It is unlikely that 100% happy expressions are more ambiguous than 100% angry expressions, as behavioural data suggests that happy expressions are detected faster and more accurately than angry faces (Calvo & Beltran, 2013). As the EPNs evoked by happy expressions did not differ based on intensity, we could speculate that resources are not recruited to process happy expressions as they are for angry ones. Interactions between behavioural data and these components might help unpack these interactions (See Chapter 4).

3.4.5. Conclusion

The main aims of this study were two-fold. Firstly, we aimed to examine how attention directed towards emotion affects processing of emotion intensity along happy and angry emotion trajectories. Secondly, we aimed to compare the effects associated with overt attention to emotion with ‘automatic’ processing of emotion by comparing results from this experiment with Experiment 1 (Chapter 2).

Taken together, results from Experiments 1 and 2 show that modulations of the N170, EPN, and LPP are affected by top-down attentional control. Results from this experiment suggest that expression intensities are processed at the ‘structural’ encoding stage of processing (see Bruce & Young, 1986), which does not seem to be sensitive to emotion-related information during passive viewing (See Chapter 2, Experiment 1). It is also possible that there is increased arousal for high expression intensities when attention is directed toward emotion. Attention might increase the modulatory feedback from the amygdala to the fusiform face regions that are thought to contribute to the N170 amplitude (see Eimer 2012; Herrington, Taylor, Grupe, Curby, Schultz, 2011). Future studies that examine expression intensities when attention is directed toward emotion should control for arousal of the expression intensities in order to examine this interaction further.

After initial stages of coding at the N170, intensities are then prioritised on the basis of both intrinsic relevance (as shown by graded EPN modulation to angry expressions in this experiment, and greater EPNs for high expression intensities in Experiment 1), as well as task relevance (as shown by greater EPN for 100% happy expressions in comparison with other intensities). Finally, the faces seem to be evaluated based on ambiguity, as defined by the task, as shown by greater LPPs to 100% (prototypical) and neutral expression than all other intensities that were not unambiguous according to the task.

Chapter 4: Behavioural significance of the EPN and LPP while evaluating emotion expression intensities along an emotion trajectory

4.1. Introduction

The time course for processing faces and prototypical emotion categories have been investigated extensively (e.g., Allison, Puce, Spencer, & McCarthy, 1999; Batty & Taylor, 2003; Blau, 2012; Eimer & Holmes, 2002). However, relatively little is known about how expression intensities are processed. In Chapters 2 and 3, we examined the time course of processing expression intensities along happy and angry emotion trajectories. In particular, we investigated how task (or lack thereof) modulates emotion related ERPs while participants viewed expressions along happy and angry emotion trajectories. Our results suggest that the N170 and EPN might reflect the recruitment of neural resources to process expression intensities. In contrast, the LPP might be dedicated to processing stimuli that are unambiguous in the context of the required task. However, it remains unclear how the modulations of these components relate with participants' behavioural responses. In this Chapter we examine the ways in which emotion related ERPs correlate with emotion evaluation and response times. Combining these behavioural and ERP measures can provide better insight into the functional significance of the ERP components.

4.1.1. N170

In Experiment 2 (Chapter 3) we found a significant main effect of expression intensity on the amplitudes of the N170, irrespective of emotion type (see Sprengelmeyer & Jentzsch, 2006 for a similar finding). Due the early time course of the N170, it is typically thought to reflect stimulus-processing, rather than a response related process (see Eimer, 2012). Typical investigations of the N170 make inferences based on the differences between the N170 evoked by systematically varied stimuli (e.g., Carmel & Bentin, 2002; Itier, Latinus, & Taylor, 2006). However, there is some evidence that the N170 might be related to behavioural responses (e.g., to participants' evaluations of expression intensities; Utama et al., 2009). In this chapter, we examine whether the differences in N170 amplitude for different expression intensities are correlated with the proportion of faces rated as 'emotion', or with reaction times.

4.1.2. EPN

In Experiment 2 (Chapter 3) we also found that the EPN was modulated as a function of expression intensity, and that EPNs evoked by emotion type interacted with expression intensity. However, only high intensities of expression evoked larger EPN in Experiment 1 (Chapter 2). Taken together, these findings contradict the idea that the EPN only reflects 'natural selective attention' to emotional stimuli, and that voluntary attention would not differentially modulate the EPN (see Olofsson et al., 2008; c.f Herbert et al., 2008; Holmes et al., 2009; Junghöfer, Bradley, Elbert, & Lang, 2001; Kissler et al., 2007, 2009; Schacht & Sommer, 2009a, 2009b; Schupp et al., 2004). However, both experiments highlight the role of EPN in processing expression intensity. As early stages of ERPs are associated with perceptual processes, there is limited work examining the relationship between EPN and LPP and their behavioural significance. However, it seems plausible that the perceived intensity would determine whether participants respond 'emotion' or 'neutral' to the same stimulus.

There is limited work that directly assesses the relationship between EPN amplitude and behavioural outcomes of evaluating facial expression intensities. Current interpretations of the behavioural significance of the EPN rely heavily on empirical work using non-face stimuli (see e.g., Olofsson, et al., 2008; Schupp, et al., 2006, for reviews). Although data using non-face stimuli seem to be similar to those using face stimuli, it has yet to be determined whether or not they involve the same processes (see Chapter 6). Therefore, we examine the relationship between EPN negativities and behavioural measures (the proportion of expressions rated as emotional and reaction times).

4.1.3. LPP

Studies that do examine the relationship between ERPs and behaviour mainly focus on the LPP (Duval et al., 2013; Leppänen et al., 2007; Pollux, 2016; c.f. Calvo & Beltrán, 2013; Utama et al., 2009). As the LPP occurs in a time range that is close to behavioural responses, and is modulated by experimental task, the LPP is thought to be an ideal candidate for elaborate task related processes (Schacht & Sommer 2009a, 2009b; Schupp et al., 2004). However, the LPP is evoked under many different experimental conditions, and for a wide range of stimulus types; for example IAPS (see Hajcak et al., 2010; Schupp et al., 2006, for reviews); prototypical expressions (Calvo & Beltrán, 2013; Schupp et al., 2014); expression intensities (Duval et al., 2013; Leppänen et al., 2007); and parts of the facial expressions (Leppänen, et al., 2008). In particular, the LPP is modulated by both the 'intrinsic' value of the stimulus, and the explicit task-related value (Schupp et al., 2000). Therefore, it is difficult to compare results directly to form a consensus interpretation about the behavioural significance of LPP. In Experiments 1 and 2 we examined how task modulates LPP using comparable tasks. In this chapter, we aim to build on this work by examining the relationship between LPPs evoked in Experiment 2 and our behavioural measures.

In Experiment 2 (Chapter 3) we found greater LPP amplitudes for neutral, 20%, and 100% emotional expressions. This seems to be consistent with the hypothesis that the LPP is enhanced for processing task related stimuli, where task relevance is defined by the experimenter's instructions (e.g., to categorise the expressions displayed on the face as 'emotion' versus 'neutral'), in addition to intrinsic task relevance based on the significance of the stimulus (e.g., emotional expressions based on their motivational relevance). LPPs evoked for 60% expression intensity in Experiment 1 were reduced in amplitude in comparison with LPPs evoked for all other intensities. We suggested that LPP modulation might reflect enhanced processing for stimuli that are unambiguously emotional or neutral (see Sun et al., 2017). Experiment 1 did not include any behavioural measure to assess stimulus ambiguity. Therefore, we could not identify the point of subjective equality where participants are equally likely to respond 'emotion' or 'neutral'. Analysing the behavioural data from Experiment 2 (Chapter 3), specifically the proportion of faces rated as 'emotion', would allow us to examine the intensities that the participants found ambiguous.

4.1.4. Rationale and aims of this Chapter

Little is known about how modulations in the amplitudes of the N170, EPN, and LPP relate with behavioural measures when processing expression intensities along emotion trajectories. Furthermore, current interpretations of the behavioural significance of the EPN and LPP rely heavily on non-face emotion-laden stimuli, as well responses to 0% (Neutral) versus 100% (prototypical) expression intensities. We aim to address these gaps in the literature by re-analysing data from Experiment 2 (Chapter 3) to examine the relationship between modulations of the N170, EPN, and LPP evoked by incremental intensities between 0% (Neutral) and 100% (prototypical) expression intensities with participants' evaluations of 'emotion' and response times. Results from theses analyses can help us better understand the neural operations underlying the processing of expression intensity and evaluation of emotion.

4.2. Method

We used the data from Experiment 2. See Chapter 3 Section 3.2 for details about Participants (Section 3.2.1), Stimuli (Section 3.2.2), and the Procedure and design (Section 3.2.3) of the experiment.

4.2.1. Behavioural data analyses

The number of ‘emotion’ and ‘neutral’ responses and average reaction times were obtained from E-Merge (Psychology Software Tools Inc., Pittsburgh; Schneider, et al., 2002a, 2002b). Trials with response times over 3000 ms were omitted from the dataset as we assume that participants were not paying attention to the task during these trials.

We then conducted 2 (Emotion type) x 5 (Intensity) rANOVAs to examine differences in the response time, and proportion of faces rated as emotion for each condition.

4.2.2. ERP analysis – subsampling ‘emotion’ responses

Processed epochs that were separated by condition (e.g., 20% happy) were split based on the participants’ response of ‘emotional’ (i.e., ‘20% happy intensity, rated as emotional’) or ‘neutral’ (i.e., ‘20% happy intensity, rated as neutral’). This resulted in insufficient numbers of trials to examine each intensity for each expression, therefore we collapsed across emotion type. This ensured that we had at least 60 trials left to analyse per emotion intensity (consistent with our previous two analyses, and Luck, n.d). 20% expressions were excluded from the analysis because there were insufficient epochs for the ‘emotion’ responses (Angry 20% *M* = 7, *SD* = 18.33; Happy 20% *M* = 3, *SD* = 21.51). Data from one more participant were rejected at this point as they did not have enough trials for 60% (8 trials) expression intensity.

We then computed the minimum of trials remaining for each intensity in each emotion type (33) and subsampled 33 trials from each condition using the randperm (n,k) function in MATLAB (The Mathworks, Inc.) to generate a unique vector of values with the number of trials to reject (k) between one to the current trial number (n). This method allowed us to select trials randomly from each data set. After subsampling, we were left with 66 trials per expression intensity per person.

4.2.3. ERP and behaviour correlations

To examine the extent to which each ERP component was related to the behavioural responses, we conducted correlation analyses between the mean amplitude values of each component, and the behavioural measures; proportion of expressions rated as emotional, and response times. We used the mean amplitude scores for each expression intensity for each participant, for a total of 76 datapoints (19 participants x 4 intensity categories: 40%, 60%, 80%, and 100%).

In order to investigate the relationship between emotion related ERP components and the evaluation of emotionality of the face, a correlation matrix was made for EPN and LPP amplitudes. Each matrix contained the behavioural measures (proportion of faces rated as 'emotion' and response time), and an average amplitude in the analysed time window.

As the data deviated from a normal distribution, we used non-parametric Spearman rank-order correlations. An alpha level cut-off of .05 was used to correct for multiple comparisons. We also computed the regression coefficient (R^2) to estimate the amount of variance accounted for in the behavioural measures as a function of the ERP component.

4.3. Results

4.3.1. Behavioural results

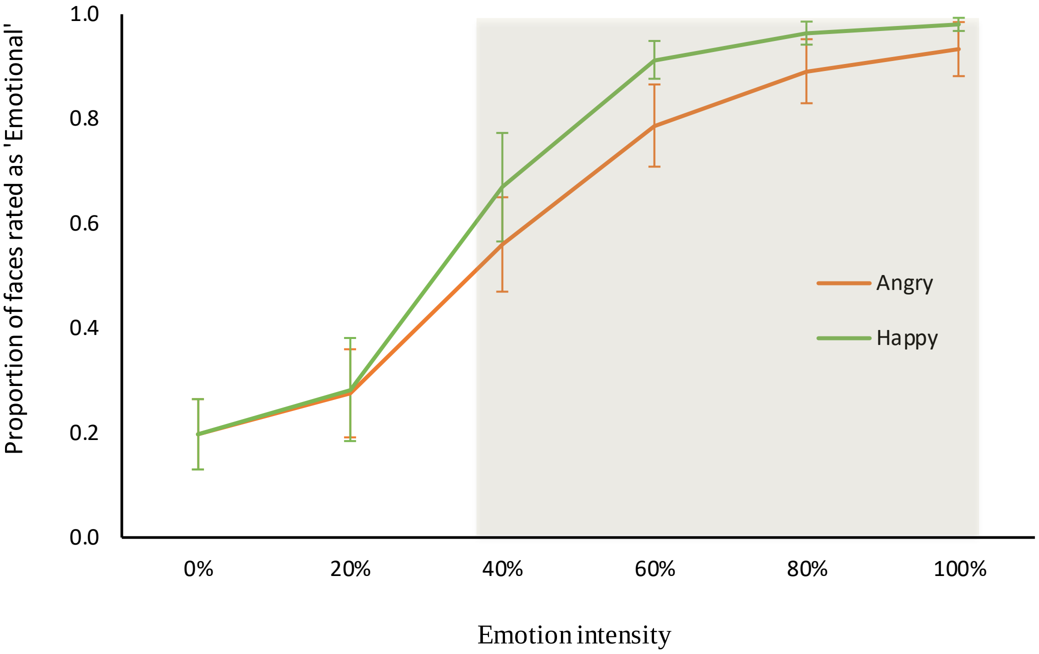


Figure 4.1. Proportion of faces rated as emotional for each expression intensity. The orange and green lines represent angry and happy expressions, respectively. Error bars represent 95% confidence intervals. For 0% (Neutral) and 20% expressions, very few trials were rated as emotional and therefore were not included EEG analysis. The grey box represents the expressions intensities with sufficient trials for further analysis in this Chapter. These were subsampled (see Section 4.1.1 for details) so that all conditions had equal numbers of trials for analysis.

Figure 4.1 shows mean percentages of emotional responses per intensity. The proportion of faces rated as ‘emotion’ increased with increasing intensities. We observed ceiling effects in emotion ratings for 80% and 100% expression intensities.

A 2 (Emotion) x 5 (Expression intensity: 20%, 40%, 60%, 80%, and 100%) rANOVA on the percentages of emotional responses showed main effects of both emotion, $F(1, 17) = 8.363$, $p = .010$, $\eta_p{}^2 = 0.330$, and intensity, $F(4, 14) = 199.133$, $p < .000$, $\eta_p{}^2 = 0.921$, $\varepsilon = 0.346$. The emotion effects were driven by more 'emotion' responses for happy expressions (*M* = 0.762, *SD* = 0.25) than angry ones (*M* = 0. 689, *SD* = 0.034).

The effects of emotion type and intensity were also modulated by an interaction between the two variables *F*(5, 15) = 4.885, *p* = .008, $\eta_p{}^2$ = 0.214, ε = 0.452. This interaction was driven by greater proportions of happy expressions rated as emotional for 40% (happy *M* = 69.350, *SD* = 5.194, angry, *M* = 59.300, *SD* = 3.745), 60% (happy *M* = 91.000, *SD* = 2.425, angry, *M* = 81.250, *SD* = 2.812), 80% (happy *M* = 95.150, *SD* = 1.710, angry, *M* = 91.100, *SD* = 1.769) intensities.

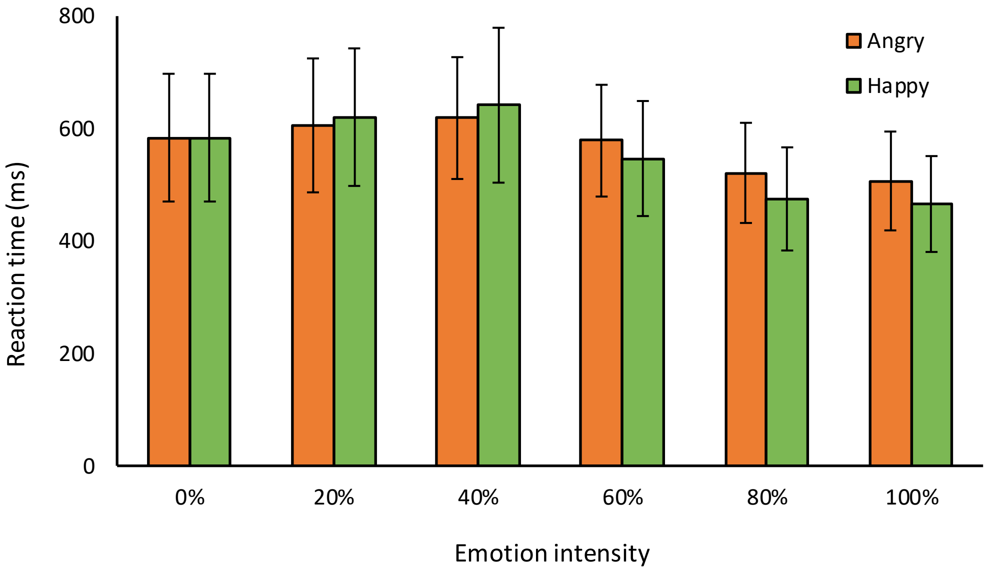


Figure 4.2. Response times for each expression intensity. The orange and green bars represent angry and happy expressions, respectively. Error bars represent 95% confidence intervals.

Figure 4.2 shows mean response times per intensity for angry and happy expressions. There was no main effect of emotion type on the response times (*p* > .05). There was a main effect of intensity, *F*(4, 14) = 12.499, *p* < .000, $\eta_p{}^2$ = 0.424, ε = 0.513. This main effect was also modulated by an interaction with emotion type, *F*(1,14) = 4.090, p = .05, $\eta_p{}^2$ = 0.194, ε = 0.668. Participants responded slightly faster for happy expressions at higher intensities (60%, 80%, and 100%) than angry expressions (see Figure 4.2)

There were no significant correlations between reaction time and proportion of expressions rated ‘emotion’ (all *p*s > .05).

4.3.2. ERPs and behaviour

4.3.2.1. N170 (136–156 ms)

When we subsampled data, there was a main effect of intensity, but not emotion type on the amplitude of the N170, *F*(3, 16) = 5.300, p = .010, $\eta_p{}^2 = 0.498$ (Figure 4.3). There was a linear decreasing trend in N170 amplitudes with respect to increasing intensities of emotion, *F*(3, 16) = 6.944, p = .017, $\eta_p{}^2 = 0.278$. However, these amplitudes did not co-vary with the proportion of expressions rated as ‘emotional’, or with response times (all *p*s > .05).

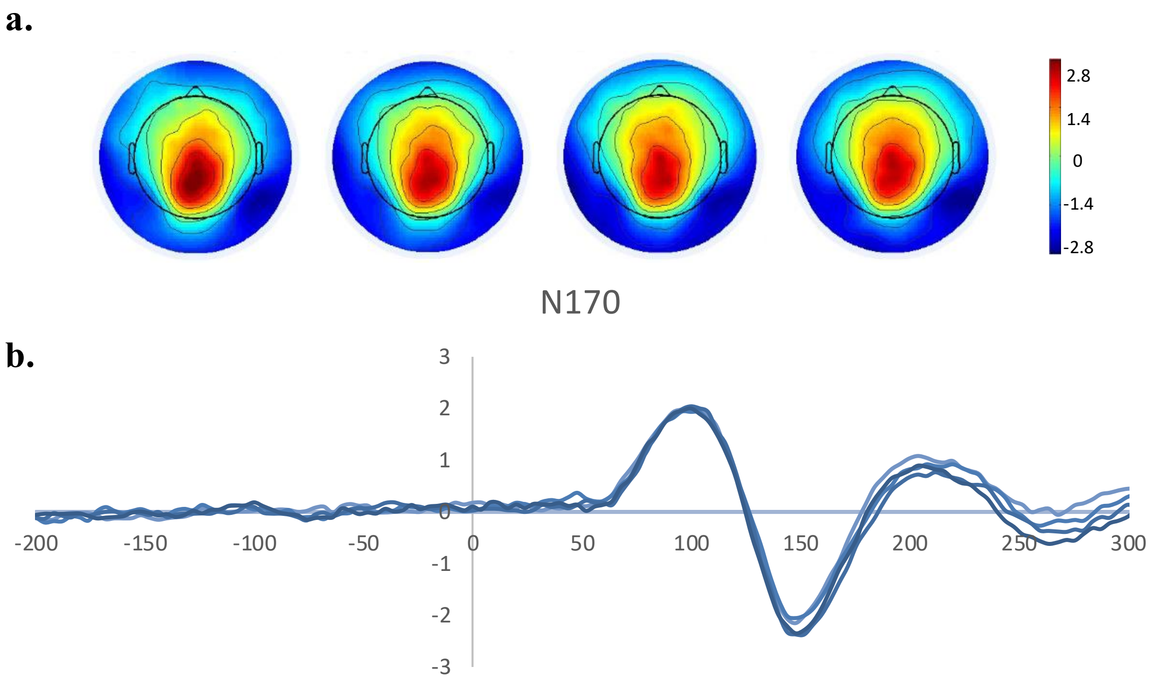


Figure 4.3. a. The topographies showing the spatial distribution of activity for each intensity between 136-156 ms. b. The N170 evoked by each intensity when participants rated the expression as 'emotional'.

4.3.2.2. EPN (202–408 ms) and behaviour

The EPN was modulated by emotion intensities in the 252-304 ms time window $F(3, 16) = 3.852$, $p = .030$, $\eta_p{}^2 = 0.419$. The negativities were graded by emotion intensity with a significant decreasing linear trend for increasing emotion intensities $F(1, 18) = 11.599$, $p = .003$, $\eta_p{}^2 = 0.220$ (see Figure 4.4b).

Figure 4.4c shows that the EPN amplitude was negatively correlated with the proportion of expressions evaluated as 'emotional' for all four intensities (i.e., greater negatives resulted in a greater proportion of that were evaluated as emotional), **40%:** $r_s(17) = -0.573$, $p = .010$; **60%:** $r_s(17) = -0.580$, $p = .009$; **80%:** $r_s(17) = -0.592$, $p = .008$; **100%:** $r_s(17) = -0.601$, $p = .006$.

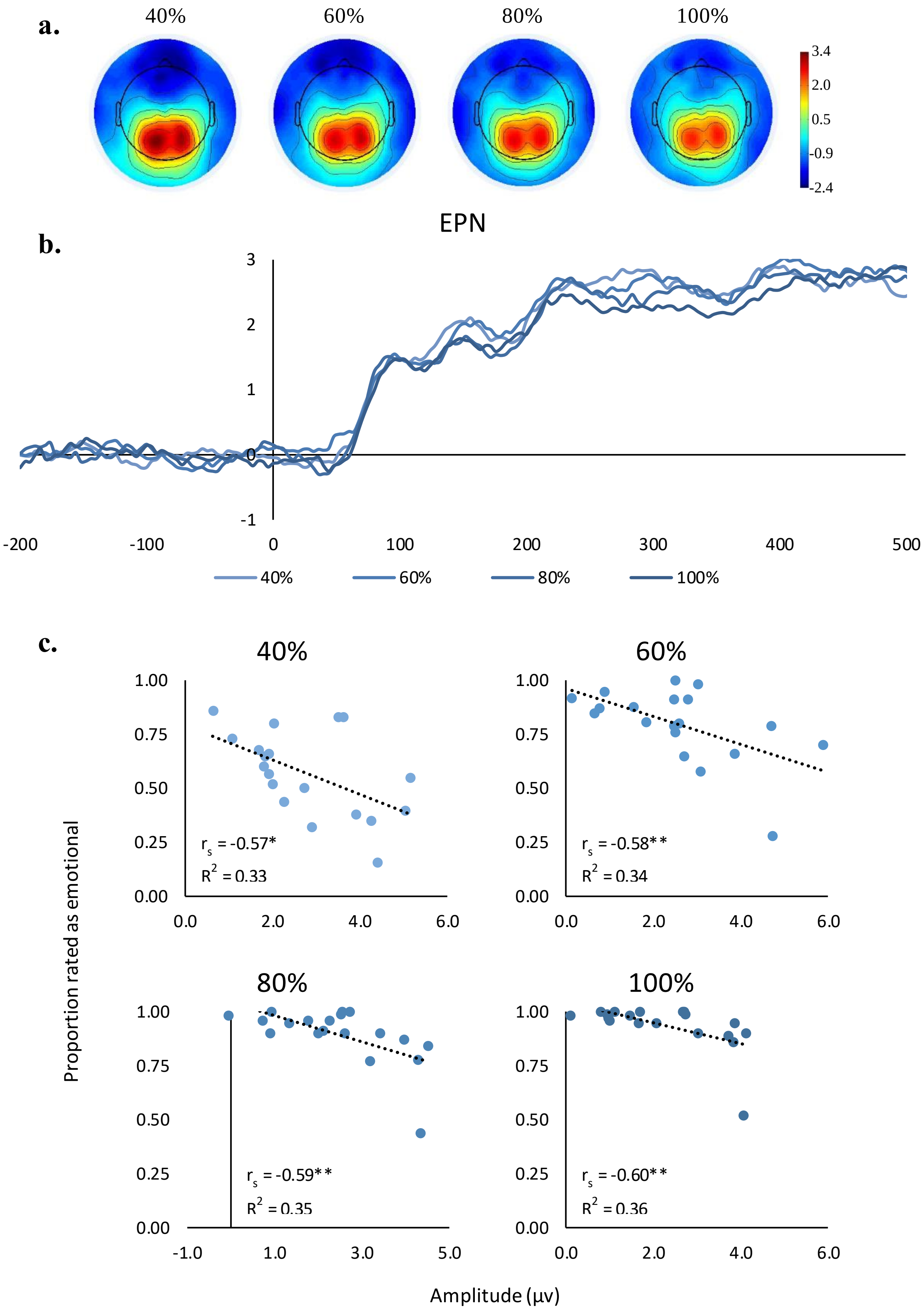


Figure 4.4. a. The topographies showing the spatial distribution of activity for each intensity between 252-304 ms. b. The EPN evoked by each intensity when participants rated the expression as ‘emotional’. c. Correlations between EPN negativities and proportion of expressions rated as ‘emotion’ for each expression intensity. *p < .05, **p < .01.

4.3.2.3. LPP and behaviour

In Chapter 3, we found a main effect of emotion on the amplitude of the LPP, however, after subsampling the main effect of emotion only approached significance, $F(1, 18) = 4.322$, $p = 0.052$, ${\eta_p}^2 = 0.194$.

We found a main effect of intensity on the amplitude of the LPP, $F(3, 16) = 3.607$, $p = 0.037$, ${\eta_p}^2 = 403$. There was a linear relationship between the LPPs amplitudes evoked for expression intensities along the emotion trajectory (i.e. greater amplitudes for greater intensities), $F(1, 18) = 10.620$, $p = 0.004$, ${\eta_p}^2 = 0.371$. Figure 4.5c shows that there were positive correlations between LPP amplitude and emotion response reaction times for all four intensities, **40%:** $r_s\,(17) = 0.493$, $p = .032$; **60%:** $r_s\,(17) = 0.518$, $p = .023$; **80%:** $r_s\,(17) = 0.588$, $p = .008$; **100%:** $r_s\,(17) = 0.577$, $p = .010$.

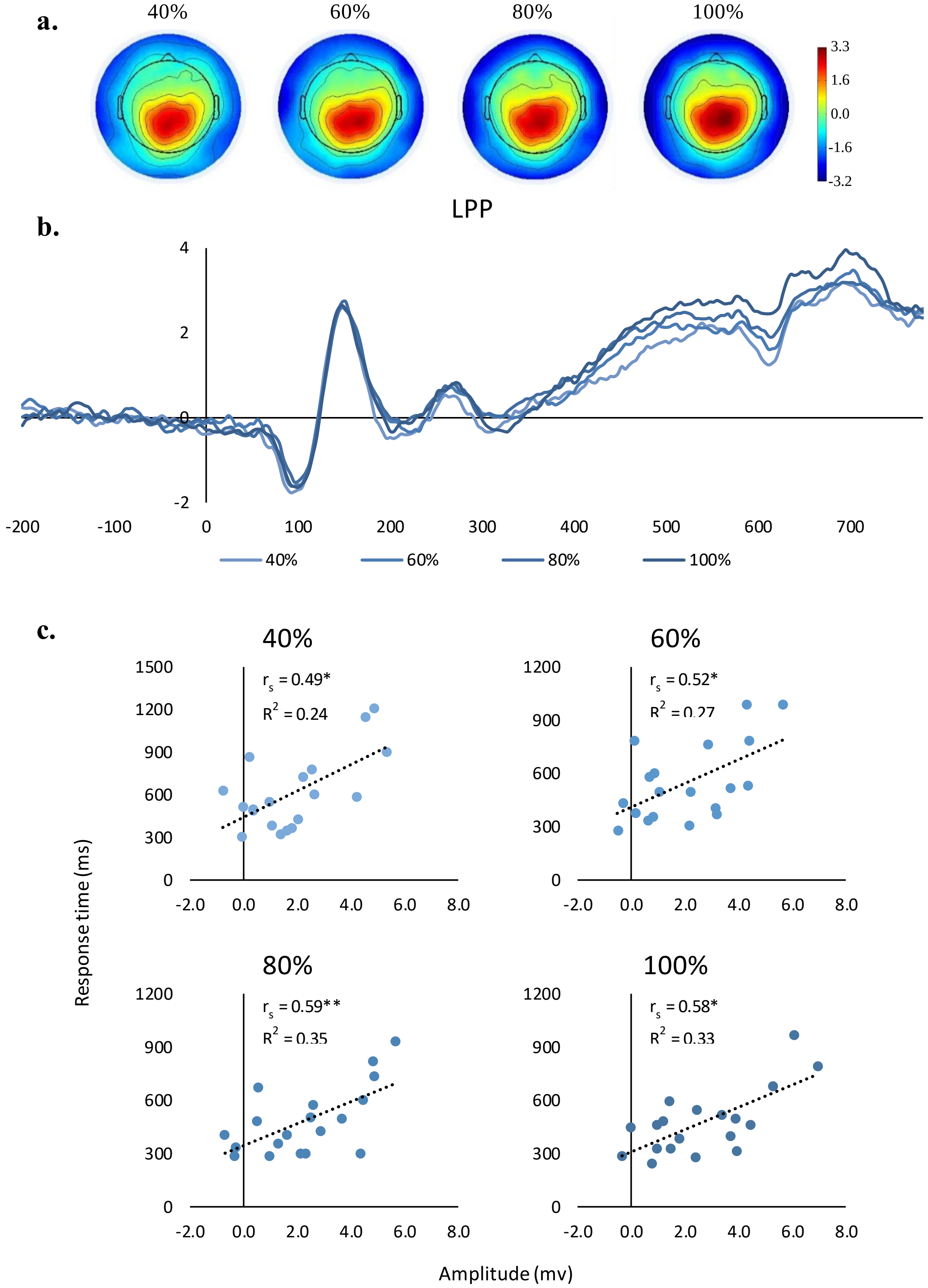


Figure 4.5.a. The topographies showing the spatial distribution of activity for each intensity between 400-600 ms. b. The LPP evoked by each intensity when participants rated the expression as ‘emotional’. c. Correlations between LPP amplitudes response times for each expression intensity. *p < .05, **p < .01.

4.4. Discussion

This chapter examines the relationship between behavioural outcomes and modulations of the N170, EPN, and LPP evoked for expression intensities along happy and angry emotion trajectories. Participants were required to view different intensities of expressions along happy and angry emotion trajectories and evaluate whether the faces were 'emotional' or 'neutral' in expression. We then separated the 'emotional' responses (see Leppänen et al., 2008; Utama et al., 2009, for similar analyses) and examined correlations between behavioural measures (participants' evaluations of emotion, and response times) with amplitudes of each component. We found significant negative correlations between the amplitude of the EPN and 'emotion' judgements; greater EPN negativity was correlated with greater proportions of faces rated as 'emotional' versus those as rated neutral. We also found positive correlations between the amplitude of the LPP and reaction times; larger LPPs were correlated with longer reaction times.

4.4.1. N170

We found no significant correlations of the amplitudes of the N170 and the proportion of expressions rated as emotional, nor response times. This is consistent with the large body of literature that suggests that the early time course of the N170 makes it a suitable candidate for examining behaviour-free stimulus processing (see Rossion & Jacques, 2011). We should note that our results are inconsistent with Utama and colleagues' (2009) results, which show that the N170 correlates with participants' evaluation of emotion intensities. However, a key difference between the two studies is the task requirement in the experiment. Utama et al. required participants to rate the intensity of expressions rather than the emotion in the expression. In contrast, in our experiment, we aimed to draw attention to the emotion in the face without prescribing specific emotion type, or expression intensities. This might have required a different depth of processing than in Utama et al.'s study. Therefore, examining the relationship between the N170 and behavioural measures in different types of tasks would allow us to examine how task modulates the amplitude of the N170, and how modulations of the N170 might relate to behavioural responses in different tasks.

4.4.2. EPN

For each expression intensity from 40%-100%, we found that the EPN amplitude correlated with the proportion of faces that were rated as expressing an 'emotion'. This contrasts with previous literature suggests that the EPN is involved in 'automatic' processing of emotion laden stimuli that occur irrespective of the task or behavioural responses (Herbert et al., 2008; Junghöfer et al., 2001; Kissler et al., 2007, 2009; Rellecke et al., 2011; Schacht & Sommer 2009a, 2009b; Schupp et al., 2004). Our results from Chapters 2 and 3 show that the EPN is associated with 'automatic' processing of high-intensity expressions, irrespective of emotion type (see also Sprengelmeyer & Jentzsch, 2006) and it can be modulated by voluntary attention. The correlational analysis offers a novel extension by showing that the amplitude of the EPN is correlated with judgement of emotion for each expression intensity. EPN correlation with the response suggests that EPN amplitude likely represents the perceptual coding of expression intensity rather than coding of physical configural changes in the stimulus.

Further investigation is required to assess modulations of the EPN as a function of emotion type, and how that interacts with expression intensity. When we split the data based on participants' responses, we did not have sufficient trials to examine the relationship between emotion type and expression intensity modulation observed in Chapter 3. Future studies can examine a single expression in a particular experiment, or focus a subset of intensities that capture the variation in our behavioural data, to investigate how the interactions between emotion type and expression intensity (see Chapter 4) would correlate with EPN.

The ways in which task modulates the EPN is also worth following up in future studies. Our task differs from other experiments that have investigated the EPN for expression intensities, as we required participants to make a judgment between ‘emotion’ versus ‘neutral’, not between two specific emotion types (e.g., ‘happy’ versus ‘angry’). Therefore, participants may have had to attend to structural aspects of the face in our experiment, rather than perform template matching, where stimuli are matched with existing representations of prototypical expressions in memory (see e.g., Valentine & Bruce, 1986). Future studies can use different emotion categorisation tasks (e.g., naming prototypical emotions, judging positive/negative valence) to assess whether modulations of the EPN for emotion intensities are robust to task effects.

4.4.3. LPP

Our analysis in this chapter revealed that the LPP amplitudes were systematically greater for higher versus lower intensities of expressions rated as ‘emotional’, and that these amplitudes are correlated with response times to the stimuli (i.e., larger LPP amplitudes were associated with longer response times). The relationship between increased amplitudes of LPPs with response times suggests that the LPP is likely associated with sustained processing of ‘task relevant’ stimuli (Schupp et al., 2000). However, we cannot rule out the explanation that higher amplitudes might reflect processing of more unambiguous stimuli based on the explicit task (see Sun et al. 2017) as we suggested in Chapters 3 and 4. In our experiment, both 0% (Neutral) and 100% (prototypical) expressions are task relevant. However, Neutral expressions evoked much larger LPPs, which could reflect the oddball response (see Chapter

3, Section 3.4.4). We designed our experiment to include 800 trials between neutral and 50% expression, and 800 between 50% and 100% expression. However, only 36% of faces were rated as ‘neutral’. As the subjective probability of seeing the ‘neutral’ faces was much lower than seeing ‘emotional’ faces, it is possible that larger P300 amplitudes were evoked by stimuli perceived as ‘Neutral’, in comparison with those evoked by stimuli perceived as ‘emotional’.

Future studies may equalise the number of trials for neutral and all the intensities included. However, this would prolong the experimental sessions substantially. As the point of subjective equality differed between individuals, it would be difficult to strictly control perceived probabilities in emotion evaluation tasks. Therefore, it might be useful to examine single expressions, or a subset of expression intensities that capture the variation in the behavioural data. The latter might could involve using a subset of intensities around the point of subjective equality. Our data suggests that this lies at about 40% intensity on average.

4.4.4. Reanalysis of ‘correct’ neutral and emotion responses

Our analysis in this chapter is based on participants’ recognition of “emotion” in response to morphed stimuli that include any portion of emotion (i.e. >0% Neutral expression). This is consistent with the way in which others have subsampled trials for analysis (see Leppänen et al., 2007; Utama et al., 2009). However, there is some inconsistency in the literature regarding how data are chosen to be analysed. For instance, Duval et al. (2013) operationally defined ‘corrects’ based on the predominant emotion in the expression. In their case, ‘Corrects’ were defined as instances in which the expression was over 50% intensity, and classified as ‘positive’ or ‘negative’, or instances in which the expression was below 50% and classified as ‘neutral’ (Duval et al., 2013).

As some responses included in Duval et al.'s (2013) analysis were classified as 'neutral' rating in our experiment, results from their analysis strategy would allow visualisation of 20% and Neutral intensities. However, the results, and therefore interpretation of the data, would differ significantly using this strategy. In order to examine these differences, we reanalysed our data by dividing 'emotion' responses to intensities over 50%, and 'neutral' responses to intensities below 50%, as 'correct'. When the data are subsampled in this way, the analysis showed substantially larger LPPs for Neutral and 20% expression intensities, in comparison with all the other intensities (see Figure 4.6b). Differences between LPPs evoked for 20% expression intensities rated as 'Neutral', and those evoked by expressions rated 'emotional' started much earlier (~100 ms), and were much larger than the differences between emotion intensities rated emotional (see Figure 4.6b).

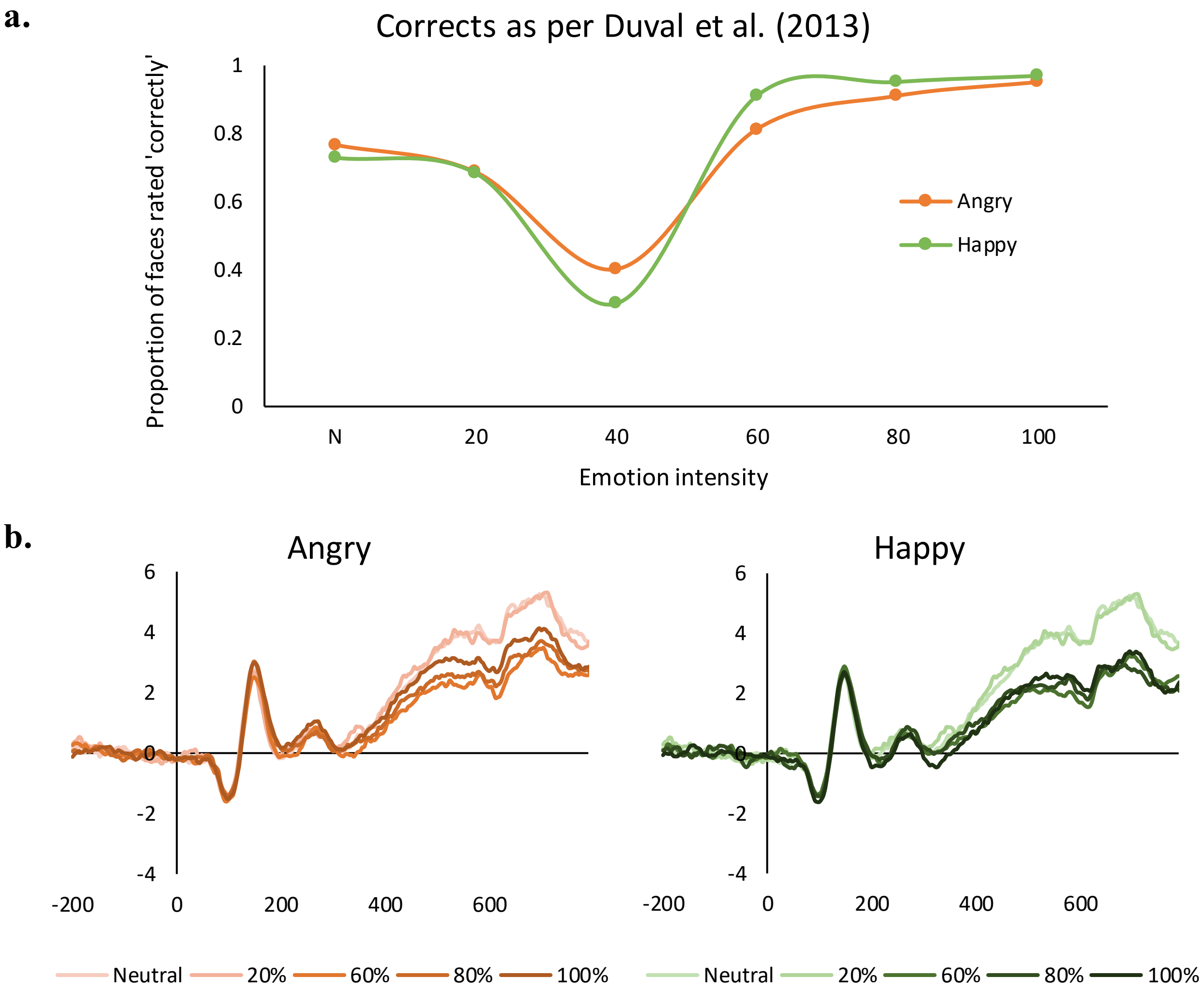


Figure 4. 6. a. Proportion of faces rated correctly, according to Duvel et al.'s (2013) definition, for each expression intensity. b. ERPs evoked for each intensity for angry expressions (right) and happy expressions (left) when participants 'correctly' rated intensities below 50% as 'neutral' and intensities above 50% as 'emotional'.

In using Duval et al.’s (2013) method to reanalyse of our data, larger amplitudes for Neutral and 20% expression intensities seem to reflect the P300 (see Kok, 2001). The P300 has been segregated into two types of positive waves that occur at around 300 ms (Kok, 2001). The first subcomponent, P3a seems to be evoked by ‘novelty’. These include conditions in which a stimulus is presented rarely, or when a stimulus that is presented at a predictable rate is missing. These effects are similar to the responses to neutral expressions that we report above.

The second subcomponent, the P3b has been modulated under many different conditions, leading to a number of contrasting hypotheses (see Kok, 2001, for discussion). Like the LPP, it has been suggested that the P3b is larger for stimuli that ‘automatically’ attract attentional resources (Delplanque, Silvert, Hot, & Sequeira, 2005); stimuli that are more difficult to perceive (Verleger, Baur, Metzner, & Smigasiewicz, 2014); stimuli that are task relevant, where ‘task’ is defined as both the experimental task, as well as things that are implicitly motivating (i.e., threatening emotions; see Kok, 2001).

We assume that task difficulty is not modulating the LPP/P3b in our task, as this would predict that more ambiguous stimuli (i.e., intensities falling near the point of subjective equality) would evoke larger LPP/P3b amplitudes, compared with expressions on the extreme ends of the emotion trajectory (i.e., neutral and prototypical emotions). We did not find evidence of this pattern during passive viewing (Experiment 1) or when emotion evaluations were made (Experiment 2).

4.4.5. Conclusion

In this chapter we examined the relationship between behavioural measures (participants' evaluations of emotion and response times) with modulations of the N170, EPN, and LPP. Consistent with the majority of previous literature, we found no correlation between the N170 and behavioural measures. We found that the amplitude of EPN negatively correlates with participants' judgments of 'emotion' in faces along both happy and angry expression trajectories. Lastly, we observed modulations of the LPP positively correlate with response times, which seems to reflect sustained processing of task related stimuli.

Chapter 5: Exploring the emotion trajectory in an adaptation/aftereffects task

5.1. Introduction

In Chapters 3 and 4, we found systematic modulations of the EPN as a function of emotion intensities along happy and angry emotion trajectories. Chapter 4 showed that the EPN amplitude is correlated with the proportion of faces evaluated as emotional for each intensity examined. These findings are consistent with behavioural adaptation/aftereffects studies (e.g., Rhodes et al., 2017), which provide converging evidence that emotions are processed continuously. In this chapter, we utilise an adaptation/aftereffects paradigm to explore whether EPN amplitudes covary with faces evaluated as emotional in an adaptation/aftereffects different paradigm, and assess the generality of our previous findings.

5.1.1. Visual adaptation/aftereffects

Visual adaptation paradigms are frequently used as tools for investigating ‘pools’ of neurons dedicated to processing specific stimuli (see Clifford et al., 2007; Webster, 2015; Webster & MacLeod, 2011, for discussions). When one stimulus follows another stimulus (the *adaptor* stimulus) of the same or similar ‘category’, the response to the second stimulus (the *test* stimulus) is attenuated as a result. As attenuation does not occur for test stimuli that are dissimilar to the adaptor, attenuation is thought to reflect a reduction in response from overlapping mechanisms used to process the two stimuli. In some instances, adaptation can give rise to aftereffects which suggest that the perception of the test stimulus has been shifted. If the mechanisms that code the adaptor and test stimuli overlap, there is an attenuation in the response to the test stimulus and perception of the test stimulus is biased towards the ‘opposite’ direction. For example, adapting to the colour red shifts the perception of white towards green (see Webster & MacLeod, 2011). Therefore, measuring the responses to systematically varied adaptor stimuli can provide insights into the common mechanisms shared between adaptors and test stimuli.

5.1.2. Facial expression adaptation/aftereffects

Neural adaptation/aftereffects have traditionally been investigated with simple stimuli that are processed in lower levels of the visual hierarchy (see Clifford et al., 2007; Webster & MacLeod, 2011, for discussions). However, more recently this paradigm has also been used to investigate the way in which more complex stimuli are represented. For example, Leopold et al. (2001) used face stimuli varying in identity, and Webster, Kaping, Mizokami, and Duchamel (2004) used face stimuli varying in gender, ethnicity, and expression. Face aftereffects seem to occur despite changes in the size and position of faces (Leopold et al., 2001; Webster & Macleod, 2011). Furthermore, expression aftereffects have been found even when the features in the face have been scrambled (Butler, Oruc, Fox, & Barton, 2007). These findings suggest that the adaptation paradigm can also tap into higher levels of processing in the visual system, which seem to be invariant to changes in lower-level stimulus properties (see Webster, 2015, for discussion).

5.1.3. Emotion trajectories in adaptation aftereffects

Few studies have examined behavioural adaptation/aftereffects for emotion expressions (e.g., Rhodes et al., 2017). There is a range of different procedural variations in the literature and each implies, or predefines, a different direction for the emotion shift (i.e., a different emotion trajectory). For instance, when a ‘happy’ face is followed by another ‘happy’ face, it is less likely to be reported as happy in a forced choice task where the alternatives are fear, happy, or sad (Hsu & Young, 2004). This suggests that the adaptor might repulse evaluation of the test, but does not predict the vector of the axis. In contrast, other studies pre-define the direction of the axis by morphing two expressions, or by creating structurally opposite expressions (Cook et al.., 2011; Skinner & Benton, 2010). These later studies typically find that evaluations of emotion shift away from the adaptor, and towards the alternative expression (i.e., the other morphed image, or the structurally opposite expression). Although these experiments predict the vector of the axis by creating morphs that vary along specific axes, the specific properties coded along the axis remain elusive.

Data from Chapters 2 – 4 suggest that expression intensity is coded continuously, as reflected by the modulation of the EPN. Behavioural adaptation/aftereffect studies of facial expressions suggest that perception of an expression can be shifted in the ‘opposite’ direction by a preceding face. If intensity is one of the properties that is coded along an emotion trajectory, we might expect that expression intensities of adaptation expressions would shift the percept of neutral test faces. For instance, a 40% expression intensity would should shift the perception of a neutral face to a greater extent than a 20% expression intensity. However, behavioural measures in adaptation/aftereffect paradigms only allow us to measure the outcomes of expression evaluations. Therefore, they give us some insight into the final decision that the participants make, but not the underlying stimulus evaluation processes. EPN amplitude, in conjunction with behavioural perceptual shifts, could provide a clearer understanding of the stimulus- and response -related processing underlying the adaptation/aftereffects to emotional expressions.

5.1.4. Physical versus perceptual coding of intensity

Exploring EPN modulation in the adaptation/aftereffects paradigm can also inform us about the nature of intensity coding. The previous experiments show modulations of the EPN that are driven by expression intensity when participants viewed images of each expression intensity. Given that these effects were enhanced with attention (see Chapters 3 and 4 versus Chapter 2), we suggested that EPN modulation might be driven by attention mechanisms that are recruited for processing intensity. However, intensity can be also be processed via the physical features of the face (e.g., the curvature of the mouth for a smile), as well as more abstract perceptual representations that require non-sensory/affective processing (see Calvo & Nummenmaa, 2016). So far, our experiments only allow us to infer how different expression intensities are processed when we varied the physical attributes of the expression intensity. However, in the broader emotion literature, the EPN is modulated by intensities of other emotion laden stimuli (e.g., IAPS; see Olofsson et al., 2008, for a review). Therefore, it seems likely that modulation of the EPN involves, at least in part, processing of abstract representations of emotion intensity. Adaptation aftereffects tasks are useful for assessing how perception of expressions with the same physical attributes may be shifted. The magnitude of these shifts are thought to be based on the intensity of the adapting stimulus. Therefore, examining the EPN modulation for each test following different intensities of adaptors should allow us to examine whether the EPN is modulated by perceptual shifts of intensity.

5.1.5. Rationale and aims of this study

We recorded EEG while participants viewed adaptor faces that were either neutral in expression, or displayed happy or angry expressions along an emotion trajectory. The emotional faces were morphed to display expressions that were 20%, 40%, or 60% intensity of happy and angry expressions. These faces were followed by a test face that was neutral in expression, and participants were required to evaluate whether the test face displayed an ‘emotion’ or whether it was ‘neutral’ in expression. We examined whether there were systematic modulations of the EPN evoked by the test face, as a function of emotion intensity of the adaptor. Furthermore, as we previously found covariance between the EPN and the proportion of expressions rated emotional (see Chapter 4), we also explored whether the EPN is greater for expressions evaluated as ‘emotional’ versus those evaluated as ‘neutral’.

5.2. Methods

5.2.1. Participants

Participants in this study were 28 volunteers (19 female) from the University of Auckland. The mean age was 21.05 (*SD* = 3.26, *range* = 18-32). Three participants were left-handed. One participant was unable to complete the full experiment, so their data were not included. Data from another 11 participants were excluded as they did not have a minimum of 30 trials per condition (irrespective of response).

Volunteers with conditions that impaired their ability to recognise facial expressions or with a history of epilepsy or migraines did not meet the criteria to participate in the study. All participants reported normal or corrected-to-normal vision. Participants provided written, informed consent prior to their participation. All participants received a $20 supermarket voucher as koha for their participation in the study. Research protocols were approved by The University of Auckland Human Participants Ethics Committee.

5.2.2. Stimuli

As the trial times in this experiment are much longer than the previous experiments, we used a subset of images from the previous chapter in this experiment (see Chapter 2 Section 2.2.2 for details of stimulus creation): 0% (Neutral), and 20%, 40%, and 60% expression intensities along the happy and angry trajectories (a total of 7 different stimuli). We limited our exploration to 60% as 60% expression intensities were perceived as emotional well above chance levels in Experiment 2 (see Figure 4.1).

5.2.3. Procedure

Participants were seated in a dimly lit faraday cage. The monitor was positioned 57 cm in front of the participant. Experimental stimuli were presented on a 21- inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh).

The experiment had a total of 540 trials which were split up into 12 blocks (45 trials per block). There were seven types of adaptor stimuli (Neutral expressions, and 20%, 40%, and 60% intensity of happy and angry expressions). Each of the 20%-60% happy and angry expressions was presented as the adaptor 45 times (i.e., there were 45 images that were presented once each). Neutral adaptors were presented 270 times (there were 45 images that were presented 6 times each). All test faces were neutral in expression (45 images presented 12 times each). We used a custom written script for E-Prime to ensure that the same neutral expression was not presented as both the adaptor and the test face on any given trial.

We adopted a similar paradigm to Kovács et al. (2006) who examined adaptation/aftereffects for faces and body parts in EEG; however, we included a temporal jitter by varying the interval between adaptor and test face presentation to prevent alpha-wave activity becoming phase locked to the presentation rate of the test stimulus (see Woodman, 2010). Consistent with the previous chapters, images were subtended 5.26° x 6.53° of visual angle. Each trial started with a cross that was displayed at the center of the screen for 500-700 ms to prompt participants to focus on the area where the stimuli would be displayed. This was followed by a face that was presented for 4600-5000 ms (the adaptor stimulus). The adaptor could be neutral in expression, or a morphed face that was 20%, 40%, or 60% intensity of happy and angry expressions. The adaptor was followed by a brief blank screen for 30-50 ms to reduce the effects of retinal adaptation, and then a neutral face (the test stimulus) was presented for 500 ms. After the test, a blank screen was presented for 2 seconds. Participants were instructed to judge whether the second face was emotional or neutral, and encouraged to respond as quickly as possible. After each block of 45 trials, a “break” slide appeared for 30 seconds, after which participants were able to press the spacebar to continue when they were ready.

Prior to the start of the experiment, we ran a practice block that contained 12 trials. These included 6 examples of neutral adaptors with neutral test face, and an example of each expression intensity as an adaptor with a neutral test face. We chose to use a different stimulus set (NimStim; Tottenham et al., 2009) for the practice block to ensure that participants did not see any of the stimuli used in the experiment. We monitored participants’ responses during the practice block to ensure that they responded after the test stimulus rather than the adaptor, and that they respond as quickly as possible. We did not provide feedback about accuracy. Instead, we emphasised the importance of responding quickly when they see the test stimulus.

Consistent with Chapter 3, participants were asked indicate via key press (labelled ‘E’ and ‘N’) whether the second face they saw was expressing an ‘emotion’, or whether it was ‘neutral’. Participants were asked to judge facial expressions they saw as ‘Emotional’ if they could identify what the expression was, or ‘Neutral’ if they did not know what expression it displayed, or if they thought the face was unemotional. The key locations were counterbalanced across participants to mitigate the effects of lateralisation during finger movements.

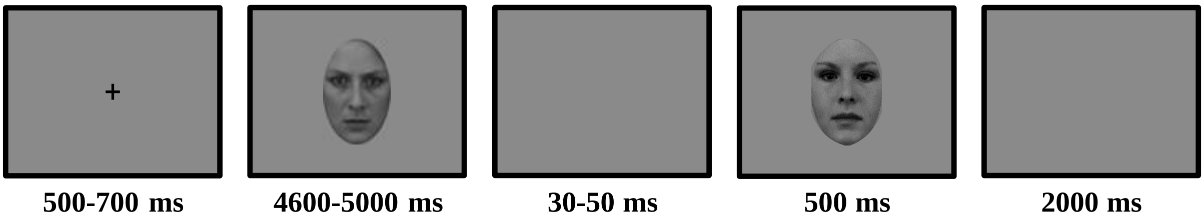


Figure 5.1. The sequence of events during each trial. Each trial began with a fixation cross that was presented for 500-700 ms, an adaptor face was then presented for 4600-5000 ms, followed by an interstimulus interval of 30-50 ms. The test face was then presented for 500 ms, and then a blank slide was presented for a maximum of 2 seconds, or until the participant responded.

5.2.4. EEG acquisition and pre-processing

Data were acquired and pre-processed in the same way as in Experiment 1 (Chapters 2) and Experiment 2 (Chapter 3; see Chapter 2 Section 2.2.4 for details).

Prior to data collection, we conducted a time test using a photocell in-order to measure the lag between trigger presentation on the EEG acquisition computer, and stimulus presentation on the experimental computer. We found a lag of 18 ms. Therefore 26 ms were added to all time points in the data. This accounts for the 18 ms lag recorded using the photocell, and the default 8 ms lag that the EGI 300 amplifier has between trigger value display on the EEG acquisition computer and image display on the experimental computer.

5.2.5. ERP analysis

Epochs were centred around the test stimulus, and they were divided per condition based on the response (‘emotion’ versus ‘neutral’) to each intensity. Grand averages were then calculated. On average, we were left with 23 trials per emotion type, however there was a large range in the number of remaining trials (*min*: 5, *max*: 35 trials). Therefore, we collapsed the data across emotion type, and computed grand averages for each response for each expression intensity irrespective of emotion type.

A baseline correction (based on the average of the 200-ms baseline period) was subtracted from each time point in the epoch. We also observed slow drift in our data which led to the conditions separating at the baseline period. We then re-epoched the data into large epochs by time locking to the adaptor. We used the baseline period for the adaptor and subtracted this throughout the time window. This also left us with ERPs that segregated during the baseline period. We then performed a linear de-trend on the epochs time locked to the test stimulus, using the de-trend function in ERP lab. This function calculates the linear trend in the data and subtracts it from each time point, effectively ‘zero-ing’ the baseline period so that comparisons can be made between the different conditions.

Electrodes for analysis were chosen on the basis of previous literature, as well as the scalp maxima of the current dataset when all the conditions were collapsed together. The P1 was measured at two homologous electrodes clusters around O1 in the left hemisphere (electrodes 70, 66, and 71), and around O2 in the right hemisphere (electrodes 83, 76, and 84). N1 was measured at two homologous electrode clusters which included P7 and P9 in the left hemisphere (electrodes 66, 55, and 59) and P8 and P10 in the right hemisphere (electrodes 90, 91, and 94). The EPN was measured at electrodes 66, 67, and 60 in the left hemisphere, and at electrodes 77, 84, and 85 in the right hemisphere. The LPP was measured at the midline electrodes Pz, Cz, and CPz.

We quantified our ERPs using the same method as in the previous chapters. For the early ERP components (P1 and N170), we computed the average in a 20-ms window around the peak of each component, with the peak identified based on the grand-average. The EPN was in analysed in 50-ms blocks from 202-408 ms as in previous chapters, and the LPP was analysed in a large time window between 400-600 ms (Leppänen et al., 2007; Rellecke et al., 2012).

5.2.6. Statistical analyses

We conducted 2 (Emotion type: Happy and angry) x 3 (Intensity) rANOVAs to examine the effects of emotion type, and expression intensity on proportions of neutral test faces rated as ‘emotion’, and reaction times.

We then conducted 2 (Response: ‘Emotion’ versus ‘Neutral’) x 2 (Hemisphere: Left and Right) x 4 (Intensity: Neutral, 20%, 40%, and 60%) rANOVAs to analyse the effects of response, and intensity on the amplitudes of the P1, N170, and EPN. As the LPP is calculated from the midline electrodes, hemisphere was not included as a factor for analysis. Instead we conducted a 2 (Response) x 4 (Intensity) rANOVA.

We used an alpha level of .05 for all statistical tests, and applied Greenhouse-Geisser corrections to degrees of freedom where appropriate.

5.3. Results

5.3.1. Behavioural results

Response times to test stimuli did not differ significantly based on the emotion type, or expression intensity of the adaptor (ps $> .05$).

The proportion of faces evaluated as emotional also did not differ significantly based on emotion type, or intensity. However, the responses were mediated by an interaction between emotion and intensity, $F(2, 14) = 5.130$, $p = .021$, $\eta_p{}^2 = 0.423$. This was driven by larger proportions of neutral test faces being rated as expressing an 'emotion' when they followed 40% angry expressions versus happy expressions, and 60% happy expressions versus angry expressions. However, at all levels of intensity, the proportion of faces rated as emotional was around 50% (see Figure 5.2).

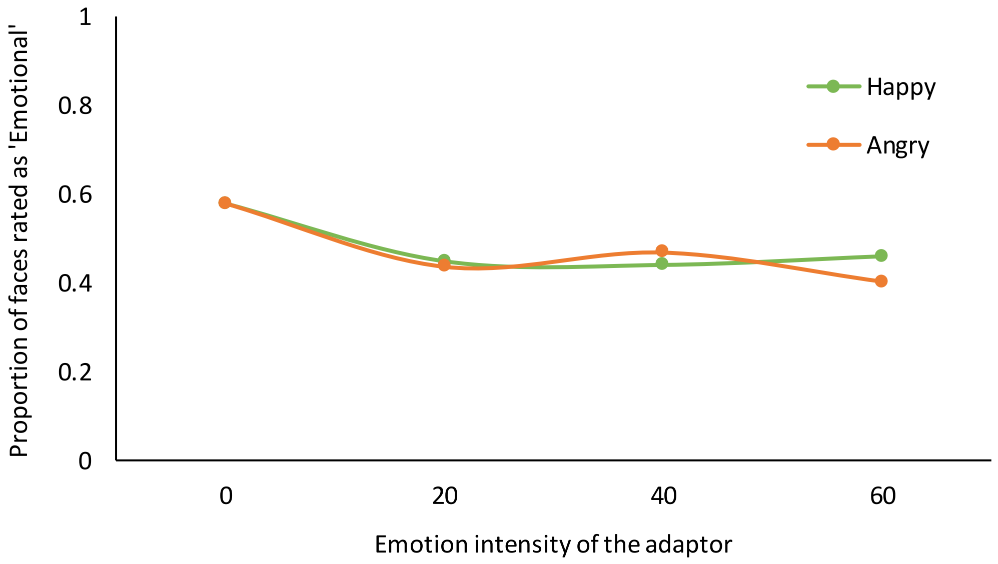


Figure 5.2. Proportion of test faces rated as emotional for each expression intensity of the adaptor. The orange and green lines represent angry and happy adaptor expressions, respectively.

5.3.2. EEG results

We found no significant effects of intensity on the amplitudes of the P1, N170, EPN or the LPP (all *ps* > .05). There were also no significant modulations of these components as a function of expression intensity when we analysed the trials per condition irrespective of response type (all *ps* > .05). Therefore, as intensity did not systematically modulate the EPN, we did not conduct follow-up correlations between EPN amplitudes and the behavioural measures.

5.4. Interim discussion

We did not find systematic modulation of the EPN based on the expression intensity of the adaptor expression. We also did not find perceptual shifts for the test stimulus to indicate that the perceived intensity of the expression varied. This seems to be the most likely explanation for our results. However, it is plausible that the EPNs evoked by the adaptor were not systematically modulated by expression intensities, and therefore did not cause a shift in the opposing direction. Therefore, before drawing conclusions based on this data, we reanalysed the data to examine whether there was a main effect of intensity on the EPN evoked by the adaptor to assess whether we replicated intensity effects for the EPN that we found in Chapters 2-4.

5.4.1. Follow up analysis: EPN evoked by the adaptor stimulus

We re-epoched the data by time locking our epochs to the adaptor stimulus. Consistent with our other analyses, data were segmented into epochs that were 1.2 seconds long (200 ms before stimulus presentation, and 1 s after). Grand average ERP waveforms were computed for each condition per participant, and for each condition collapsed across participants. A baseline correction (based on the average of the 200-ms baseline period) was subtracted from each time point in the epoch. We then computed EPN amplitudes for the adaptor in the same time windows analysed for the test stimulus, consistent with the previous chapters (i.e., 50 ms blocks between 200-400 ms). We conducted 2 (Hemisphere: Left and Right) x 4 (Intensity: Neutral, 20%, 40%, and 60%) rANOVAs to analyse the effects of response and intensity on the amplitude of the EPN evoked for the adaptor.

5.4.2. Results and Discussion

Consistent with our previous findings, there was a main effect of the intensity of the adaptor on the amplitude of the EPN from 252-304 ms, $F(2, 14) = 7.611$, $p = .006$, ${\eta_p}^2 = 0.521$. There was a significant linear trend for greater EPN negativities for higher intensities of emotional expressions $F(1, 15) = 13.446$, $p = .007$, ${\eta_p}^2 = 0.396$. We then checked whether this EPN modulation was correlated with proportion of faces evaluated as emotional; there were no significant correlations except for 60% intensity angry faces, where EPN amplitude was positively correlated with proportion of faces evaluated as emotion $r_s(14) = 0.624$, $p = .010$.

5.4.3. Follow up behavioural study

The behavioural results of our EEG experiment show that participants evaluated test faces as emotional about 50% of the time, irrespective of the intensity of the adaptor. This is inconsistent with our hypothesis that a greater proportion of test faces would be rated as ‘emotional’ at higher intensities of adaptors. As all test faces were neutral, participants may have been biased towards reporting faces as neutral. To explore this further, we conducted a behavioural study in which we also included 60% intensities of happy and angry faces as test stimuli.

5.4.4. Method

5.4.4.1. Participants

Participants in this study were 16 volunteers (12 female) from the University of Auckland. The mean age was 23.93 (*SD* = 7.56, *range* = 18-34). One person was left-handed. All participants’ data were included in the analysis.

Volunteers with conditions that impaired their ability to recognise facial expressions or with a history of epilepsy or migraines did not meet the criteria to participate in the study. All participants reported normal or corrected-to-normal vision. Participants provided written, informed consent prior to their participation. All participants received a $20 supermarket voucher as koha for their participation in the study. Research protocols were approved by The University of Auckland Human Participants Ethics Committee.

5.4.4.2. Stimuli

We used the same stimuli as in the main experiment (see Chapter 2 Section 2.2.2, for details about stimulus creation).

5.4.4.3. Procedure

The experiment was similar to the behavioural task in the adaptation/aftereffects EEG experiment. However, we added more conditions by presenting both 60% happy and 60% angry faces as test stimuli. As these additions further prolonged the experiment, we reduced the number of trials per condition to 36, instead of 45 as in the EEG study. We ensured that we maintained the same proportion of expressive and neutral adaptors as in the EEG experiment.

The experiment had a total of 480 trials which were split up into 10 blocks (48 trials per block). There were seven types of adaptor stimuli (Neutral expressions, and 20%, 40%, and 60% intensity of happy and angry expressions), and three types of test stimuli (Neutral expressions, 60% Angry expressions, and 60% Happy expressions). Each of the 20-60% happy and angry expressions were presented as adaptors 40 times (there were 40 images that were presented once each). These were followed by neutral test expressions 36 times, 60%

happy expressions twice, and 60% angry expressions twice. Neutral adaptors were presented 240 times (there were 48 images that were presented 5 times each). These were followed by neutral test expressions 216 times, 60% happy expressions six times, and 60% angry expressions six times. We used a custom written script for E-Prime to ensure that the same neutral expression was not presented as the adaptor and the test face on any given trial.

5.4.4.4. Statistical analyses

We conducted 2 (Adaptor Emotion type: Happy and angry) x 3 (Adaptor Expression Intensity: 20% 40%, 60%), x 3 (Test Expression: Neutral, 60% Happy, 60% Angry) rANOVAs to examine the effects of emotion type and expression intensity on reaction times and the proportions of test faces rated as ‘emotion’.

5.4.4.5. Results

There was were no significant differences in the proportion of test faces rated as emotion based on emotion type $F(1, 15) = 0.214$, $p = .650$ ${\eta_p}^2 = 0.0.014$, or intensity of the adaptor $F(2, 14) = 0.994$, $p = .650$ ${\eta_p}^2 = .014$, or the test face type $F(2, 14) = 0.774$, $p = .410$, ${\eta_p}^2 = 0.049$, $\varepsilon = 0.583$.

There was a significant difference in response times based on the intensity of the adaptor expression, $F(2, 14) = 4.182$, $p = .049$, ${\eta_p}^2 = 0.218$, $\varepsilon = 0.604$ (see Figure 5.4). This was driven by longer response times to 60% ($M = 710.55$ ms, $SD = 113.88$) expression intensity than 20% ($M = 528.23$ ms, $SD = 54.17$) or 40% ($M = 571.21$ ms, $SD = 53.10$).

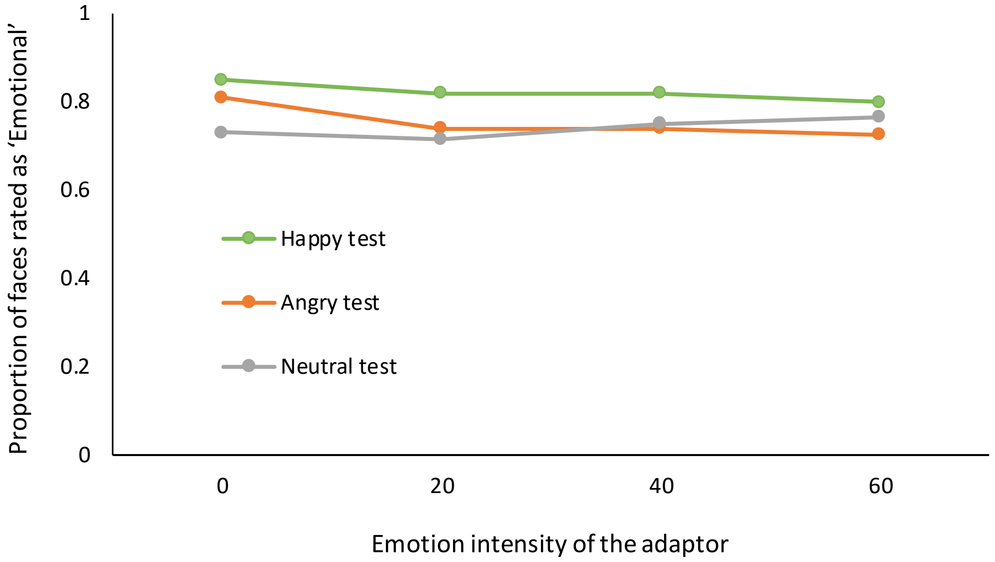


Figure 5.3. Proportion of test faces rated as emotional for each expression intensity of the adaptor. The orange and green lines represent 60% angry and 60% happy test faces, respectively. The grey line represents neutral test faces.

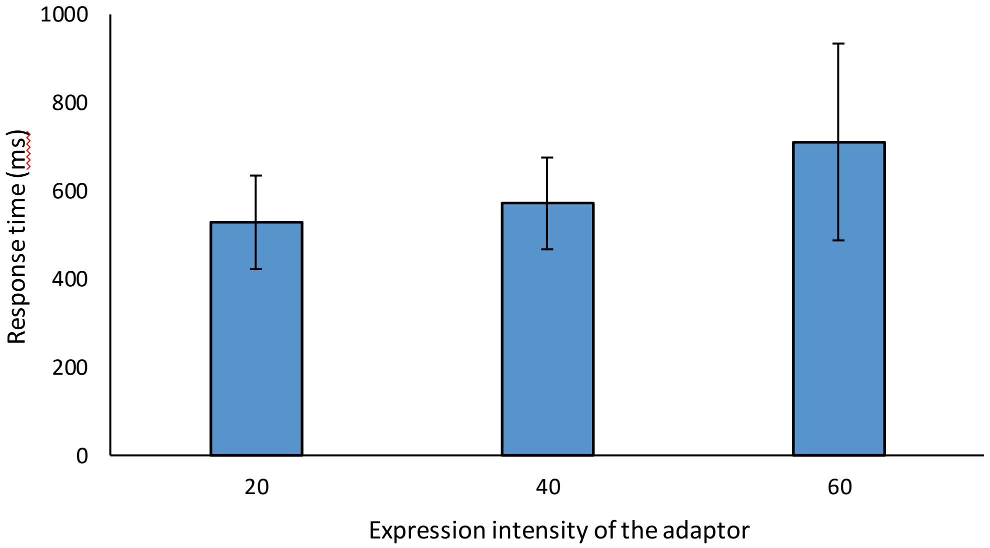


Figure 5.4. Response times for test faces at each expression intensity of the adaptor when emotion type was collapsed. Error bars represent 95% confidence intervals.

5.5. Discussion

In this chapter we examined whether the EPN might reflect behavioural evaluations observed in adaptation aftereffects. Contrary to expected, the proportion of neutral faces evaluated as emotional did not increase as adaptor intensities increased. Instead, we found that participants rated test faces as 'emotional' about 50% of the time following adaptors of any expression intensity. Furthermore, we found no significant effects of intensity on the EPN evoked for the test face, despite systematic modulation of the EPN evoked by the adaptor.

EPN modulations were systematically affected by intensity differences in the adaptor stimulus, but not the test stimulus. One interpretation of these results could be that EPN is driven by expression intensity only when the morphological differences in features that represent intensity are presented on screen versus a shift in percept of expression intensity. This may seem to be a parsimonious explanation for the data presented thus far. However, the behavioural data suggest that participants' evaluations of emotion did not shift systematically as the intensity of adaptor expression increased. Therefore, we were unable to examine EPN modulations for perceptual shifts in expression intensity. Furthermore, participants performed at chance levels and it is possible that their responses were biased by the presentation of only neutral test faces.

In the follow-up behavioural experiment, the inclusion of 60% intensity angry and happy expressions as test stimuli led to an increase in all test faces being evaluated as emotional, irrespective of the intensity level of the adaptor (see Figure 5.3 versus Figure 5.2). This shift in evaluation included neutral test faces followed by neutral adaptors, which were rated as emotional 58% of the time in the EEG task, versus an average of 81% in the behavioural task. This shift in evaluation likely reflects a shift in overall bias towards reporting 'emotion'. The proportion of neutral adaptors in the EEG experiment and the follow up task were kept consistent. Therefore, it is unlikely that participants were biased towards responding to the adaptor face rather than the test; in which case, neutral expressions would be rated emotional about 50% of the time in both experiments. However, the variation in evaluations was very large across individual participants. Therefore, it is possible that the bias in the averaged data was due to different individuals using different expression processing strategies.

Future studies are needed to examine the procedural parameters to ameliorate the effects of bias in this procedure. One way to address this might be to make participants respond faster to the stimuli. Adaptation typically produces transient afterimages (see Webster & MacLeod, 2011); therefore, rapid response times are required to capture the shifts in perception. Although we verbally encouraged participants to respond quickly, average response times were fairly slow (*M* = 648.50 ms, *SD* = 212.53 ms). In future, forcing a response in shorter time windows could help capture aftereffects.

Another possible reason for our unsystematic findings is that the strength of the adaptors was insufficient to produce aftereffects. Evidence for this interpretation comes from our analysis of the EPN amplitudes evoked by the adaptors, and their relationship with the proportion of faces evaluated as expressing emotion. Only when the adaptor was 60% intensity angry were the amplitude of the EPN positively correlated with the proportion of test faces rated as emotional. This is the opposite correlation seen in the previous chapter, where EPN amplitudes were negatively correlated with the proportion of faces rated as emotional. Therefore, it is possible that only the 60% intensity angry expressions had enough adaptive strength to shift the perception of the test stimulus. This interpretation is consistent with the idea that threat-related information is prioritised in processing (Le Doux, 1996; Morris et al., 1999). However, we can only speculate regarding emotion specific information as we had an insufficient number of trials to investigate the EPN following each intensity per emotion type.

The trial duration in this experiment was much longer than in the previous experiments. This limited the number of trials we could run in the EEG experiment. Long trial times also contributed to our decision to limit the exploration if adaptors intensities to between neutral and 60%. This window of analysis was chosen based on our previous experiment (see Chapter 4, Figure 4.1) which showed that evaluations of expressions tend to plateau at around 60% intensity. However, testing higher adaptor intensities (e.g., prototypical or caricaturised intensities) in future studies may shed light on whether greater expression intensities result in more robust findings.

Consistent with behavioural adaptation/aftereffects paradigms (e.g., Fox, Oruc, & Barton, 2008), we used adaptation durations of 4600-5000 ms. We choose to use longer adaptation times because it has been suggested that shorter adaptation times, as used in some EEG studies (e.g., Nemredov & Itier, 2011), do not reflect category-specific neural adaptation (Kovács, Zimmer, Volberg, Lavric, & Rossion., 2013; Nemrodov & Itier, 2012). However, similar to Burton, Jeffery, Bonner, and Rhodes’s (2016) exploration of temporal parameters in behavioural adaptation/aftereffects paradigms, the timing of adaptors, interstimulus intervals, and test stimuli also need to be examined more thoroughly to establish the current EEG procedure as a paradigm for probing adaptation/aftereffects.

5.5.1. Emotion trajectories in continuous processing versus adaptation/aftereffects literature

A broader consideration for future experiments is the inconsistency between the emotion trajectories investigated in the categorical/continuous processing literature and those in adaptation/aftereffects paradigms. While investigating continuous processing, we made use of morphed images that change from 0% (Neutral) intensity to 100% (Prototypical). This is based on the two-dimensional space models that suggest that the underlying axes that expressions are coded on is based on ‘valence’ (i.e., how pleasant or unpleasant’ they are) and ‘arousal’ (the response intensity that they evoke). Neutral faces can be represented in the center of this space, as there should be equal representation by the channels that code the axes (i.e. a neutral face is equally coded by mechanisms that code for pleasant-ness and unpleasant-ness). If this is the case, faces that are ‘neutral’ in expression should represent a ‘null’ point (Webster, 2015). The ‘null’ point is created when two pools of neurons that fire maximally and equally for two extremities of a stimulus property (e.g., intensity of expression in this case). Therefore, at the null point, the dimension that is coded by the pools of neurons is not distinguishable as either extremity (see Webster, 2015, for a discussion). However, face identity adaptation/aftereffects studies suggest that faces might be represented with respect to a central ‘norm’, which is the average of all the faces in our repertoire of faces (see Rhodes et al., 2005, for discussion). It has recently been suggested that expressions may also be coded in the same space as identity (Rhodes et al., 2017), which suggests that the proper ‘null’ point may be the ‘norm’ face, rather than faces that are neutral in expression. Therefore, it is possible that we did not find behavioural shifts in perception as our test stimulus did not represent a central point, around which perception can be shifted. Utilising the ‘norm’ face as the test stimulus in an EEG adaptation/aftereffects procedure might help elucidate whether the EPN amplitude correlates with systematic shifts of the test faces for expression intensities.

5.5.2. Conclusion

In this chapter we aimed to explore whether the amplitude of the EPN evoked by neutral test faces correlates with the proportion of faces evaluated as ‘emotion’ in an adaptation aftereffects paradigm. There were no significant differences between EPN amplitudes for test stimuli evaluated as ‘emotional’ versus ‘neutral’, nor were there differences in EPN amplitude across different adaptor intensities. Furthermore, the proportion of faces evaluated as emotion did not vary across different expression intensities of the adaptor. Nevertheless, consistent with Chapters 3-5, the EPN evoked by the adaptor was systematically more negative for greater expression intensities. In addition, there was a positive correlation between EPN amplitude and the proportion of expressions evaluated as emotional when the adaptor was 60% angry. This suggests that stronger adaptors may be necessary to induce significant perceptual shifts of the test expressions. Further refinement of the temporal and stimulus parameters could help assess whether EPN amplitudes covary with shifts in the evaluations of ‘emotion’ in expressions.

Chapter 6: General discussion

This thesis presents three main experiments that systematically explore how expression intensities are processed along happy and angry emotion trajectories, and how processing of expression intensity interacts with emotion type. In this chapter, we review the main findings from the experimental chapters and consider the theoretical significance of our findings, including avenues for future research.

6.1. Summary of main findings

In Chapter 2, we explored whether emotion intensity is processed ‘automatically’ (i.e., when the expression is not task relevant). We found that high intensities of expressions (80% and prototypical expressions) were processed automatically, irrespective of emotion type. We also found greater EPN negativities for angry versus happy expressions, suggesting that emotion type is also processed automatically. Differences in EPN negativities for emotion type preceded negativities for expression intensity, suggesting that we might process expressions ‘categorically’ (perhaps into ‘basic emotion’ categories; see Ekman, 1992; Izard, 1994) before we process expression intensity. In addition, we did not find evidence for the hypothesis that the LPP reflects automaticity in emotion processing when there are no task constraints (c.f. Hajcak et al., 2010; Schupp, 2000). Instead, we found lower amplitudes of the LPP for 60% expression intensities than all other intensities examined. This could reflect greater processing of unambiguous stimuli, as proposed by Sun et al. (2017).

In Chapter 3, we investigated how expression intensities are processed when voluntary attention is directed to the emotion in expressions (i.e., when the emotional expression is task relevant). We found that N170, EPN, and LPP amplitudes were modulated a function of expression intensity. Consistent with Sprengelmeyer and Jentzsch (2006), we found that the

N170 was more negative for greater expression intensities, but was not modulated systematically by emotion type. Overall, EPN amplitudes were graded with respect to expression intensity (i.e., more negative for greater expression intensities). However, these effects interacted with emotion type. Angry expressions evoked EPN negativities that were graded with respect to expression intensity (i.e., more negative for greater intensities). In contrast, only 100% (prototypical) happy expressions evoked more negative EPN amplitudes than all other intensities of happy expressions. This suggests that voluntary attention might have asymmetric effects on facilitating intensity processing for threat-related (angry) versus friendly (happy) expressions. When emotion type was collapsed, LPP intensity effects appeared to be driven by larger responses to neutral and 100% (prototypical) expressions. Separating the LPPs based on emotion type showed that the main effect of intensity for angry expressions were driven by larger responses to 0% (Neutral) faces and 100% (Prototypical) angry expression intensities. However, for happy expressions 0% (Neutral) and 20% expression intensities evoked the largest LPPs.

In Chapter 4, we explored the relationship between modulations of the N170, EPN, and LPP observed in Experiment 2 (Chapter 3) with behavioural measures (response times and the proportion of faces evaluated as emotional) per expression intensity. In contrast to past literature, which focused on the LPP to examine decision-related processes, we found that the proportion of faces rated as emotional at each intensity level was correlated with greater negativities of the EPN. The LPP was however positively correlated with response times. This suggests that LPP amplitude might reflect elaborative assessment of stimuli (Schacht & Sommer 2009a, 2009b; Schupp et al., 2004, 2006).

Given our robust intensity effects on the EPN in Experiments 1 and 2, in Chapter 5 we explored whether EPN amplitudes could index perceptual shifts of neutral test faces in an adaptation/aftereffects paradigm. However, neither the proportion of faces rated as emotional nor the EPN amplitude evoked by the neutral test faces varied systematically with the intensity of the adaptor. Therefore, we did not observe perceptual shifts to assess the relationship between EPN amplitudes and the perception of emotion. A follow-up behavioural study suggests that our participants’ responses may have been biased by presentation of only neutral test faces. Therefore, future studies should further refine the parameters of the behavioural task to utilise in EEG to explore the relationship between the EPN and perceptual shifts.

6.2. Theoretical significance of our results

6.2.1. Implications for categorical and continuous processing

Our data provides evidence of both categorical and continuous processing as reflected by EPN and LPP modulations. We observed greater EPN negativities evoked for angry expressions than happy expressions in Experiment 1, and greater LPPs evoked for angry expressions than happy ones in both Experiments 1 and 2. These results suggest that emotion type is coded by both of the EPN and LPP components.

The expressions we used differed in expression category (angry versus happy) as well as valence (negative versus positive). Therefore, we cannot determine whether our results reflect differences in emotion categories as described in the basic emotions framework (Ekman & Friesen, 1992, 1994,), or whether they reflect valence processing as per the two-dimensional continuous processing model (Posner, et al., 2005; Russell, 1980). Sprengelmeyer and Jentsch (2006) examined EPN for expression intensities for three negative valence expressions (fear, disgust, and anger), and reported main effects of emotion type on the EPN. As they found differential modulation of EPN for prototypical expressions of the same valence, the parsimonious explanation for our results is that the EPN was driven by prototypical emotion type rather than valence.

One limitation to this explanation is that Sprengelmeyer and Jentsch's (2006) experiment involved evaluation of every face in the set, which meant that participants had to direct more attention towards each face in their set than in ours. Given that the EPN seems to be modulated by attentional control, future studies can use the same parameters as Experiments 1 and 2 to compare pairs of expressions that differ in emotion type but not emotion valence when attention is not directed toward the emotion.

We also found that the EPN was modulated by expression intensities in all three experiments, suggesting that expression intensities are systematically coded in the brain. These results also converge with fMRI evidence (Harris et al., 2012) suggesting that there are distinct areas for processing expression intensities (pSTS) and emotion type (amygdala).

6.2.2. Implications for attention and emotional expression processing

Given their motivational and biological significance, emotional expressions are thought to be processed 'automatically' (Öhman, 2002). One of the aims of this thesis was to examine automaticity of expression intensity processing, and how it interacts with processing emotion type. Here we examine implications for of our findings for automaticity of emotion processing, threat specificity in processing emotional expressions, and discuss the implications for alternative operational definitions of automaticity.

6.2.2.1. Implications for 'Automaticity' of expression intensity processing

In Experiment 1 (Chapter 2), we defined 'automaticity' as processing that occurs when emotion is not task relevant. Our results show that emotion type was processed automatically and earlier than intensities of expressions. Furthermore, only high intensities of expression were coded 'automatically', irrespective of emotion type. These results contrast with Sprengelmeyer and Jentzsch's (2006) findings, which show the effects of expression intensity prior to emotion type; and that EPN amplitude had a linear relationship with the expression intensity (i.e., was more negative for greater intensities). The differences between our tasks, and range of expression intensities, might help explain these differences in results. We discuss these below.

In Experiment 1, we asked participants to simply view expression intensities, and respond to an unrelated face that was presented 10% of the time. In contrast, Sprengelmeyer and Jentzsch (2006) used a gender discrimination task. Although neither task draws attention to emotion directly, the gender discrimination task might draw more attention towards each face in the study (see Rellecke, et al., 2012,). Therefore, their effects may be driven by modulatory influences of attention that is directed towards the faces, rather than automatic emotion related processes. This explanation is consistent with our results from Experiment 2 (Chapters 3 and 4), where we direct attention towards emotion in the face and also found graded modulations of the EPN for emotional expressions.

Another difference between Sprengelmeyer and Jentzch's (2006) study and ours is that they used a different range of expression intensities (50%, 100%, and 150%) to those used in our tasks (0%, 20%, 40%, 60%, 80%, and 100%). When emotion was not task related, we found differences between 0% expression intensity and 80% and 100% intensities. Therefore, if we removed all intensities from our analysis except 50% and 100%, to examine a subset of the intensities in their study, we would also find a linear relationship between EPN amplitude and expression intensity. This seems to be the most parsimonious explanation of the discrepancy between our results. In sum, it seems as though only high expression intensities are processed automatically.

6.2.2.2. Limitations to inferring automaticity

While our first experiment did not explicitly draw attention to emotion in the face, it was not a ‘true passive task’ as we asked participants to identify a distinctive face from a different stimulus set. We choose for two reasons: the first was to ensure participants were looking at the screen, and not disengaging or falling asleep; the second was because we operationally defined automaticity as processing without *explicit* attention to emotion. Automaticity can also be defined as processing without *any* attention. To examine the latter, we would need to omit a task all together as it is that participants were paying more attention to the expressions on screen than they would had not included any task.

In the broader context of participating in an experiment, any stimulus that is presented may be perceived as task relevant. Furthermore, the majority of faces shown throughout the experiment expressed different emotional expressions. Therefore, although participants were not explicitly instructed to evaluate emotion or intensity in the experiment, it is possible that participants were processing them anyway. Equalising the number of unrelated behavioural trials, and trials per condition, would not be practical as these additions would extend the EEG session time substantially. Although this is a general consideration, it does not diminish the significance of the systematic differences between emotion type, and high intensities versus low intensities. However, it does suggest that we should be careful before suggesting that there is ‘no attention’ directed towards the emotion in Experiment 1.

6.2.3. Implications for threat prioritisation

Our results from Experiments 1 and 2 support the idea that threat-related expressions are prioritised in processing (Le Doux, 2000). In Experiment 1, we found larger EPN negativities for angry expressions than for happy expressions (see also Schupp et al., 2004). We also found that high expression intensities evoked more negative EPN negativities than low intensities, irrespective of emotion type. This contrasts with Leppänen et al.'s (2007) results, which show intensity effects on the EPN for fearful but not happy faces. They suggested that expression intensity might be coded only for threatening expressions. The differing results from Experiment 1 and Leppänen et al. may be due to the differences between our tasks; Leppänen et al.'s study required participants to categorise expressions into prototypical expression categories, whereas we only required participants to respond to an infrequently presented face. This discrepancy might suggest that threat-specific effects only occur when there is voluntary attention directed towards the face.

While the results of Experiment 2 showed main effects of expression intensity on the EPN, irrespective of emotion type, data from Experiment 2 also showed that the facilitatory effects of voluntary attention could be asymmetric for processing threat-related (angry) versus friendly (happy) expression intensities. The amplitude of the EPN was graded for angry expressions. In contrast, only 100% intensity (prototypical) happy expressions evoked larger amplitudes of the EPN than all other intensities. These findings may align with Morris et al.’s (1998) findings showing increased amygdala activation was associated with increasing intensities of fear. It is plausible that the modulatory effects of amygdala are strengthened for processing expression intensities of threat related information. However, Morris et al. also showed that decreasing amygdala activity was associated with increasing intensities of happy expressions. This does not fit our data, as we also observed greater EPN negativities for 100% happy expression intensity. However, it is possible that the attenuation of the amygdala activity is mediated by voluntary task related attention (as 100% happy expressions needed to be categorised as 'emotion' in the task).

It is also possible that the graded effects for angry expressions reflect increased arousal to threatening expressions that is modulated by attention, and perhaps decreased arousal for happy expressions. These effects may be driven by increased modulatory feedback from the amygdala that enhances arousal responses (see Herrington et al., 2011). These interpretations remain speculative, as our experiments used EEG which does not allow us to record from the areas identified by Morris et al. and Herrington et al. Future studies integrating fMRI and EEG that control for arousal can help elucidate the relationship between attention, intensity and arousal.

6.2.4. Implications for different types of automaticity

Automaticity does not have a consistent operational definition in the literature. Automaticity could refer to processing without explicit intention to process the emotion (Rellecke et al., 2012), without attention (Öhman, 2002), without awareness (Pegna, Landis, & Khateb, 2008), or without inhibitory control (Vuilleumier et al., 2001). The interpretation of experimental results may vary drastically depending on the definition used by the experimenter.

6.2.4.1. Automaticity as processing without awareness

Automaticity can be defined as perception without awareness. Evidence for this form of automaticity comes from backwards masking tasks; these experiments involve briefly presenting an emotional expression, followed by a mask which is intended to disrupt emotion perception (e.g., Pegna et al., 2008). Although we asked participants to do an unrelated task in Experiment 1 (Chapter 2), our results should not be conflated to reflect a lack of 'awareness' of the emotion, or expression intensity. We presented the stimuli at the center of the screen for 500 ms to ensure participants were able to see our stimuli. Furthermore, participants viewed many trials for each expression intensities. Therefore, limited conclusions can be drawn for this definition of automaticity based on our data.

6.2.4.2. Automaticity as independence from attentional resources

We explored whether attention modulates intensity processing when there is an infrequent unrelated task which would be considered low load; and when the primary task is to distinguish between emotional and neutral expressions. A remaining question is whether or not intensity processing *depends* on available attentional resources. There is some evidence that highly salient emotional images can attract attentional resources, irrespective of other task demands, or even when emotions are presented to the unattended side of space in hemi-spatial neglect (Vuilleumier & Schwartz, 2001). However, others have demonstrated that processing for emotion type is affected by the availability of attentional resources (Pessoa et al., 2008; Pessoa et al., 2002). Furthermore, Müller-Bardorff et al. (2016) demonstrated that the effects of attention on processing emotion type are only attenuated when attentional resources are limited by an alternative task. However, processing of expression intensity was not affected by task demands. This suggests that emotion intensity processing is not sensitive to attentional load in the same way that emotion type is. However, as intensity effects were enhanced by attentional control from Experiment 2, we might expect that intensity effects would be attenuated when attentional resources are depleted in the presence of another task. Further research using tasks that differentially engage attentional resources can enhance our understanding of how attentional resources impact emotion expression processing.

6.2.5. Future directions

6.2.5.1. Investigating alternative emotion trajectories

For the purposes of our experiments, we created stimuli that ranged from 0% (Neutral) to 100% (prototypical) expression intensities that we defined as 'emotion trajectories'. These were based on other studies in the continuous processing literature (e.g., Harris et al., 2012; Morris et al., 1996). This approach integrates both categorical and continuous frameworks, as prototypical expressions from the categorical framework are varied along the intensity dimension. Evidence from Experiments 1-3 show systematic effects of intensity on the modulations of the EPN. However, there are multiple types of emotion trajectories in the literature. For instance, some behavioural adaptation/aftereffects use trajectories that intersect through a 'norm', which is the average of all the faces in our repertoire (see e.g., Leopold et al., 2001). Others create trajectories along orthogonal axes, connecting two 'exemplar' expressions together (Pell & Richards, 2011). These differing conceptions of expression trajectories could be possible avenues for future research.

6.2.6. Domain generality of emotion effects

In this thesis we examined emotion related ERPs for processing expression intensities. The EPN and LPP results we found are similar to those reported for other emotion laden stimuli (see Olofsson et al., 2008; Schupp et al., 2006). This suggests that intensity may not be specific to facial expressions, but instead may be a general construct. As we only used face stimuli, we cannot directly assess the domain generality of our observed effects. If this is the case, we need to account for a system that can process intensities across multiple domains and sensory systems. However, it is also possible that the effects that we observed relate to the morphological changes in the face, rather than intensity per se. We aimed to examine this issue in Experiment 3, where we hoped to examine responses of ‘emotion’ and ‘neutral’ to neutral test faces in an adaptation/aftereffects paradigm. As responses would be to the same stimulus, if there were EPN differences for test stimuli that varied depending on the magnitude of adaptor intensity, we could infer that the EPN reflects perceptual shifts in intensity perception rather than physical shifts.

6.3. Conclusion

ERP research on emotional expression processing is a vast and active field of research. However, most research is based on the categorical framework which suggests that there are distinct categories of expressions that are represented by specific neural areas (Ekman & Friesen, 1972). This thesis provides evidence that both expressions are coded both categorically and continuously. It also shows that high intensities of positive and negative expressions can be coded automatically (without explicit attention to emotion) and that negative expression intensities are enhanced in processing when attention is explicitly directed towards emotion. In contrast, only prototypical positive expressions are prioritised in processing when attention is directed towards emotion. We found EPN component of the ERP seems to be associated with perceptual processing of expression intensities, and attempted to use the ERP technique to index perceptual shifts in adaptation/aftereffects paradigm. The combination of these two methods could be a useful tool to investigating perceptual processing of expression intensities in future.

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