Perceiving direct and averted gaze during emotion discrimination, affective empathy and affective theory of mind judgements: electrophysiological and behavioural effects

by

Sarah McCrackin

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Examining Committee Membership

The following served on the Examining Committee for this thesis. The decision of the Examining Committee is by majority vote.

External Examiner	Dr. Aina Puce, PhD Professor, Psychological and Brain Sciences, Indiana University
Supervisor	Dr. Roxane Itier, PhD Associate Professor, Psychology, University of Waterloo
Internal Member	Dr. Mike Dixon, PhD Professor, Psychology, University of Waterloo
Internal Member	Dr. Heather Henderson, PhD Professor, Psychology, University of Waterloo
Internal-external Member	Dr. Michael Barnett-Cowan, PhD Associate Professor, Kinesiology, University of Waterloo

Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

Sarah McCrackin was the sole author of Chapters 1 and 5, which were written under the supervision of Dr. Roxane Itier and were not written for publication.

In addition to Chapters 1 and 5, this thesis consists of three manuscripts (Chapters 2, 3 and 4) written for publication. Exceptions to sole authorship of material are as follows:

Research presented in Chapters 2, 3, and 4:

Dr. Roxane Itier was the primary investigator on the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant #418431), Ontario government (Early Researcher Award, ER11-08-172), Canada Foundation for Innovation (CFI, #213322), and Canada Research Chair (CRC, #213322 and #230407) grants which supported conducting this work.

The research in each of these chapters was conducted at the University of Waterloo by Sarah McCrackin under the supervision of Dr. Roxane Itier. Sarah McCrackin and Dr. Roxane Itier contributed to study conceptualization and design. Sarah McCrackin programmed the experiments and ran the participants. She cleaned the participant data and analysed it with input from Dr. Roxane Itier. Sarah McCrackin was first author of all manuscripts, to which Dr. Roxane Itier contributed intellectual input and editing.

The research in Chapter 2 has been published (see citation below), and Chapters 3 and 4 are in the process of revision and submission respectively.

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Abstract

Our observations about the eye-gaze of others inform how we interact with them. Perception of direct gaze has been shown to impact emotional and self-referential processing differently than perception of averted gaze, which in turn may impact how we relate emotionally to others. However, it is still unclear how the use of eye-gaze varies depending on the type of social task being performed, and how direct and averted gaze processing vary during each task. A set of three Event-related Potential (ERP) studies investigated the time-course of direct and averted gaze perception, and the impact of gaze processing on different social and emotional abilities. In Study 1, participants were asked to use the same direct and averted gaze faces to make three kinds of discriminations based on facial cues – direction of attention discrimination from eye-gaze, emotion discrimination from facial expressions, and gender discrimination. In Studies 2 and 3, written sentences describing positive, negative, and neutral scenarios were presented before face stimuli and acted as emotional context. Participants then viewed direct and averted gaze faces of the individuals that had been described as experiencing the various scenarios. After seeing each face, participants rated their affective empathy (Study 2) for the gazer, or made affective theory of mind judgements about what the gazer was feeling (Study 3). Event-related potentials (ERP) were recorded to the onset of direct and averted gaze faces in each study, while participants performed each task. The impact of direct and averted gaze perception on behavioural performance was examined, and ERPs tracked the time-course of how direct and averted gaze perception interacted with affective task processing. A mass univariate approach was used to analyse several key components: i) the frontocentral N100 and N200, thought to reflect the initial activation of emotion areas in response to affective stimuli; ii) the face-sensitive N170, thought to reflect structural encoding of the face; iii) the EPN, thought to reflect attentional selection of motivationally relevant stimuli; iv) the P300 and LPP, thought to reflect the cognitive appraisal of those stimuli. Behavioural results demonstrated that relative to the other gaze condition, direct gaze perception facilitated emotion discrimination, while averted gaze facilitated attention discrimination (Study 1). The perception of direct gaze within positive contexts was associated with increased empathy for the gazer, and increased positive emotion for the observer (Study 2). Participants rated that the gazer was feeling more positive when they displayed direct gaze as opposed to averted gaze, and that they were feeling more aroused during negative contexts with averted gaze than direct gaze (Study 3). At the neural level, eye-gaze perception interacted with emotional aspects of each task, during both early and late time-windows known to be sensitive to emotional processing. Eye-gaze interacted with task demands to modulate N200 activity in Study 1, with different patterns of eye-gaze effects seen in each task. Eye-gaze and sentence valence also interacted to modulate the N100 and P200 in Study 2, during the affective empathy task. These early N100, N200 and P200 effects may reflect eye-gaze modulation of a frontocentral brain network that responds to emotional stimuli. During the affective theory of mind task in Study 3, eye-gaze and sentence valence interacted later, on the centroparietal LPP and the P300 tail end. This gaze modulation appeared to reflect a unique modulation linked to cognitive appraisal of emotional content. The pattern of results suggests that early neural eye-gaze effects may reflect the initial processing of emotional stimuli and may be responsible for the eye-gaze effects seen behaviourally on the observer's emotional state. In contrast, later neural eye-gaze effects may reflect the cognitive appraisal of eye-gaze linked to higher social processes, and these may be responsible for the impact of eye-gaze on emotional appraisals of the gazer. These results have implications for understanding neurotypical eye-gaze processing as well as clinical populations that present with both altered eye-gaze processing and social impairment.

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Dedication

This dissertation is dedicated to my parents, who have always believed in me, supported me in so many different ways, and instilled a love of science in me from a young age. If I typed out everything I owe to you, this thesis would be another hundred pages, so I'll spare my committee and just say: thank you for everything, and I love you. Who would have thought that all those science fairs would eventually lead here?

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Chapter 1: General Introduction

The importance of observing the eyes during social interactions is unquestioned. We are sensitive to the eyes of others even as infants (e.g. Wahl et al. 2019; Vernetti et al. 2018; Keemick et al. 2019), and it is believed that processing the eyes is a key part of our social development and functioning (see Itier & Batty, 2009; Cañigueral & Hamilton 2019; George & Conty, 2008 for reviews). We use our own eyes to engage with the world around us, and as such, we understand that if we look at someone else's eyes, we can gain valuable insight into their internal state. This is reflected in many colloquial expressions, like "I can see it in your eyes", "trying to catch someone's eye", or "seeing through another's eyes". These expressions are not really about the eyes themselves – they are about trying to relate to the minds behind them.

The most salient cue that the eye-region carries is the direction of eye-gaze, which tells us if someone is attending to us or to something else (George & Conty, 2008; Itier & Batty, 2009). Discerning gaze direction is thought to have been so important in our evolutionary history that selective pressures led to the development of an eye with a large sclera and a smaller dark iris, adaptations that make gaze direction much easier to identify (Kobayashi & Kohshima, 2001; see Emery, 2000 for a review). In this thesis, I define direct gaze as forward facing eye-gaze, such that if an observer was looking at the eye-region it would result in eye-contact with the image. Averted gaze is defined as eye-gaze averted to the left or right side, with enough of a deviation from the center (approximately 45°) that it is easily judged as not central.

As reviewed below, there is accumulating evidence that the perception of direct compared to averted gaze elicits different neural activation and has unique cognitive and behavioral effects. In particular, this evidence suggests that direct and averted gaze perception have differential impacts on self-referential processing (i.e. related to the self) and emotional processing (see Hietanen, 2018 and Hamilton, 2016 for reviews), which are believed to have a strong impact on the way we relate to those around us (Lieberman, 2007; Joireman & Hammersla, 2002; Mitchell, Banaji & Macrae, 2005; Lombardo et al. 2007). In this thesis, I present three event related potential (ERP) studies focusing on how the perception of direct and averted gaze impacts the way in which we understand a gazer's emotional state and the way in which we relate to the gazer on an emotional level.

1.1 The Attentional and Emotional Effects of Direct and Averted Gaze Perception

1.1.1 Attentional Effects – Directing Attention Towards or Away from the Self

The primary function of observing gaze direction is that it provides information about the gazers' attentional state (George & Conty, 2008; Itier & Batty, 2009). Averted gaze typically signifies that the gazer is attending to the object or location they are gazing at, while direct gaze signifies to an observer that they are the focus of attention (Conty et al., 2016; Itier & Batty, 2009; George & Conty, 2008). Using the eye-gaze of others to infer attentional state is thought to be a key part of how we make inferences during social interactions. For example, Baron-Cohen's influential "mind-reading" model proposes the existence of an innate Eye-Direction Detector (EDD; Baron-Cohen; 1992) which discerns gaze direction and helps an observer understand what the gazer perceives. Perrett and Emery's (1994) Direction of Attention Detector (DAD) model is similar but integrates information from multiple sources about the direction of attention, including eye-gaze, head orientation, and other body cues. Indeed, it is important to acknowledge that other cues like head orientation can impact eye-gaze discrimination (Itier et al. 2007; Palancia & Itier, 2014; Seyama & Nagayama, 2005), and interact with gaze direction to signify direction of attention (e.g. Langton, 2000) and to shift an observer's attention (Hietanen, 1999). However, below I specifically review eye-gaze effects on attention while holding head position and other facial and body cues constant.

Direct gaze is thought to be attention grabbing, as it is discriminated more quickly and accurately than averted gaze within a crowd of gazing faces as distractors (the so-called "stare in the crowd effect"; Von Grünau & Anston, 1995; Senju & Hasegawa., 2005; Doi, Ueda, & Shinohara, 2009; Palancia & Itier, 2011). There is also evidence that discriminating direct from averted gaze is unaffected by dual tasking designed to divide attention, while discriminating averted left from averted right gaze suffers (Yokoyama et al. 2014). The tendency to attend to direct gaze faces has also been inferred from studies showing that people preferentially look towards direct gaze. Not only is this effect robust in adults (Mojzisch et al. 2006; Palancia & Itier, 2012), but it can be observed in neonates (see Senju & Johnson, 2009b for a review), who preferentially look at direct gaze faces compared to those with closed eyes (Batki et al., 2000) or averted gaze (Farroni et al. 2002).

In turn, seeing eye-gaze also appears to impact the observer's attentional state, with direct and averted gaze impacting attention differently. Perceiving direct gaze is thought to result in increased self-focus (see Hamilton, 2016 for review). Seeing direct gaze signifies that one is being watched and direct gaze images have been shown to produce similar brain activation as hearing one’s name being called (Kampe, et al., 2003). Direct gaze images may also produce a similar effect as reading self-referential statements, as these statements interact with eye-gaze direction to impact electrophysiological responses to faces (McCrackin & Itier, 2018a) and seeing direct gaze results in the increased use of first-person pronouns (Hietanen & Hietanen, 2017). The impact of direct gaze on self-attention appears to be linked to the social significance of direct gaze (Hamilton, 2016) as it is enhanced by seeing a real face with direct gaze instead of a picture. For example, Pönkänen, Peltola, & Hietanen (2011) demonstrated that live direct gaze was associated with increases in self-awareness (measured by the Situational Self-Awareness Scale; Govern & Marsch, 2001), while photos of direct gaze did not produce the same effect.

When averted gaze is perceived, there is a different impact on attention. The observer's attention is spontaneously oriented to the gazed-at location (Friesen & Kingstone, 1998; Driver et al., 1999; see Frischen et al., 2007 for a review), a phenomenon known as gaze-cuing or gaze-oriented attention. This gaze-cuing can even be found in 3-month olds (Hood, Willen & Driver, 1998) and is thought to facilitate social interactions by leading to joint attention, where two individuals attend to the same target while simultaneously being aware of the other's interest (Frischen, Bayliss, & Tipper, 2007). Accordingly, there is evidence to suggest that gaze-cuing in neurotypical individuals is positively related to social competence (Hayward & Ristic, 2017), and inversely related to psychopathic traits (Hoppenbrouwers et al., 2017). Alterations in gaze-cuing have also been documented in those with autism spectrum disorder (e.g. Gillespie-Lynch et al., 2013; Uono, Sato, & Toichi, 2009) which is characterized by social impairment (e.g. Tanguay et al. 1998), and in neurotypical individuals with higher levels of autistic-like traits (McCrackin & Itier, 2019a; Bayliss et al. 2005; Hayward and Ristic, 2017; Lassalle and Itier, 2015; but see Bayliss and Tipper, 2006, for null results). Gaze-cuing is also thought to be vital for survival. Gaze-cuing is faster if the gazer is smiling or fearful, which likely helps an observer attend faster to threats, and possibly rewards, in the environment (e.g. Bayless et al., 2011; McCrackin & Itier, 2018b, 2019a, 2019b; Neath et al. 2013; Lassalle & Itier, 2013, 2015a, 2015b; Graham et al. 2010).

1.1.2 Emotional Effects – The Link between Direct Gaze and Affective Processing

Both direct and averted gaze can vary in their emotional significance depending on a variety of contextual factors. For example, seeing someone look at you may be either desired or feared depending on the situation. Likewise, seeing someone avert their gaze could either mean they are ignoring you or looking at something interesting. However, when contextual factors are eliminated or controlled, direct gaze appears to produce a stronger and more positive emotional response than averted gaze (see Hietanen, 2018 for a review), potentially because it is a typical signal of inclusion and attention (Wirth et al. 2010). Indeed, relative to averted gaze, the perception of direct gaze is associated with increased self-reported positive affect (McCrackin & Itier, 2018a; Uono & Hietanen; 2015; but see Chen, 2017) and studies using an implicit association test have shown that individuals associate direct gaze faces with positive words more than averted gaze faces (Chen, 2017; Lawson, 2015).

The perception of direct gaze not only makes an observer feel more positive, but it makes an observer have a more positive evaluation of the gazer. Individuals pictured with direct gaze are liked more than those with averted gaze (Mason et al. 2005), and avatars making direct gaze shifts are liked more than those making averted gaze shifts (Kuzmanovic et al., 2009). Individuals who display more direct gaze are also associated with other positive personality traits like trustworthiness, competence and credibility (see Kleinke, 1986 for a review), social rank and dominance (see Hall et al. 2005), and even increased physical attractiveness (Conway et al., 2008; Ewing et al., 2010; Mason et al., 2005, Palancia & Itier, 2012).

Finally, direct gaze perception has been associated with increased arousal relative to averted gaze. This has been shown using many different paradigms, including paradigms which require self-reporting of arousal (McCrackin & Itier, 2018a) and those which use physiological measures like galvanic skin response (Conty et al., 2010; Helminen et al. 2011, Hietanen et al., 2008; Nichols & Champness, 1971; Myllyneva & Hietanen, 2015; Pönkänen et al., 2011) and pupil dilation (Porter et al., 2006). Participants also appear to have increased awareness of their own arousal responses to emotional stimuli after viewing direct gaze compared to averted gaze (Baltazar et al., 2014).

1.2 Emotional Hallmarks in Interpersonal Relationships and Proposed Relation to Gaze

The unique emotional and attentional effects of eye-gaze perception likely have a strong effect on our social interactions. However, the impact of eye-gaze perception on many areas of social cognition is still unknown. In this thesis, I focus on how the perception of direct and averted gaze impacts three emotional hallmarks in interpersonal relationships: discrimination of facial expressions of emotion (hereafter emotion discrimination), affective empathy, and affective theory of mind. I define each of these socio-cognitive abilities and review support for potential links between them and eye-gaze processing below.

1.2.1 Emotion Discrimination

Emotion discrimination refers to the ability to discern emotional state from physical cues, and in this thesis I specifically refer to it as discerning emotion from facial expressions. There is some preliminary evidence to suggest that emotion discrimination may be impacted by perceived gaze direction. At the clinical level, deficits in emotion discrimination are associated with poor social functioning in individuals with schizophrenia (Hooker & Park, 2002) and autism spectrum disorder (e.g. Pelphrey et al., 2002; Senju & Johnson, 2009a), both of which have been associated with altered eye-gaze processing (Akiyama, et al. 2008; Kington et al., 2000; Kohler et al., 2008; Lajiness-O’Neill et al, 2014; Pelphrey et al., 2005; Senju et al. 2005). However, it is unclear if the altered eye-gaze processing and emotion discrimination have distinct or common causes.

In neurotypical individuals, some have found that happy and angry expressions are easier to perceive when those faces have direct gaze, while fear and sadness are perceived more easily with averted gaze (Adams & Kleck; 2003, 2005; Sander et al., 2007). Adams and Kleck (2003) proposed that direct gaze signals approach from a gazer, and that this approach signal is shared with "approach" emotions like happiness and anger. In contrast, averted gaze signals avoidance, and enhances the perception of "avoidance" emotions like fear and sadness. However, there is mixed support for this theory. For example, while these original studies were promising, support for the shared signal hypothesis was largely found to be tied to the specific stimuli used (Bindemann et al., 2008; Graham & Labar, 2007). More recent studies have nevertheless suggested that emotional expression processing and eye-gaze processing do interact (e.g. Ulloa et al. 2014), and as reviewed above, direct gaze perception has an impact on many types of emotional processing. This may facilitate emotion discrimination from some facial expressions.

1.2.2 Affective Empathy

Once another person's emotional state is discriminated, an observer sometimes experiences a similar emotional state as a result. Affective empathy refers to the capacity to become affectively aroused by another person’s emotional valence and intensity (Decety et al., 2015; de Vignemont & Singer, 2006; Kanske et al. 2015; Lieberman, 2007), while being aware that the other person is the source of the emotion. This affective sharing can occur for both positive and negative emotional states (Morelli et al., 2015a; 2015b). As with emotion discrimination, there appears to be a link between altered eye-gaze processing and altered affective empathy in clinical populations, including psychopathy (e.g. Dadds et al., 2008; 2012; Gillespe et al., 2015) and social anxiety disorder, the latter of which has recently been linked to impaired affective empathy for positive emotions (Morrison et al., 2016). Again, this link is tentative, and has not yet been tested with an experimental manipulation.

Perceiving direct gaze may facilitate affective empathy for a few potential reasons. Direct gaze appears to result in spontaneous emotional processing (see Hietanen, 2018 for a review), and this may facilitate the emotional processing that occurs when sharing someone’s emotions. Direct gaze has also been linked to mimicking behavior (Wang et al., 2010), which some have argued can facilitate affective sharing (e.g. Prochazkova & Kret, 2017; Schuler et al., 2016). Finally, as self-focused attention may aid in the simulation of others’ affective states within the self (Joireman & Hammersla, 2002; Lieberman, 2007; but see Boyraz & Waits, 2015 for null results), the increased self-referential processing that comes with processing direct gaze (e.g. Hamilton, 2016; Hietanen & Hietanen, 2017; Kampe et al. 2003) may facilitate empathy.

1.2.3 Affective Theory of Mind

While affective empathy may coincide with emotion discrimination, it also likely coincides with affective theory of mind, which refers to our ability to make inferences about the emotional states of others (Decety et al. 2015; de Vignemont & Singer, 2006; Kanske et al. 2015; Lieberman, 2007). Indeed, while identifying an emotional expression does not require inferring a mind behind the eyes (e.g. identifying a frown does not require considering what that frown means or why it is there), affective theory of mind requires the inference about a mental state that is attached to the emotional experience (Decety et al., 2015; Stewart et al. 2019).

There is some support for the idea that eye-gaze processing may facilitate affective theory of mind. First, there is a tentative clinical link between altered theory of mind (Baron-cohen, 1997; Baron-cohen et al. 1997; Bora et al., 2009; Cui et al., 2017; Hezel & McNally, 2014; Mathersul et al. 2013; Sprong et al., 2007) and altered eye-gaze processing in autism spectrum disorder (Lajiness-O'Neill et al, 2014; Pelphrey et al., 2005; Senju et al. 2005), schizophrenia (Akiyama, et al. 2008; Kington et al., 2000; Kohler et al., 2008) and social anxiety disorder (Weeks et al., 2013; Wieser et al. 2009).

Second, a few neuroimaging studies have observed that direct and averted eye-gaze elicit differential activation in brain areas that have been implicated in theory of mind (e.g. Calder et al., 2002; Conty et al., 2007; Hooker et al., 2003; Wicker et al., 1998). This observed overlap has led to the suggestion that simply seeing the eyes results in activation of the brain areas involved in making mental state inferences (Calder et al., 2002; Conty et al., 2007; Hooker et al., 2003; Wicker et al., 1998). Inferences about another's emotional state may be particularly impacted by eye-gaze, given that direct and averted gaze have differential impacts on emotional processing.

Finally, different affective states are associated with different patterns of eye gaze behavior (e.g. Allard & Kensinger, 2018; Demeyer et al., 2017; Isaacowitz & Choi, 2011; Isaacowitz et al., 2008; Natale, 1977; Kim et al., 2018; Kleinke, 1986; Wadlinger & Isaacowitz, 2006), and changes in gaze behavior are used to regulate emotions (see Isaacowitz et al. 2006 for a review). This suggests that if we are tuned to typical associations between eye-gaze behavior and affective state, we may make better affective theory of mind judgements by incorporating eye-gaze information.

1.3 Neural Correlates of Eye-gaze Perception

The link between different socioemotional abilities and eye-gaze processing is better understood by considering the neural correlates of eye-gaze perception. In particular, understanding how these neural substrates give rise to the attentional and emotional effects of gaze perception can help us start to understand the mechanism by which direct and averted gaze elicit these effects. Functional neuroimaging studies have determined that eye-gaze is processed by a network of brain areas, with main nodes including the superior temporal sulcus, amygdala, medial prefrontal cortex, orbitofrontal cortex, and parietal regions including the intraparietal sulcus (for reviews, see Carlin & Calder, 2013; George & Conty, 2008; Grosbras et al., 2005; Itier & Batty, 2009; Numenmaa & Calder, 2009). While many studies have reported that these areas are sensitive to gaze direction, the areas reported in each study, as well as the direction of direct and averted gaze differences, have been quite mixed. This is likely because these brain areas play different roles in driving the unique attentional and emotional effects of gaze perception, which vary greatly as a function of the tasks that participants have performed. I briefly review the key brain areas implicated in eye-gaze perception below, along with their proposed relation to the effects of seeing direct and averted gaze.

1.3.1 Implicated Brain Areas and Link to Attentional and Emotional Outcomes

The superior temporal sulcus (STS) appears to be one of the most common neural correlates of eye-gaze (but see Pageler et al., 2003; Wicker et al., 1998 for null results) with either increased activation for direct gaze relative to averted gaze (Calder et al., 2002; Pelphrey et al., 2004; Wicker et al., 2003), or vice versa (Hoffman & Haxby, 2000). The anterior STS is thought to contain clusters tuned to respond preferentially to left and right averted gaze (Calder et al. 2007; Numenmaa & Calder, 2009). In contrast, the posterior STS is proposed to be more broadly involved in the detection of biological motion (Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000; Puce & Perrett, 2003) and as such responds to stimuli with varied gaze directions or emotional expressions, as eye-gaze and expression are the primary changeable aspects of the face. When averted gaze is perceived, the STS interacts with regions of parietal cortex (Hoffman & Haxby, 2000; Materna et al. 2008; Nagata et al. 2012) and it is believed that these parietal areas mediate the attention shifts that spontaneously occur towards gazed-at locations (Grosbras et al., 2005; Materna et al., 2008; Nummenmaa et al. 2010).

The medial prefrontal cortex (mPFC) is another common correlate of eye-gaze perception. Increases in mPFC activity have been reported for averted compared to direct gaze (Calder et al. 2002), for averted and direct gaze relative to closed or downcast eyes (Calder et al. 2002; Wicker et al., 1998), or for dynamic gaze sequences relative to control conditions (Hooker et al., 2003). Preference for direct and averted gaze may vary depending on the mPFC location, as Conty et al. (2007) found that the lateral and medial mPFC responded preferentially to direct and averted gaze, respectively. It is thought that the mPFC may work with the STS to facilitate the use of eye-gaze while making theory of mind judgements (Calder et al., 2002; Conty et al., 2007; Hooker et al., 2003; Wicker et al. 1998), as they have long been implicated as key nodes in the theory of mind network (see Abu-Akel & Shamay-Tsoory, 2011; Carrington & Bailey, 2009; Saxe, & Baron-Cohen, 2006; Schurz et al. 2014; for reviews). The medial prefrontal cortex is heavily implicated in self-referential processing (e.g. Schwarz et al., 2012; Schmitz et al. 2007; Schmitz et al. 2004; Macrae et al., 2004; Mitchell et al., 2005), so it seems likely that activation of the mPFC by direct gaze may be responsible for the increase in self-awareness and reflection that occurs following direct gaze perception. Self-referential processing is also theorized to aid in the simulation of others' affective and mental states within the self (Frith & Frith, 1999; Joireman & Hammersla, 2002; Lieberman, 2007; but see Boyraz & Waits, 2015 for null results), and may facilitate theory of mind attributions made from the eye-gaze of others. Accordingly, recent studies have reported increased activation of the mPFC when engaging in joint attention from another individual's eye-gaze (Redcay et al, 2012; 2010; Schilbach et al. 2010; Williams et al. 2005a).

In general, the perception of direct gaze appears to result in increased amygdala activation, regardless of whether the faces have neutral or emotional expressions (Burra et al. 2013; George et al., 2001; Kawashima et al., 1999), though some have reported more activation for averted than direct gaze (Hooker et al., 2003; Wicker et al., 2003), or even no amygdala sensitivity to gaze direction (Pageler et al., 2003). As the amygdala is heavily implicated in the production of affective arousal (e.g. Laine et al., 2009; LeDoux, 2000; Mangina & Beuzeron-Mangina, 1996; Williams et al., 2005b;), Hietanen (2018) proposed that the amygdala may produce the increased arousal commonly associated with direct gaze perception (Conty et al., 2010; Hietanen et al., 2008; Helminen et al., 2011; McCrackin & Itier, 2018a; Myllyneva & Hietanen, 2015; Nichols & Champness, 1971; Pönkänen et al., 2011; Porter et al., 2006). The amygdala is also responsive to both positive and negative emotional expressions (e.g. Garavan, et al. 2001; Hooker et al. 2006; Juruena et al., 2010; Murray, 2007; Sander et al., 2003), and has been proposed to interact with parietal areas to enhance attentional orienting by averted gaze when the gazer bears a positive or negative facial expression compared to a neutral one (Itier & Batty, 2009; McCrackin & Itier, 2018b; 2019a; 2019b; Numenmaa & Calder, 2009).

Amygdala activation may also be responsible for increases in positive affect (Chen, 2017; McCrackin & Itier, 2018a; Lawson, 2015; Uono & Hietanen; 2015) and positive ratings of the gazer (Ewing, 2010; Hall et al. 2005; Kleinke, 1986) following direct gaze. However, it seems more likely that the positivity effects are driven by increased activation of the reward system (see Berridge & Kringelbach, 2015; Rolls, 2000; Schultz, 2006). Relative to averted gaze, the perception of direct gaze photos is associated with increased ventral striatum activity (Kampe et al. 2001) and direct gaze shifts are associated with increased anterior insula (Ethofer et al. 2011) and orbitofrontal cortex (Conty et al. 2007) activity. Finally, direct gaze from a live person is associated with increased activity in a number of reward areas, including the anterior insula, anterior cingulate, and the globus pallidus (Cavallo et al., 2015).

1.3.2 Time course of Eye-gaze Perception Assessed with Event Related Potentials

Along with attempts to localize networks in the brain, several studies have investigated the time-course of gaze processing using scalp-recorded Event-Related Potentials (ERPs). These studies typically compare the amplitude of ERP components elicited by perceiving direct gaze shifts or static direct gaze face images to that elicited by averted gaze counterparts. The impact of eye-gaze direction on ERP components has no clear consensus and only a few components have been commonly investigated. As with the results from functional magnetic resonance imaging studies, the results from these studies appear quite mixed. However, there are likely factors at play that can explain differences between eye-gaze processing in each study, including task demands and differences in ERP analysis and processing (e.g. which reference site is used).

There is some evidence that eye-gaze can impact the posterior P100 component, which typically occurs 80-130ms after face presentation. While few studies have looked at gaze effects on this early component, Burra et al. (2018) recently found that P100 amplitude was more positive in response to direct gaze than averted gaze, while Schmitz et al. (2012) found the opposite pattern at a similar timing. The P100 is thought to reflect early visual processing that is sensitive to low-level stimulus features like luminance (e.g. Bieniek et al. 2013; Shaw & Cant, 1980; Tobimatsu et al. 1993) and contrast (e.g. MacKay & Jeffreys, 1973), so it is possible that low-level differences between direct and averted gaze stimuli drove these effects. However, the P100 is also modulated by attention (Hillyard et al., 1998; Luck & Hillyard, 1995; Luck et al., 1994; Rugg et al., 1987; Taylor, 2002) and Burra et al. (2018) argued their effects were likely attentional, given that gaze modulation was present in a task that required looking at the face, but not in an oddball task, where faces were irrelevant.

The majority of ERP studies on eye-gaze perception have focused on the N170, which is a negative component occurring over occipitotemporal sites from approximately 130-200ms following face presentation (Bentin et al., 1996; Eimer, 2000; George et al., 1996). The N170 is thought to reflect the structural encoding of the face (i.e. integration of face features into one percept) and its enhancement following face presentation, compared to most other visual stimuli, has led to the suggestion that it is the earliest "face-sensitive" component (Bentin et al., 1996; Eimer, 2000; George et al., 1996). The direction of gaze effects on the N170 appears on the surface to be quite mixed. Many have found that the N170 is more negative in response to averted gaze shifts (Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015) or averted gaze face images (Itier et al., 2007; Watanabe et al., 2002) than to direct gaze counterparts. Others have found the opposite pattern of results, with more negative N170 amplitude following direct gaze images (Burra et al., 2017; see also Pönkänen et al., 2010 who found this for live faces but not face pictures) and direct gaze shifts (Conty et al., 2007; Watanabe et al. 2006). In contrast, some studies have found no detectable difference between direct or averted gaze processing on the N170 (see Pönkänen et al., 2010 for null results with face pictures but not live faces; Taylor et al., 2001; Schweinberger et al., 2007; Rossi et al., 2014 for null results with line drawn faces).

A few factors have been proposed to drive the N170 effects. The first is the dynamicity of the stimuli (Contry et al. 2007). The N170 gaze effect has been proposed to be due to local changes in eye-region luminance and contrast during the perception of gaze stimuli with apparent motion (see Puce et al. 2015, for a review), and seems to be independent of the size of the gaze shift (Latinus et al., 2015). These dynamic gaze studies typically found a more negative N170 in response to averted gaze shifts (Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015). Accordingly, the effect seems to require realistic face stimuli as the effect does not occur in response to line drawn faces (Rossi et al., 2014; Rossi et al., 2015). This proposed response to eye-motion also does not seem to require a condition in which the observer is looked at, as a similar M170 effect with MEG has been reported in a paradigm in which participants watched others gaze behaviour change without being involved with direct eye-contact (Ulloa et al., 2010). However, this is not to say that the social significance of the stimuli does not seem to matter. In fact, as discussed above, discrepant results with dynamic stimuli were found by Conty et al.

(2007), but their task asked participants to indicate whether the gaze shift moved towards or away from them. This arguably instates more of a social context than simply asking an observer if the gaze is left or right (see Puce et al., 2015). In a recent follow-up, Latinus et al. (2015) demonstrated that when participants used dynamic gaze shifts to complete the common left/right discrimination task, the typical larger N170 for averted gaze shifts was observed. However, when the same participants were asked to complete the more social task, the N170 gaze effect was reduced and lateralized to the left hemisphere, thought to reflect increased gain of the sensory system for this more important task. While Latinus et al. (2015) did not find identical results to Conty et al. (2007), the authors further proposed that differing head orientations may have also played a role.

Beside the P100 and N170, gaze effects have also been reported on the P300, a centroparietal ERP component occurring approximately 250-500ms and thought to reflect stimulus evaluation or categorization (Polich and Kok, 1995). An adaptation study comparing left and right gaze directions found sensitivity to eye-gaze 250-300ms post face presentation (Schweinberger et al., 2007). A few more studies have found that direct gaze and direct gaze shift produced more positive P300 amplitudes than averted gaze and averted gaze shift from 300-600ms (Conty et al., 2007; Burra et al., 2018; Itier et al., 2007; Myllyneva & Hietanen; 2015). Burra et al. (2018) and Carrick et al. (2007; though note that Carrick et al. found both a P300 and P500 eye-gaze effect without comparing to a direct gaze condition) have proposed that P300 gaze effects reflect cognitive evaluation of gaze linked to a higher level of social cognition than attentional or structural encoding effects. Accordingly, Myllyneva & Hietanen (2015) recently demonstrated that participants' P300 amplitudes (and their arousal) were enhanced by eye-gaze only when they believed the gazer could see them. Similarly, Sabbagh et al. (2004) found the P300 was larger when participants engaged in emotion discrimination from images of the eye-region relative to when they engaged in gender discrimination. I review the P300 further in the section below.

1.4 Event Related Potentials Associated with Emotional Processing

A field of ERP research has led to the identification of ERPs that are commonly modulated by emotional processing (see Hajcak et al. 2010; Olofsson et al. 2008; and Schupp, 2006 for reviews). These ERPs are valuable tools to investigate how direct and averted gaze perception impact neural measures of emotion discrimination, affective empathy, and affective theory of mind.

As Amodio et al. (2014) emphasize, there is always a temptation to assume that if activity from an ERP component is modulated by a certain task, it reflects neural activation unique to that task. However, as reviewed below, modulation of the ERPs I examine likely reflects activation recruited during many different types of emotional tasks. For example, there is no "affective empathy ERP component". Instead, an affective empathy task likely modulates ERPs associated with emotional processing in many different types of emotional tasks. What these components truly reflect is an ongoing and important question and the claims that we can make are limited by our understanding of them. As such, while the components analyzed in each study vary based on specific *a priori* hypotheses, I make an effort throughout this thesis to draw parallels between the modulations of ERPs for each study. These comparisons are between participant groups, so they are not as strong as within-participant comparisons. However, they are particularly important given that there has been relatively little research which has recorded ERP activity during affective theory of mind and affective empathy tasks, and even less describing gaze effects on affective processing. The affective ERP components that appear in this thesis are summarized below, along with descriptions of what the field currently believes they reflect.

1.4.1 The Frontal N100

The N100 is a negative component typically measured from approximately 50-120ms at frontocentral sites. While the direction of N100 amplitude differences has been very mixed (Coll, 2018), the N100 is modulated by attentional state (Doallo et al., 2007) and is sensitive to differences between emotional stimuli, including facial expressions of emotion (Luo et al. 2010), body language (Jessen & Kotz, 2011), images and scenes (Doallo et al., 2007), and the perception of pain-inducing stimuli relative to neutral stimuli (Fan & Han, 2008; see Coll, 2018 for a review). It has been argued that emotion effects on the N100 reflect an initial automatic activation of emotion areas (Fan & Han, 2008) potentially through mirror neuron activation (Gallese & Goldman, 1998), including the orbitofrontal cortex via modulation of the amygdala (Luo et al. 2010). This activation of emotion areas is thought to contribute to the later “emotional sharing” response during affective empathy (Fan & Han, 2008) that occurs when participants view pain-inducing stimuli. According to this idea, perceiving these stimuli result in automatic activation of emotion areas, which results in "emotional contagion". As a very early component, it is not thought to reflect the cognitive evaluation of affective empathy, but rather the initial activation of emotion areas that occurs during emotional contagion (Fan & Han, 2008).

1.4.2 The Frontal N200

The N200 component is a negative component typically measured over frontocentral sites (occasionally measured as a positive P200 over posterior sites) from approximately 200-350ms. The N200 is modulated by emotional stimuli, including the perception of pain-inducing stimuli such as hands being stabbed (see Coll, 2018 for a review), words (Kanske, & Kotz, 2010; Zhang et al. 2019) and facial expressions (Balconi & Canavesio, 2016) with inconsistent effect directions (Coll, 2018). Along with the N100, the modulation of the N200 by emotional stimuli is thought to reflect initial automatic activation of emotion areas. Again, this emotion activation is thought to be part of the emotional contagion that occurs during affective empathy (Fan & Han, 2008). Accordingly, Decety et al. (2015) recently found greater N200 amplitudes for pain-inducing images than neutral images from 175-275ms, with the difference between the two categories being larger during an affective sharing task (indicating the perceived pain intensity), than during an emotional compassion task (indicating how sorry they felt for the suffering individual). Furthermore, source localization has identified the anterior cingulate cortex as one of the potential generators of the N200 (Carretie et al., 2004), which has been implicated in attentional regulation of emotional processing (see Allman et al. 2001 for a review).

1.4.3 The Early Posterior Negativity (EPN)

The EPN is typically measured over occipitotemporal sites from approximately 200-350ms (see Schupp et al. 2006 and Olofsson et al. 2008 for reviews). The EPN does not appear to be modulated by basic physical characteristics of stimuli like colour (Junghöfer et al., 2001), but rather is believed to be part of an attentional selection process that enhances processing of emotionally arousing stimuli (Junghöfer et al., 2001; Schupp et al., 2004a). It is characterized by an increased negativity for both positive and negative stimuli relative to neutral stimuli (e.g. Herbert et al., 2008; Kissler et al., 2009; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Sato et al., 2001; Schupp et al., 2006; Rellecke et al., 2012) and sometimes for negative stimuli relative to positive stimuli (Rellecke et al., 2011; 2013; Schupp et al 2004a). The EPN's enhancement by emotion is present for many types of emotional stimuli, including faces with emotional expressions (Aguado et al. 2012; Itier & Neath-Tavares, 2017; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Rellecke et al., 2012; Schupp et al. 2004b), neutral faces primed with affective sentences (Klein et al., 2015; McCrackin & Itier, 2018a; Wieser et al., 2014; Wieser & Moscovitch, 2015), verbal material (Herbert et al., 2008; Kissler et al., 2009; Schacht & Sommer, 2009) and visual scenes (Junghöfer et al. 2001; Schupp et al., 2003; 2004a).

1.4.4 The P300

The P300 is usually measured over centro-parietal sites from 300-500ms (see Hajcak et al. 2010; Olofsson et al. 2008 and Polich & Kok, 1995 for reviews). It is believed that P300 reflects an allocation of resources towards stimuli that are motivationally relevant. For example, during oddball tasks (i.e. tasks which require a response to an infrequent stimulus), the P300 is more positive to oddball trials, which a participant is instructed to respond to (e.g. Fogarty et al., 2019; Polich & Margala, 1997). It is believed that emotional stimuli are inherently motivationally relevant, and as such, the P300 is also more positive in response to positive and negative scenes (Cano et al. 2009; Conroy and Polich, 2007; Delplanque et al., 2005; Keil et al. 2002; Mini et al., 1996; Rozenkrants and Polich, 2008), faces (Lang et al., 1990), body parts in painful situations (see Coll, 2018 for a review) and words (Naumann et al., 1992), compared to neutral counterparts. This appears to be driven by both arousal (Delplanque et al., 2005; Keil et al., 2002; Mini et al., 1996; Rozenkrants and Polich, 2008; Schupp et al., 2000) and valence, even when arousal is controlled for (Cano et al., 2009; Conroy and Polich, 2007; Rozenkrants & Polich, 2008).

1.4.5 The Late Positive Potential (LPP)

The LPP is measured from around 400-600ms over frontocentral and centroparietal sites (see Schupp et al. 2006, Hajcak et al. 2010, and Olofsson et al. 2008 for reviews), though some measure it up to timings as late as 1000-1200ms (e.g. Decety et al. 2015; Hajcak & Olvet, 2008). It is sometimes considered to be the later portion of the P300 (Olofsson et al. 2008; Schupp et al. 2006), and is thought to reflect elaborative cognitive appraisal of emotional content and emotional meaning, independent of non-affective physical characteristics like size (De Cesarei & Codispoti, 2006) or perceptual complexity (Bradley et al., 2007). Like the P300, it is more positive in response to positive and negative stimuli relative to neutral stimuli, including images or scenes (Hajcak et al., 2006, 2007; Hajcak & Nieuwenhuis, 2006; Hajcak & Olvet, 2008; Schupp et al. 2001; 2004a), body parts interacting with pain-inducing stimuli (Decety et al., 2010; see Coll, 2018 for a review), words (Fischler & Bradley, 2006, Naumann et al., 1992; 1997; Schact & Sommer, 2009), phrases (Eimer & Holmes, 2007; Fischler and Bradley, 2006), and faces (Eimer et al. 2003; Schupp et al. 2004b; Williams et al. 2006; 2007). The LPP also appears to be sensitive to the emotional context under which a stimulus is viewed. For example, like the EPN, the LPP to emotional (Aguado et al 2019; Dieguez-Risco et al 2013; 2015) and neutral faces (Klein et al., 2015; McCrackin & Itier, 2018a, Wieser et al., 2014; Wieser & Moscovitch, 2015) is impacted by the emotional significance of preceding sentences.

1.5 Summary of Overall Thesis Objectives

As reviewed above, we are becoming increasingly aware that eye-gaze processing, and its social impact, may vary greatly as a function of what the observer is trying to do. However, there is much that we still do not know about how eye-gaze processing varies in certain social scenarios, and the impact that it has on social interactions. As such, the three studies included in this thesis investigated the interaction between eye-gaze processing and the unique socioemotional abilities reviewed above.

I first focused on the behavioural and neural impact of eye-gaze on three discrimination tasks using facial cues (Study 1). Importantly, participants used the same direct and averted gaze faces to complete each task, and I investigated whether eye-gaze processing varied within the same individuals depending on the social task being performed. The first task was discriminating direction of attention from eye-gaze, which is thought to be the primary cue extracted from eye-gaze (e.g. Baron-Cohen & Cross, 1992). The second was emotion discrimination of happy and angry facial expressions. Importantly, both of these tasks are thought to be precursors to more complex theory of mind processes (Baron-Cohen & Cross, 1992; Clark et al., 2008). The third task was gender discrimination, which also requires the use of physical facial cues, but is not typically associated with eye-gaze perception. This first study was designed to demonstrate that the perception of eye-gaze varies within the same participants as a function of the task they are performing. I hypothesized that there would be differences in the neural processing of eye-gaze during each task, either in spatial location (different electrodes) and/or the time course, though the specifics of this interaction were difficult to predict given mixed previous reports of eye-gaze ERP modulations. I also hypothesized that eye-gaze would differentially impact accuracy during each task. In particular, I predicted that participants would be more accurate at emotion discrimination for direct gaze faces than averted gaze faces based on previous research suggesting that direct gaze elicits activation of emotion areas likely to be involved in emotion judgements. In contrast, I had no specific predictions about the impact of eye-gaze on attention and gender discrimination.

Next, I investigated whether perceiving direct and averted gaze would impact how much positive and negative affective empathy individuals felt for the gazer (Study 2). Participants read sentences about protagonists experiencing positive, negative, or neutral events before seeing the protagonists' face with direct or averted gaze. They rated how much affective empathy they felt for each person, and I examined whether the gaze direction would interact with the sentence valence to impact responses. I hypothesized that direct gaze perception would result in increased positive and negative empathy, as direct gaze perception is implicated in processes thought to be important for empathy, such as mimicry, emotional, and self-referential processing.

Finally, I investigated whether perceived gaze direction would impact affective theory of mind judgements about the gazer (Study 3). Participants viewed the (same) positive, negative and neutral sentences, and then saw direct and averted gaze face pictures of each person. They then made affective theory of mind judgements about how the protagonist was feeling, allowing me to examine whether eye-gaze direction would impact their judgments. Previous studies have noted that eye-gaze processing occurs in brain areas implicated in theory of mind, and eye-gaze behaviour acts to regulate the gazer's mood. In particular, previous work suggests that individuals make more eye-contact when feeling more positive, so I predicted that direct gazers would be interpreted as feeling more positive than averted gazers.

In each study, event-related potentials were time-locked to the onset of each face to investigate whether direct and averted gaze perception had differential impacts on neural processing associated with each task, and the time course of these cognitive processes. In particular, my focus was on the face-sensitive N170, and the aforementioned ERP markers sensitive to emotional processing, namely the N100, N200, EPN, P300 and LPP. As each study involved emotional tasks, I predicted that these ERPs would be sensitive to task differences in

Study 1, and the valence of sentence contexts in Studies 2 and 3. All ERP data were analysed using the recently developed mass univariate ERP technique, as described below.

1.6 The Mass Univariate Event Related Potential Analysis Technique

Electroencephalography (EEG) generates massive data sets, as it collects measures of neural activity across many electrodes at numerous time-points. The large scale of these data sets means that if enough analyses are run, there is a large chance of finding a significant effect, even if it is due to random noise (Luck & Gaspellin, 2017). Unfortunately we are becoming increasingly aware that some traditional methods for analyzing ERP data amplify the likelihood of these type I errors. One practice that is commonly used and particularly problematic involves the visual examination of ERP averages at the group level before committing to a method of analyzing data. For example, a researcher may notice that there appears to be a significant difference between conditions of interest over posterior sites during a specific time-window, and so may choose to focus their analyses there. The problem with this practice is that the researcher is essentially performing their own implicit comparisons, which are not corrected for (Luck & Gaspellin, 2017). It is quite likely that type I error due to these practices has contributed to inconsistencies in the ERP literature on eye-gaze processing, and other fields, like investigations of empathy (see Coll, 2018 for a review). One solution is to develop specific *a priori* hypotheses and plans for analysis before ever looking at the waveforms. For example, a researcher may focus on ERP components previously shown to be impacted by emotional processing if they are investigating performance in an emotional task. However, this approach has the unfortunate side effect of increasing type II errors, as it prevents the discovery of real, but unpredicted effects.

One main goal of this thesis was to analyze all ERP data using a novel mass univariate approach, as it has been found to be much more robust against both type I and type II errors (Fields & Kuperberg, 2018; Groppe et al., 2011; Luck & Gaspelin, 2017; Pernet, et al., 2011; 2015). The term "mass univariate" describes performing a separate hypothesis test on each electrode and time-point of interest, instead of the traditional practice of performing one analysis of variance on amplitudes averaged across time-points and electrodes. While this involves a large number of statistical comparisons, corrections are applied for the number of comparisons run, allowing a researcher to have careful control of the familywise error rate. Alongside hypothesis testing, an exploratory analysis can also be run on all electrodes and time-points recorded to allow for the discovery of unpredicted effects (Groppe et al., 2011). This can reduce type II error, with the caveat that this analysis will have low power following multiple comparison correction (due to the large number of comparisons made).

The correction technique used in the present studies is the Permutation Based Cluster Mass technique (Groppe et al., 2011; Maris & Oostenveld, 2007), which was adapted for ERP research from functional magnetic resonance imaging studies. This technique operates on the principle that true ERP effects will cluster across multiple adjacent electrodes and time-points, while noise is more likely to occur in smaller time-periods and across fewer electrodes (Groppe et al., 2011; Maris & Oostenveld, 2007). First, a distribution of *F*-values is generated across all analysed time-points and electrodes. Then, data points that are spatially and temporally adjacent and that exceed a statistical threshold for inclusion are considered a cluster. If a cluster forms, all *F*-values in the cluster are summed and compared to a null distribution, estimated by performing the same tests on many permutations of the data created by randomly assigning trials to conditions. The more permutations run, the better the estimate is of a true null distribution. Here, the recommended number of 100,000 permutations (Fields, 2017) was used in each study.

Chapter 2: Eye-gaze processing during discrimination of facial emotion, direction of attention, and gender[1]

2.1 Introduction

There is much support for the idea that key differences exist between our response to direct and averted gaze (Conty et al., 2016; George & Conty, 2008; Itier & Batty, 2009; Kampe, et al., 2003). While averted gaze typically signals attention towards the gazed-at object, direct gaze signals attention towards the observer and has been more heavily implicated in emotional processing (see Section 1.1.2; Hamilton, 2016 & Hietanen, 2018 for reviews).

Accumulating evidence from neuroimaging and event-related potential (ERP) studies suggests that direct and averted eye-gaze are also processed differently in the brain (for reviews, see George & Conty, 2008; Grosbras et al., 2005; Itier & Batty, 2009; Numenmaa & Calder, 2009). However, as reviewed earlier (see Section 1.3.1), inconsistencies have been noted. Across studies, the same brain areas (e.g. the superior temporal sulcus or orbitofrontal cortex) have shown increased activation for direct gaze relative to averted gaze or the exact opposite, and some have simply found no gaze difference at all. Similar inconsistencies have been found in the Event Related Potential (ERP) literature (see Section 1.3.2), with eye-gaze effects of varying direction being reported post-face presentation as early as 100-140ms (Burra et al., 2018; Schmitz et al., 2012), during the N170 time-window (Burra et al., 2017; Conty et al., 2007; Itier et al., 2007; Latinus et al., 2015; Pönkänen et al., 2010; Puce et al., 2000; Rossi et al., 2015 Watanabe et al., 2002; 2006), or after the N170, between 250-350ms (Schweinberger et al., 2007) or 300-600ms (Conty et al., 2007; Burra et al., 2018; Itier et al., 2007), coinciding with EPN and P3-like components.

One likely contributor to these inconsistencies is the type of experimental paradigm used. Given that direct and averted gaze can be interpreted differently in different social circumstances (Hamilton, 2016), it is likely that these gaze cues are processed differently depending on the task participants are asked to complete. Common tasks given to participants while they are shown direct and averted gaze images include oddball tasks (i.e. responding to an infrequent stimulus presented among frequent other stimuli; e.g. Burra et al., 2018; Rossi et al., 2015) and passive

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[1] A version of this chapter is published in *Frontiers in Neuroscience*, in a special issue on eye-gaze processing (McCrackin & Itier, 2019c).

viewing tasks (George et al., 2001; Puce et al., 2000; Pönkänen et al., 2010; Taylor et al., 2001; Watanabe et al., 2002; 2006), as well as tasks requiring the discrimination of gender (Burra et al., 2018), gaze direction (Conty et al., 2007; Hoffman & Haxby, 2000; Hooker et al., 2003; Itier et al. 2007; Latinus et al. 2015; Schweinberger et al., 2007), emotional expression (Akechi et al., 2010), identity (Hoffman & Haxby, 2000) or head orientation (Itier et al., 2007). While both the ERP and the neuroimaging literatures have begun to explore how eye-gaze processing differs based on what participants are asked to do (Burra et al., 2018; Hoffman & Haxby, 2000; Hooker et al., 2003; Latinus et al., 2015), few studies have employed direct task comparisons within the same participants. Within-subject designs are, however, more powerful statistically than between-subject designs and are necessary to draw conclusions regarding possible task effects on the neural processing of direct versus averted gaze.

As far as we know, the limited number of within-subject ERP studies that have directly compared tasks have focused on the processing of facial expressions of emotion, using Gender Discrimination (GD) and Emotion Discrimination (ED) judgements. The stimuli used were eye-region stimuli (Sabbagh et al., 2004) or faces (Itier & Neath-Tavares, 2017; Rellecke et al., 2012; Wronka & Wallentowska, 2011), but always with direct gaze. One exception includes the comparison of an ED task to judgements of looking direction and of object choice based on averted gaze faces only (Cao et al., 2012). These studies suggest that ED and GD tasks differentiate mainly after the N170 component. While Rellecke et al. (2012) and Wronka and Wallentowska (2011) found no ERP difference between the two tasks, Sabbagh et al. (2004) found that the ED task resulted in more negative ERPs than the GD task over inferior frontal and anterior temporal sites from 270-400ms. The ED task also resulted in more positive ERPs than the GD task from 300-500ms over posterior central and parietal sites (Sabbagh et al., 2004), a similar finding to Itier and Neath-Tavares (2017)'s report of more positive ERPs elicited by the GD task than the ED task over posterior sites from 200-350ms (the latest tested time-window).

The present study examines the time-course of direct and averted gaze perception within three different discrimination tasks that have been commonly used in the gaze processing literature. Using the exact same stimuli for each task, i.e. male and female faces expressing anger or joy and with direct or averted eye-gaze, participants indicated whether the face expressed anger or joy (ED task), whether the face was male or female (GD task) and whether the face was attending to them or away from them (Attention Discrimination – AD task). Importantly, explicit processing of gaze direction was required by the AD task while gaze was irrelevant to the GD and ED tasks. ERPs time-locked to the presentation of the face stimuli were used to track the time-course of when gaze and task processing were occurring and interacting. If direct and averted gaze differentially impacted these three cognitive processes, we expected to see dissociations at the neural level, in spatial location (different electrodes) and/or in the time course of the interaction, as well as at the behavioural level.

We used the recently-developed mass-univariate technique (Fields & Kuperberg, 2018; Groppe et al., 2011; Luck & Gaspelin, 2017; Pernet, et al., 2011; 2015) to analyse the ERP data. We first performed an exploratory analysis over all electrodes and time-points. Then we analyzed occipitotemporal sites from 130-200ms to capture the N170, given the mixed findings reported on this component. We also analysed frontal sites between 200-400ms, as the findings from the gaze and ERP literature on different tasks suggested that we might pick up a gaze and task interaction over these sites, after both gaze (e.g. Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015; Watanabe et al., 2002) and ED and GD task differences (Sabbagh, et al., 2004) are processed. Finally, we analysed posterior sites from 200-500ms and parieto-occipital sites from 300-500ms, as gaze effects are traditionally picked up over parieto-occipital sites (Itier & Batty, 2009), and posterior central and parietal sites have been shown to discriminate between ED and GD tasks from 200-500ms (Cao et al., 2012; Sabbagh et al., 2004; Itier & Neath-Tavares, 2017).

2.2 Methods

2.2.1 Participants

Thirty-six [36] undergraduate students from the University of Waterloo (UW) participated in the study and received course credit upon completion. All were 18-29 years old and had normal or corrected-to-normal vision. All participants had lived in Canada or the United States for the past five years or more. They reported no history of neurological or psychiatric illness and no drug use (psychiatric or otherwise). All participants rated themselves at least a 7 out of 10 on Likert-type scales when describing their ability to recognize people and emotional expressions (from 0 -extremely poor- to 10 -extremely good). In total, ten participants were excluded before analysis due to technical issues during recording (*N* = 2), problems with eye-tracking calibration (*N*=2), poor response accuracy (i.e. less than 80%; *N* = 2), or EEG data that had less than 50 trials per condition after cleaning (*N*=4). This left a final sample of 26 participants (17 females, 9 males; *mean age* = 19.67, *SD* = 1.69) for analysis. Participant ethnicity varied (Caucasian: *n*=17, Chinese *n*=5, African: *n*=1, Korean: *n*=1, Middle Eastern: *n*=1, and Other Not Listed: *n*=1). The study received ethics clearance from the UW Research Ethics Board and all participants gave written informed consent in accordance with the Declaration of Helsinki.

2.2.2 Face Stimuli

Five male and five female Caucasian identities were selected from the Radboud database (Langner et al., 2010)[2]. Each individual displayed an angry expression and a happy expression with direct gaze, averted left gaze and averted right gaze (Figure 1). All gaze deviations were of equal magnitude. The images were cropped with the GNU Image Manipulation Program (GIMP 2.8) so that only the individual's upper shoulders, head and neck were visible. All images were then mirrored to control for any asymmetry between the left and right image halves by creating a second set of images (e.g. an angry averted right image mirrored became a new angry averted left image). Images were equated on mean pixel intensity (*M* = 0.56, *SD* = 0.0003) and root mean square (RMS) contrast (*M* = 0.48, SD = 0.0002) with the SHINE package (Willenbockel et al., 2010). Custom Matlab scripts were then used to add the colour information back into each image for added realism.

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[2] Identities 10, 15, 19, 30, 31, 32, 33, 37 were used in the study blocks, while identities 7 and 14 were used in the practice block.

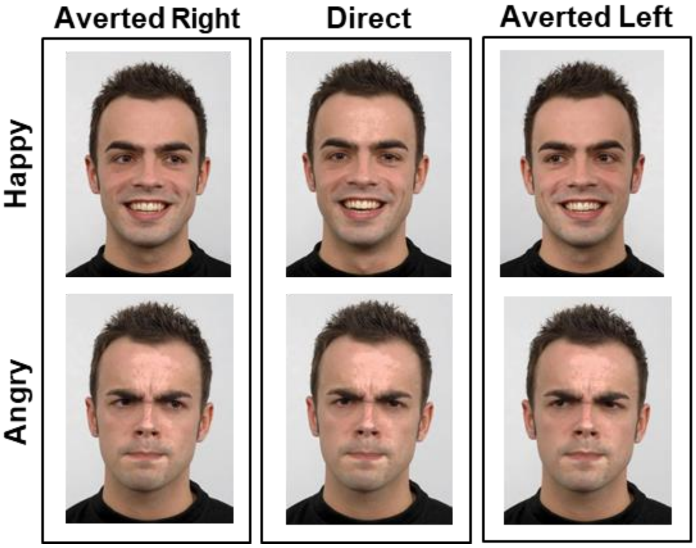

Figure 1. Sample Study 1 face stimuli

Sample images of one individual with happy and angry expressions displaying direct, averted left and averted right gaze.

2.2.3 Experimental Design

Participants first provided informed consent, and then filled out a demographic questionnaire. They were fitted with an EEG cap and led to a sound-attenuated faraday cage with dim lighting for the experiment, which was presented on a CRT monitor with a refresh rate of 85Hz and a resolution of 1280x960. A chinrest helped participants keep their heads still at a distance of 65cm away from the monitor. Participants' dominant eyes were determined using the Miles test (Miles, 1930) and then tracked at a 1000Hz sampling rate with an Eyelink 1000 eye-tracker, which was recalibrated whenever necessary.

Participants were told that they would see pictures of individuals and complete three tasks, and that a prompt at the beginning of each trial would let them know which task to perform for that trial. The first task required identifying the emotional expression (Emotion Discrimination Task, hereafter ED task; prompted by the words "Happy/Angry"). The second task required indicating whether the person was directing their attention at them (the participant) or away from them (Attention Discrimination task, hereafter AD task; prompted by "At Me/Away" words). The third task required indicating whether the person was male or female (Gender

Discrimination task, hereafter GD task; prompted by “Male/Female” words). Participants were asked to indicate their answer when prompted using the left and right arrow keys.

Figure 2 depicts a typical trial progression. At the trial start, the task prompt appeared, notifying the participant of the task and visually reminding them (with arrows) which answers corresponded to the left and right arrow keys. Task type was randomized and there were an equal number of trials for each task presented in each block. The response mapping for the arrow keys was counterbalanced between participants (i.e. half pressed the right arrow key for “angry”, and half pressed the left arrow key; half pressed the right arrow key for direct gaze and half pressed the left arrow key; half pressed the right arrow key for male and half pressed the left arrow key). Participants were instructed to press the space bar when they had read the prompt, and this key press triggered the appearance of a white screen with a fixation cross (18.43° down on the horizontal midline). Participants were asked to fixate on the cross for a minimum of 300ms within a 1.92^o x 1.92^o margin to advance the trial to the face screen. This ensured that participants were fixated between the nasion and the nose when the face appeared. If ten seconds elapsed without this requirement being met, a drift correction occurred, cancelling the trial. If the requirement was met, the trial advanced by presenting the face image (subtending 10.64° horizontally and 15.08° vertically) on a white background for 500ms. There were an equal number of direct and averted gaze faces, with half of the averted gaze trials consisting of faces looking to the left and half to the right (all averted gaze trials were grouped together for analysis). Face identity was randomized, and each was presented an equal number of times within each block and within each condition. The face was followed by a 300ms blank screen after which participants were prompted to indicate their answer by pressing the left or right arrow key. This procedure ensured that the neural activity until 800ms post face onset would not be contaminated by motor preparation and motor artefacts. However, in doing so, the response times collected were not clearly interpretable and are not further discussed.

SR Research’s Experiment Builder 1.10.1385 was used to program and run the experiment. Participants completed a minimum of four practice trials to ensure they were comfortable with the tasks before starting the study blocks. In total, there were 8 blocks of 96 trials each. There were six within-subject conditions, corresponding to the face’s gaze direction (direct or averted) in each of the three tasks performed (ED, AD and GD), with facial expression trials collapsed. Thus, across the experiment, there were a total of 128 trials per each of the 6 conditions.

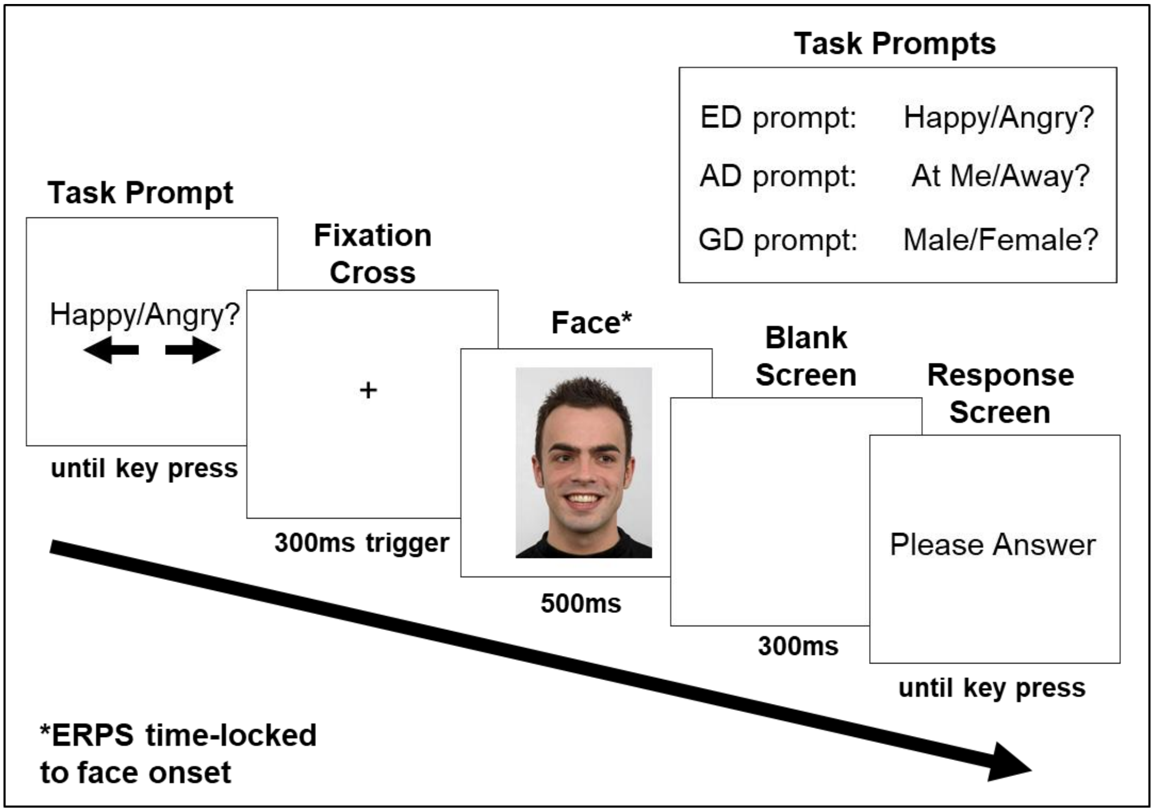

Figure 2. Sample Study 1 trial progression

Sample trial with an averted gaze trial in the ED task. ERPs were recorded to the onset of the face stimulus. The three task prompts are shown in the top right corner.

2.2.4 EEG Recording

EEG data were recorded with the Active-two Biosemi EEG system at a sampling rate of 512Hz, time-locked to the presentation of the face stimulus. Electrode offset was kept within a ±20 mV range. There were 66 electrodes on the custom-made caps under the 10/20 system, the 64 classic locations plus PO9 and PO10 electrodes added for increased posterior coverage. In addition, one electrode was placed over each mastoid, infra-orbital ridge, and the outer canthus of each eye, for a total of 72 recording electrodes. These ensured that blinks and large lateral eye-movements (saccades) would be clearly detected with visual inspection of the data later on. A Common Mode Sense (CMS) active-electrode and a Driven Right Leg (DRL) passive-electrode were used as the ground[3].

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[3] The Biosemi Active-Two system does not use an actual recording reference site.

2.2.5 Data Preprocessing and Cleaning

To ensure that participants read the task prompt on each trial, we used the eye-tracking data to exclude trials where participants did not fixate at least twice on the prompt screen within a rectangular region of interest (ROI) spanning the text (subtending 32.71^{o} horizontally and 3.72^{o} vertically, positioned $17.43\ ^{o}$ down and centered horizontally). This resulted in excluding an average of only 0.81 trials per participant (*SD* = 1.04). We also excluded trials in which participants did not fixate the spot encompassing the eyes, and nasion (a circular 5.50^{o} ROI) that was cued by the fixation cross for at least the first 250ms of face presentation. As the N170, the earliest face sensitive ERP component, can be modulated by what part of the face is fixated (de Lissa et al., 2014; Itier & Preston, 2018; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014; Parkington & Itier, 2018), this step ensured that fixation location would not play a role in any N170 modulation and that participants were encoding the gaze direction for each face. This resulted in excluding an average of 3.23 trials per participant (*SD* = 4.98). Next, trials with incorrect responses were removed (an average of 4.72 trials/participant, *SD* = 2.09).

EEG data were processed using the EEGLab (version 13.6.5b; Derlome & Makeig, 2004) and ERPLab (version 5.1.1.0; http://erpinfo.org/erplab) toolboxes in Matlab 2014b. An average reference was computed offline and data were band-pass filtered (0.01-30Hz) and then cleaned. Trials were epoched from a -100ms baseline (before the face) to 800ms post-face. First, trials were removed if they exceeded ±70µV on any non-frontal and non-ocular channels (i.e. excluding: Fp1, Fpz, Fp2, AF3, AFz, AF4, AF8, AF7, IO1, IO2, LO1, and LO2), which removed most trials with muscle or movement artifacts. Any of these channels that were consistently noisy were removed for later interpolation. Then, data were visually inspected for eye-blinks and saccades, which were detected most strongly on the electrodes positioned under and beside the eyes. For cases where there were few eye artifacts, the data were manually cleaned, and any removed electrodes were added back in and interpolated with EEGlab's spherical splines tool. For cases where there were many eye-artifacts, Independent Component Analysis (ICA; using the EEGLab "runica" function) was used to remove saccades and eye-blinks before adding back and interpolating electrodes. The number of ICA components generated matched the number of channels. An average of .93 (*SD* = 1.62) components were removed per participant. Remaining noisy trials were then manually removed when necessary, including any trials in which artifacts from muscle movement occurred. An average of 97.29 trials/condition (*SD*=22.34) were included in the final ERP waveforms.

2.2.6 Behavioural Data Analysis

Correct answers for each condition were those in which the participant pressed the arrow key corresponding to the correct gender (GD task), emotional expression (ED task) or gaze direction (AD task). An ANOVA with the within-subjects factors of gaze direction (2; direct gaze, averted gaze) and task (3; GD, ED, AD) was run on participants' average accuracy using SPSS 25. Greenhouse-Geisser corrected degrees of freedom were reported when Mauchly's Test of sphericity was significant. The follow up t-tests for the gaze and task interactions were planned based on the theoretical motivation behind this paper. However, for transparency, the raw *p*-values for all follow-up paired t-tests are reported, such that those with $p<.05$ would be considered significant with Fischer's LSD test, and those with $p<.016$ would be considered significant after Bonferroni-correction (0.05/3 comparisons).

2.2.7 EEG Data Analysis

EEG data were analyzed using the Factorial Mass Univariate Toolbox (FMUT) extension (Fields, 2017) for the Mass Univariate Toolbox (MUT; Groppe et al., 2011). FMUT uses robust statistics to test each time-point included in the time-window of interest for the selected electrodes, and then control for the familywise error rate. Each ANOVA was corrected for multiple comparisons with the Permutation Based Cluster Mass technique (Maris & Oostenveld, 2007; Groppe et al., 2011). With this technique, data points that are spatially and temporally adjacent and that exceed the threshold for inclusion are considered a cluster. All *F*-values in the cluster are then summed, and compared to a null distribution for cluster mass significance estimated with permutations. We used the recommended number of 100,000 permutations and alpha of 0.05, such that clusters exceeding the 1 - α percentile of the resulting distribution were considered significant. As discussed by Groppe et al. (2011) and Marie & Oostenveld (2007), true ERP effects are more likely than noise to occur across multiple adjacent electrodes and time-points, and thus ERP effects will typically stand out more clearly from noise using cluster-based statistics.

One exploratory ANOVA with the within-subjects factors of gaze direction (2; direct gaze, averted gaze) and task (3; GD, ED and AD) was run over all electrodes and relevant time-points (50-800ms) post-face to allow for the discovery of unpredicted effects. Based on the main effect of task that we observed in this analysis, three follow-up ANOVAs were performed to compare the activations associated with each task (the use of ANOVAs instead of t-tests as follow-up tests is recommended for the Permutation Based Cluster Mass technique; Fields, 2017). We performed these follow up ANOVAs over the time-points (400-800ms) and electrodes that were significant in the omnibus ANOVA with an alpha level set to 0.016 to correct for the three comparisons. As in the original ANOVA, 100,000 permutations were calculated.

For our hypothesis driven analyses, one ANOVA with the within-subjects factors of gaze direction (2; direct gaze, averted gaze) and task (3; GD, ED and AD) was run over i) a posterior cluster (P9, P10, PO9. PO10, P7, P8) between 130-200ms encompassing the N170 component, ii) a frontal electrode cluster (Fp1, Fp2, Fpz, AF3, AF4, AFz, F4, F3, F1, F2, Fz) from 200-400ms, and iii) parieto-occipital electrodes (Pz, POz, PO4, PO3, P1, P2, Oz, O1, O2) from 200-500ms. Based on the gaze direction by task interaction that we observed in the omnibus ANOVA at frontal sites during 200-400ms, three follow-up ANOVAs were performed with FMUT to compare the activations associated with direct and averted gaze in each of the three tasks. Again, we performed these follow up ANOVAs over the sites and time-points (220-290ms) that were significant in the omnibus ANOVA with an alpha level set to 0.016.

2.3 Results

The behavioural results and the FMUT results files analysed in the present study are available in the Open Science Framework Repository at (https://osf.io/am4zv/?view_only=eac91ae8a07e44f7ab5aca550fc19da2).

2.3.1 Behavioural Results

2.3.1.1 Participant Accuracy

There was a main effect of task on response accuracy[4], *F*(2,50) = 31.98, *MSE*=30.16, *p* <.001, ηp^2=.56 (Figure 3), driven by greater accuracy in the GD than both the ED task (*t*(25) =

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[4] For the interested reader, the RT time-locked to the onset of the answer prompt displayed a similar pattern as the accuracy data: the main effect of task (*F*(1.40,34.96) = 13.14, *MSE* = 13908.60, *p* < .001, ηp^2 = .34) was driven by

3.71, *SE* = .83, *p*=.001) and the AD task (*t*(25) = 7.61, *SE* = 1.12, *p*<.001), and by greater accuracy in the ED task than in the AD task (*t*(25) = 4.37, *SE* = 1.24, *p*<.001).

Although there was no main effect of gaze, *F*(1,25) = 2.82, *MSE*=12.78, *p* = .11, ηp^2=.11, there was a strong interaction between gaze direction and task, *F*(1.37, 34.16)= 12.10, *MSE*= 18.70, *p*< .001, ηp^2 = .33 (Figure 3). Planned paired comparisons comparing gaze conditions for each task revealed that participants were more accurate during the AD task in the averted gaze condition than in the direct gaze condition (*t*(25) = 3.18, *SE* = 1.77, *p*=.004). In contrast, during the ED task, participants were more accurate in the direct gaze condition than in the averted gaze condition (*t*(25) = -3.51, *SE* = .67, *p* =.002). Finally, there was no accuracy difference between the two gaze conditions for the GD task (*t*(25) = -.81, *SE* = .52, *p* = .42).

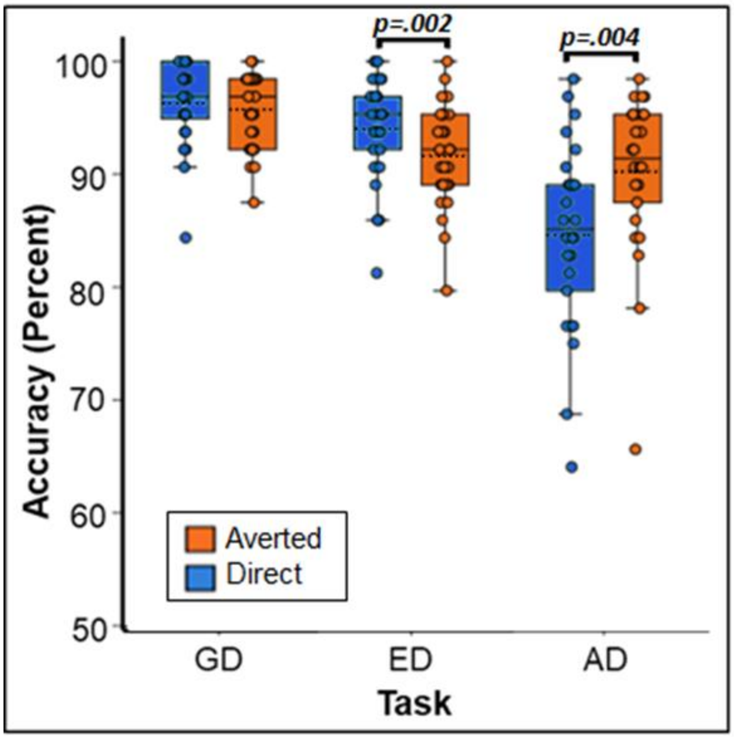

Figure 3. Gaze effects on task accuracy during the three tasks

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faster responses during the GD than both the ED (*t*(25) = -4.24, *SE* = 11.52, *p* <.001) and AD (*t*(25) =-4.29, *SE* = 23.09, *p* <.001) tasks, as well as faster responses during the ED than the AD task (*t*(25) = -2.35, *SE* = 21.36, *p* = .027). There was no main effect of gaze (*F*=1.02, *p*=.32), though there was a significant interaction between task and gaze (*F*(2,50) = 6.17, *MSE*=3568.78, *p* =.004, ηp^2=.20). RTs were faster for the averted gaze than the direct gaze condition during the AD task (*t*(25) = -2.72, *SE* = 17.96, *p*=.012). The opposite pattern, though not significant, was observed in the ED task, with faster RTs during the direct gaze than the averted gaze condition (*t*(25) = 1.80, *SE* = 14.57, *p*=.084). There was no RT difference between gaze conditions for the GD task (*t*(25) = .024, *SE* = 9.94, *p*=.98).

Data points represent the accuracy for individual participants. Boxes encompass data points between the 25th and 75th percentiles, and within each box the mean (dotted horizontal line) and median (solid horizontal line) are indicated. The threshold for significance with Bonferroni correction is $p<.016$.

2.3.2 EEG results

2.3.2.1 Exploratory Analysis Over All Electrodes (50-800ms)

The exploratory analysis over all electrodes and time-points (excluding the first 50ms post-face; between 50-800ms) revealed a widespread main effect of task (Figure 4a; two significant clusters; *ps*=.019 and .000020). It was most pronounced from 400-800ms over posterior and fronto-central sites. Follow up comparisons indicated that this effect was driven by differences between the GD and ED tasks (Figure 4b; $p=.00046$), the GD and AD tasks (Figure 4c; two clusters; *ps*=.0065 and .000020), and the ED and AD tasks (Figure 4d; $p=.000020$). Over posterior sites, ERP amplitudes were most negative in the AD task, intermediate in the ED task, and most positive in the GD task (Figure 4e, P10). The opposite pattern was found over fronto-central sites (Figure 4e, CP1). There was no task by gaze direction interaction ($p=.55$), nor a main effect of gaze direction ($p=.40$).

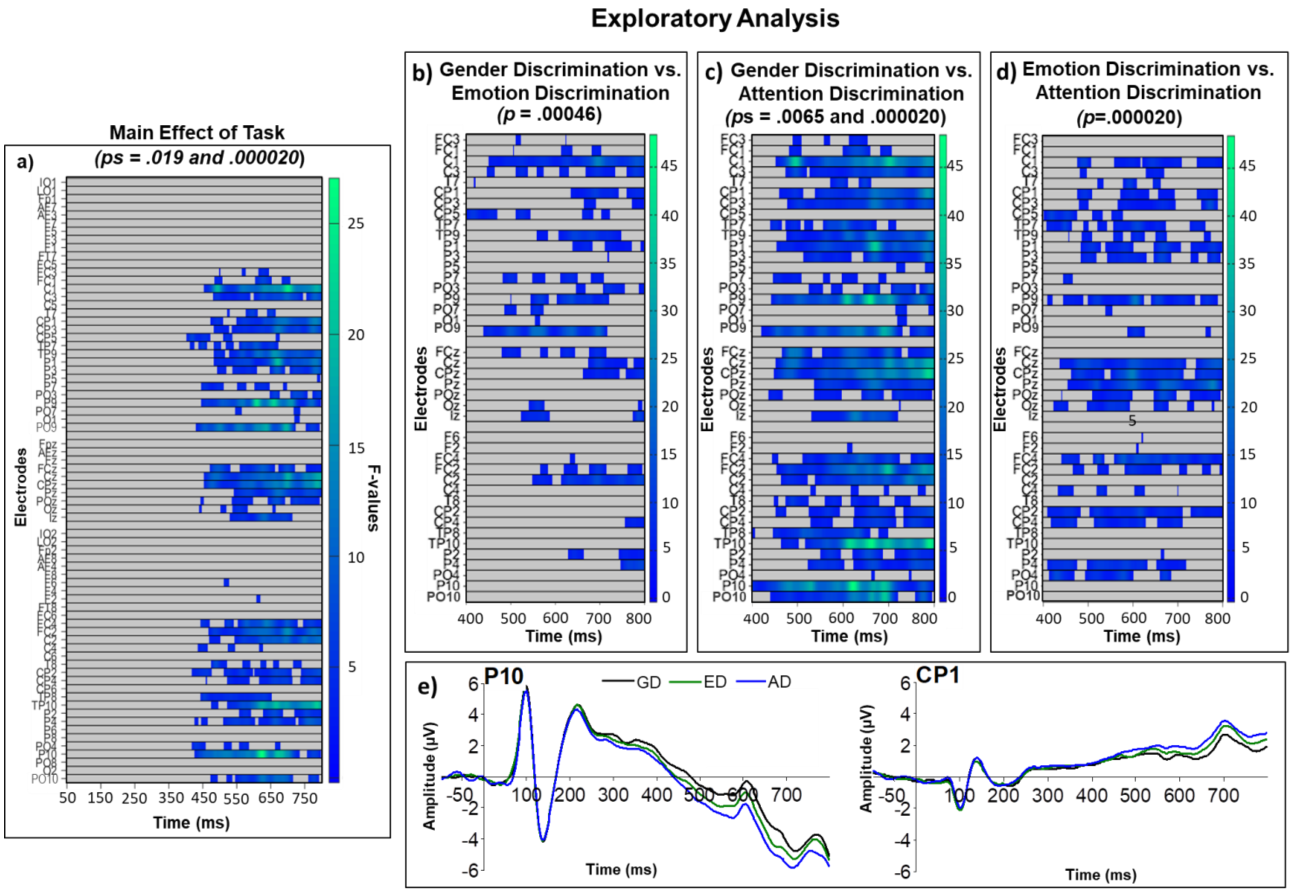

Figure 4. Exploratory analysis task effect

a) Task effect in the exploratory analysis. Panels depict significant F-values corrected with a Permutation Based Cluster Mass technique at $p<.05$. Electrodes are plotted on the y-axes and time points following face presentation are plotted along the x-axis. The colour of the "blocks" in these panels corresponds to the magnitude of significance as indicated by the right-hand colour bar. Comparisons of the **b)** gender and emotion discrimination tasks **c)** gender and attention discrimination tasks and **d)** emotion and attention discrimination tasks. These post-hoc analyses were run on the 400-800ms time widow during which the task effect was significant in the omnibus ANOVA with a corrected significance value of $p<.016$. **e)** Mean ERP amplitudes for each task are shown on representative posterior (P10) and central (CP1) electrodes.

2.3.2.2 Posterior Sites During the N170 Time-window (130-200ms)

The N170 ANOVA over posterior sites from 130-200ms did not reveal any significant effects of gaze direction (*p*=.094), task (*p*=.33), nor an interaction between the two (*p*=.39).

2.3.2.3 Frontocentral Sites (200-400ms)

The omnibus ANOVA over frontal sites from 200-400ms revealed an interaction between gaze direction and task on ERP amplitudes (Figure 5a; *p*=.031), but no main effect of gaze direction (*p*=.053) or task (*p*=.88). While caution must be taken when making inferences about effect latency or location with cluster-based permutation tests (Sassenhagen & Draschkow, 2019), in this latency range the interaction was most pronounced from approximately 220-290ms over electrodes F3, F1, AFz and FPz. Our follow-up comparisons during that time window (with *p*<.016) of how direct and averted gaze are processed in each task revealed that in the ED task direct gaze produced more positive ERP amplitudes than averted gaze (Figure 5b *p*=.015). In contrast, the opposite pattern was seen in the GD task, with more positive ERP amplitudes for averted gaze than direct gaze (Figure 5c, *p*=.0057). Finally, there was no detectable effect of gaze direction in the AD task (Figure 5d, *p*=.10).

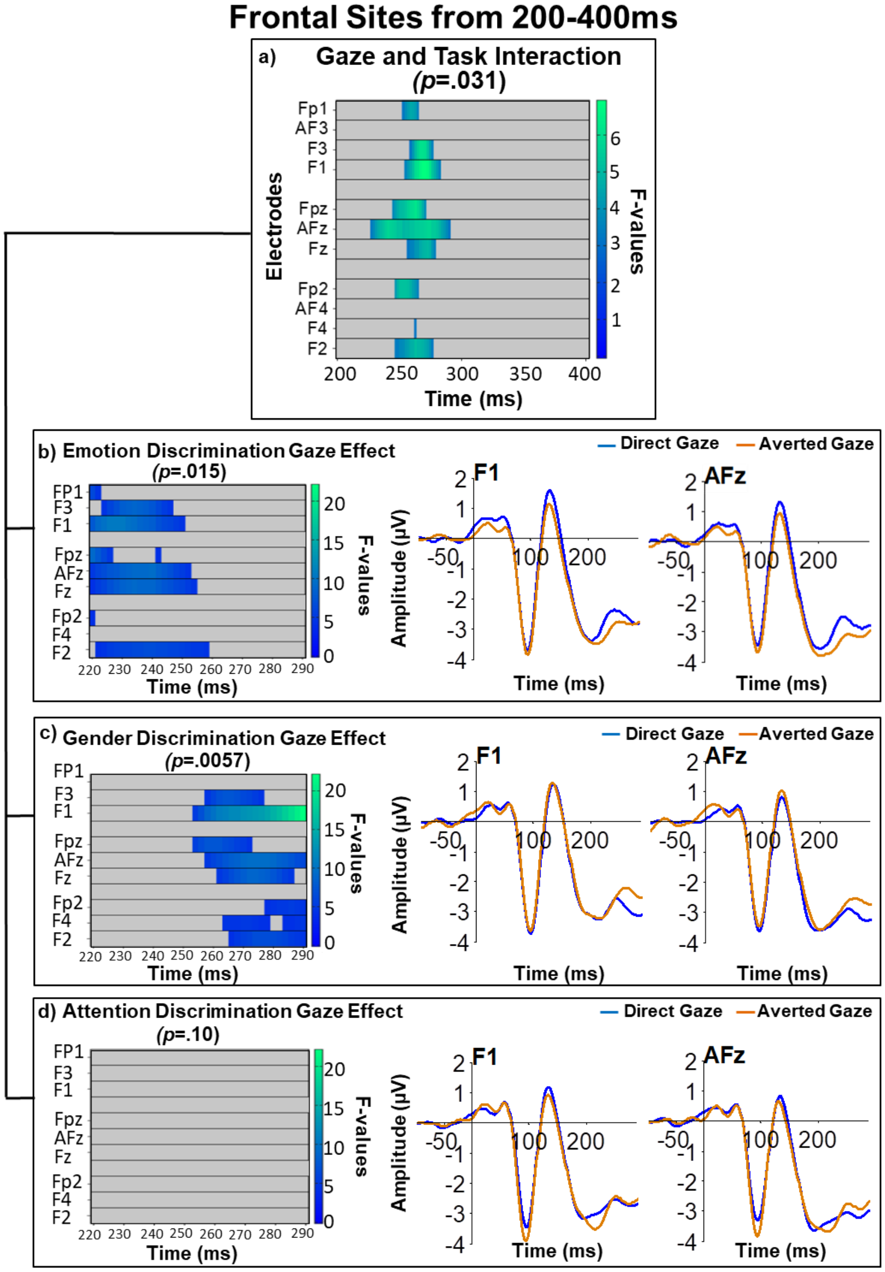

Figure 5. Frontal interaction between gaze and task

a) The interaction between task and gaze over frontal sites between 200-400ms, corrected for multiple comparisons with the Permutation Based Cluster Mass technique. The electrodes included in each analysis are plotted on the y-axes, while the x-axis represents time (post face onset). Coloured "blocks" represent significant *F* values, with the magnitude of the *F* value plotted according to the right-hand colour bar. A comparison of direct and averted gaze over frontal sites is shown for the **b)** emotion discrimination **c)** gender discrimination and **d)** attention discrimination tasks. These post-hoc analyses were run at $p<.016$ on the 220-290ms time widow that was significant in the omnibus interaction. The difference between the two gaze conditions in each task is shown on representative electrodes F1 and AFz.

2.3.2.4 Parieto-occipital Sites (200-500ms)

There were no significant effects of task (*p*=.42), gaze direction (*p*=.27), or an interaction (*p*=.48) over parieto-occipital sites from 200-500ms.

2.4 Discussion

The importance of eye-gaze processing during social interactions is undisputed (Emery, 2000; George & Conty, 2008; Itier & Batty, 2009; Kleinke, 1986 for reviews) and the clinical significance of altered eye-gaze processing in disorders such as Autism Spectrum Disorder (Madipakkam et al., 2017; Pelphrey et al., 2002; Senju & Johnson, 2009a) and Social Anxiety Disorder (Schneier et al., 2011) has led to a field of research devoted to understanding how direct and averted gaze are processed in the brain.

While there has been much interest in examining the neural correlates of eye-gaze processing, there does not seem to be a consensus about where and when direct and averted gaze are differentiated in the brain. One of the likely reasons for this lack of consensus is that the experimental tasks in studies of gaze processing vary quite substantially (Burra et al., 2018; Carrick et al., 2007; Hoffman & Haxby, 2000; Hooker et al., 2003; Latinus et al., 2015). Direct and averted gaze are used to make many types of inferences about the gazer and can be interpreted differently in different social circumstances (Hamilton, 2016). It seems probable, then, that these gaze cues are processed differently depending on the type of task participants are asked to complete. To this end, we examined how viewing individuals with direct and averted gaze would affect performance during three different tasks commonly used in the field, in a within-subjects design. These tasks have been previously used to study gaze processing in separate samples (one task at a time) and included an Emotion Discrimination (ED) task, where participants discriminated between two facial expressions, an Attention Discrimination (AD) task that required participants to infer the direction of the individual’s attention based on gaze cues, and a Gender Discrimination (GD) task. We found that direct and averted gaze elicited different behavioural effects depending on the task that participants were performing (Fig.3). Direct gaze was associated with better accuracy than averted gaze during the ED task, while averted gaze was associated with better accuracy in the AD task. However, there was no significant effect of gaze direction on performance in the GD task.

Although we believe our behavioural interactions between gaze and task reflect interactions between gaze processing and AD and ED task demands, other potential explanations should be noted. First, previous literature has reported that direct gaze has a facilitatory effect on a myriad of tasks including capturing attention (Yokoyama et al., 2014), facilitating recognition memory (Vuilleumier et al., 2005) and gender discrimination (Burra et al., 2018; Macrae et al., 2002; but see Vuilleumier et al., 2005). While it is possible that a general facilitatory effect of direct gaze may explain our behavioural findings in the ED task, we do not believe this is the case because no significant effect of gaze direction was found in the GD task. This would suggest that the facilitatory effect of direct gaze during the ED task was above any standard facilitation effect. Furthermore, the AD task was associated with worse performance for direct gaze, which goes against this explanation. It is important to highlight that all previous studies reporting facilitated effects for direct gaze studied only one task at a time, in contrast to the present within-subject design which directly compared three tasks in the same individuals.

A similar argument could be made regarding the possibility of gaze cuing effects influencing the results. Given that the gaze cuing literature suggests that spontaneous attention shifts occur towards gazed-at locations even when gaze direction is task irrelevant (Driver et al., 1999; Friesen & Kingstone, 1998), one could argue that averted gaze may have oriented participants’ attention away from the stimuli during the tasks. However, there is no reason why this potential attention shift should have affected tasks differently, and because there was no effect of gaze direction on accuracy in the GD task, and opposite effects of gaze direction in the ED and AD tasks, it is unlikely that covert attention shifts in the direction of averted gaze could explain the pattern of results.

It must be noted that others have reported that direct gaze is associated with improved ED. Adams and Kleck (2003, 3005) and Sander et al. (2007) also found that angry and happy facial expressions (as used in the present study) were perceived more easily when paired with direct gaze than with averted gaze. However, they also found that fear and sadness were perceived more easily when paired with *averted* gaze than with direct gaze. Adams and Kleck (2003) proposed that direct gaze enhances the perception of facial expressions signaling behavioural approach from the gazer (e.g. angry and happy expressions), while averted gaze enhances the perception of facial expressions signaling behavioural avoidance (e.g. sadness and fear) due to a “shared signal” between gaze and emotion expression decoding. Although the support for the shared signal hypothesis was largely found to be tied to the specific stimuli used (Bindemann et al., 2008; Graham & Labar, 2007), it is still possible that gaze direction may facilitate or impair ED differently depending on the emotional expression on the face. Replication of the present findings and extension to more facial expressions is needed to examine this possibility further.

There is also another potential explanation for our behavioural gaze effects, which concerns the inherently self-referential nature of direct gaze (see Section 1.1.1; Conty et al., 2016). Direct gaze signals to us that we are the subject of someone's attention (Conty et al., 2016; Itier & Batty, 2009; George & Conty, 2008), and has been shown to produce similar fMRI brain activation as hearing one's name being called (Kampe et al., 2003). Gaze processing has also been shown to interact with the self-relevance of contextual sentences at the ERP level (McCrackin & Itier, 2018a). In the attention discrimination task, participants indicated whether the individuals were directing their attention at them or away from them. This may have primed self-referential processing, which could have impacted how direct gaze was processed. However, if this was the case, one would expect participants to be more accurate at responding to direct gaze faces in the AD task, while the opposite was observed.

We also found that gaze processing interacted with task at the ERP level, although the pattern of results did not map directly onto the pattern of behavioural results. Gaze processing differed between the three tasks from 200-400ms over frontal sites. While there was no gaze difference in ERP amplitudes in the AD task over these sites, direct gaze elicited more positive amplitudes than averted gaze in the ED task, but less positive amplitudes than averted gaze in the GD task. The interaction between gaze direction and task indicated that these two effects overlapped in time, although the ED gaze effect appeared earlier (around 220ms) than the GD gaze effect (around 255ms).

Interestingly, the frontal gaze activity occurs in a time-window during which decoding of emotions typically occurs. At frontal sites such as those measured here, the N200 ERP component occurs from approximately 200-350ms, and is commonly found to be modulated by emotional stimuli (see Coll, 2018 for a review), words (Kanske, & Kotz, 2010; Zhang et al. 2019) and facial expressions (Balconi & Canavesio, 2016), albeit with inconsistent effect directions (see Section 1.4.2; Coll, 2018). It has been proposed that modulation of the N200 reflects initial automatic activation of emotion areas when perceiving emotional stimuli, and this emotion activation is thought to be part of the emotional contagion process that occurs during when we share in someone else's emotional state during empathy (Fan & Han, 2008). At posterior sites, the Early Posterior Negativity (EPN; see Section 1.4.3) is also often reported between 150-250ms and up to 350ms and typically differentiates between different facial expressions, in particular fearful and angry compared to happy facial expressions (e.g. Herbert et al. 2008; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Rellecke et al., 2012; Kissler et al. 2009; Sato et al., 2001; Schupp et al. 2006; Wronka & Wallentowska, 2011). Given that direct gaze has been implicated in emotion processing (see Section 1.1.2; Hamilton, 2016; Kampe et al., 2001; Strick, Holland, & van Knippenberg, 2008) and affects participants' arousal (Conty et al., 2010; Nichols & Champness, 1971; McCrackin & Itier, 2018a) and introspective reporting of emotional state (Baltazar et al., 2014), the present frontal activation in the ED task may be indicative of overlap between the neural correlates associated with emotion processing and gaze processing.

Despite its excellent temporal resolution, EEG has poor spatial resolution, so caution must be taken when making inferences about possible neural generators. Nevertheless, we speculate that the frontal activity recorded may be linked to orbitofrontal (OFC) activity, given the involvement of the OFC in emotion processing, gaze processing and higher order theory of mind tasks (Amodio & Frith, 2006; Calder et al., 2002; Conty et al., 2007; Dixon et al., 2017). The 220-290ms during which the task by gaze interaction was found significant at this frontal cluster falls in between timings reported by two independent studies to be sensitive to gaze (Conty et al. 2007) and task (Sabbagh et al. 2004), respectively. Conty et al. (2007) reported that OFC activation differentiated between direct and averted gaze from 190-220ms (picked up first over frontocentral and centroparietal sites -e.g. Fz, Cz-, then later over occipital-temporal sites -e.g. P9, P10). In another study, source localization pointed to the OFC as the source of ERP amplitude differences found between 270-400ms and differentiating between a GD task and an ED task close to our own (over frontal sites including FP2 and F4, as well as parieto-occipital sites), which asked participants to decode emotional state from eye-regions with direct gaze (Sabbagh et al., 2004). We thus find it plausible that the OFC would be involved in the gaze by task interaction picked up at frontal sites during similar timing.

One of the limitations of this study concerns the differences between the demands associated with each task, and it is unclear what differences between tasks are responsible for the differences in how gaze was processed during each. For example, while we assume that the key factor differentiating the ED from the GD and AD tasks is the recruitment of frontocentral emotion processing centres in the ED task, in particular the orbitofrontal cortex, the tasks also differ in terms of featural versus holistic processing. Indeed, the AD task may have required featural processing of the eyes, while both ED and GD judgements are generally considered to require holistic face processing (e.g. Calder & Jansen, 2005; McKelvie, 1995; Prkachin, 2003; Zhao et al., 2010). However, as opposite gaze effects were seen between the GD and ED tasks at the neural level, this featural versus holistic processing difference cannot easily explain our neural interaction. Similarly, while it has been demonstrated that the presence of teeth can impact early ERPs to faces (daSilva et al., 2015), we believe it is unlikely that the presence of teeth in the happy face stimuli impacted our findings. First, the same exact faces were present in each task condition and second, the modulation of early ERPs by happy expressions appears to only occur when participants fixate on the mouth (Neath-Tavares and Itier, 2016), whereas fixation to the eyes was enforced here.

In contrast, a featural/holistic difference in processing may account for overall task differences found from 400-800ms post-stimulus that may be related to task difficulty. Over occipitotemporal sites, the most positive ERP amplitudes were elicited by the GD task, intermediate amplitudes by the ED task, and the most negative amplitudes were elicited by the AD task. The reverse pattern was seen over centro-parietal sites, likely reflecting the opposite end of the same dipole. Similar task effects have been reported in studies in which participants used eye-regions (Sabbagh et al. 2004) or faces (Itier & Neath-Tavares, 2017; but see Rellecke et al. 2012 for null results) to complete similar ED and GD tasks. Itier and Neath-Tavares (2017) reported more positive ERPs in the GD than the ED task over posterior sites but at much earlier timings (from 200-350ms, the latest measured time window due to much shorter response times). Sabbagh et al. (2004) reported more positive ERPs for the ED task than the GD task over posterior, central and parietal sites at a timing closer to our own timing (300-500ms, where as our task effect began at 400ms). These timing differences may be related to the fact that in the present study and the Sabbagh et al. (2004) study, participants were asked to wait until the response prompt to press the keys while in the Itier & Neath-Tavares (2017) study, responses occurred as soon as possible after the presentation of the stimulus. Similar task effects have also been found when participants were asked to perform visual discrimination tasks with differing levels of complexity (Senkowski & Herrmann, 2002). Our behavioural data support the idea that task complexity might be responsible for these general effects of tasks, given the accuracy gradient followed the same pattern as the ERP amplitude gradient. Accuracy was indeed highest in the GD task, intermediate in the ED task, and worst in the AD task. Similar response time (Rellecke et al., 2012; Wronka & Wallentowska, 2011) and accuracy (Wronka & Wallentowska, 2011) gradients were previously reported by groups using similar GD and ED tasks. Overall, the general task effects seen at the ERP level seem related to task difficulty and future studies could investigate whether this difficulty is related to featural/holistic processing differences or to other task-specific factors.

We should also note that it was surprising to find neither a main effect of gaze direction, nor an interaction between gaze and task, over posterior sites during the 130-200ms window encompassing the N1710, given past reports of gaze effects on this ERP component. These previous reports have varied, with some finding enhanced N170 amplitudes in response to averted gaze (Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015; Watanabe et al., 2002), some to direct gaze (Burra et al., 2017; Conty et al., 2007; Pönkänen et al., 2010; Watanabe et al. 2006), and others, like the present study, finding no gaze effect at all (Taylor, Itier et al., 2001; Schweinberger et al., 2007). One possibility is that this was due to our use of static stimuli as opposed to dynamic stimuli (see Sections 1.3.2 and 5.2.1 for further discussion of this point). Another is that there is a lot of variation in how gaze is processed at the individual level over these sites (the N170 itself can range in latency from 130-200ms between individuals). While there may be some similarities in timing and location, significant individual differences could have impacted our ability to detect gaze effects at the group level using a mass-univariate approach. Moreover, this literature on gaze effects almost always used neutral faces, while the present study used emotional expressions, which may have impacted the early processing of gaze. The other alternative is that previously reported findings regarding N170 modulations by static gaze images were type I errors that may be related to the lack of control of gaze position. Indeed, as far as we know, the present study is the first ERP study on gaze perception to have controlled for gaze position using a gaze-contingent approach, a particularly important aspect given the growing literature showing modulations of the N170 amplitude with gaze fixation location, in particular to the eyes (de Lissa et al., 2014; Itier & Preston, 2018; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014; Parkington & Itier, 2018). Those possible caveats represent an important topic for further research to address. In any case, from the present within-subject design, there is no evidence of early gaze effects during the time window encompassing the N170 component, as least when using facial expressions of emotion.

In summary, the present study is one of the first ERP investigations demonstrating that direct and averted gaze are processed differently during emotion, attention and gender discrimination judgements performed by the same participants. Gaze direction did not affect GD task performance, while processing direct gaze facilitated emotion discrimination relative to averted gaze, and processing averted gaze facilitated the attention direction judgement relative to direct gaze. These results provide support for the idea that gaze perception impacts attention and emotion discrimination judgements, which are likely key initial steps in our everyday theory of mind. Finally, if there are brain areas that are recruited commonly for both emotional and eye-gaze processing, an important next step is to investigate the impact of eye-gaze on the other ways that we related to one another on an emotional level. Accordingly, Study 2 (Chapter 3) investigates how the perception of eye-gaze impacts our affective empathy, our ability to share the emotional state of others (Decety et al. 2015; de Vignemont & Singer, 2006; Lieberman, 2007; Kanske et al. 2015).

Chapter 3: Eye-gaze processing during affective empathy judgements[5]

3.1 Introduction

The layman's expressions “the eyes are the windows to the soul” and “the eyes always tell the truth”, reflect that we look to the eyes of others to help us understand their thoughts and emotions, a cognitive process called theory of mind (Baron-Cohen & Cross, 1992). Furthermore, it has been shown that eye gaze also impacts our own emotional state (see Section 1.1.2; Baltazar et al., 2014; Conty et al., 2010; Hietanen, 2018; Nichols & Champness, 1971; McCrackin & Itier, 2018a). It is thus surprising that the impact of eye gaze on empathy (colloquially described as “seeing through another’s eyes”) has yet to be investigated, given that it is an everyday social process requiring both theory of mind abilities and an emotional reaction.

Although different definitions of empathy exist, in the present study we define empathy as the sharing of another’s emotional state while being aware that the other person is the source of the emotion. That is, the capacity to share or become affectively aroused by the other’s valence and intensity (Decety et al. 2015; de Vignemont & Singer, 2006; Kanske et al. 2015; Lieberman, 2007), which can occur in response to either positive or negative stimuli (see Morelli et al. 2015a for a review). As argued by Decety et al. (2015), this emotional or affective empathy can be distinguished from theory of mind (what some refer to as “cognitive empathy”), and from empathic concern, which is argued to be the motivational aspect of empathy. In the present study, we investigated the behavioural and electrophysiological impact of perceiving direct and averted eye-gaze on affective empathy judgements in neurotypical individuals.

Perceiving direct gaze results in different cognitive effects than perceiving averted gaze, and these cognitive processes may make it easier for an individual to affectively empathize with others when they display direct gaze. First, direct gaze may facilitate the emotional contagion that occurs during affective empathy (e.g. Schuler et al. 2016; Prochazkova & Kret, 2017). Not only does direct gaze elicit an emotional response within an observer (see Section 1.1.2; Hietanen, 2018 for a review) but perceiving direct gaze appears to increase the mimicry of the gazer's actions (Wang et al., 2010), which is associated with affective empathy (Sonnby-Borgström et al. 2003) and argued to facilitate emotional contagion that occurs during affective

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[5] A version of this chapter has been submitted to *Neuroimage* (McCrackin & Itier, 2020, under revision).

empathy (e.g. Schuler et al. 2016; Prochazkova & Kret, 2017). Second, direct gaze may facilitate better understanding of another's emotional state. Direct gaze is associated with more accurate discrimination of happy and angry facial expressions (Study 2; Adams & Kleck, 2003; 2005; Sander 2007), and while emotion discrimination is arguably different from understanding or sharing those emotions, it may facilitate later emotional understanding and sharing (Clark et al., 2008). Finally, the impact of direct gaze on self-referential processing (see Section 1.1.1; Conty et al., 2016 and Hamilton, 2016 for reviews) may also allow an individual to draw on their own experiences while making mental state inferences (Joireman & Hammersla, 2002; Lombardo et al. 2007; Mitchell et al., 2005) and help simulate others' affective states within the self (Lieberman, 2007; Joireman & Hammersla, 2002; but see Boyraz & Waits, 2015 for null results).

The present study combined electroencephalography (EEG) with behavioural measures of affective empathy to test the hypothesis that, compared to averted gaze, direct gaze might facilitate both positive empathy (i.e. sharing in a positive emotion) and negative empathy (i.e. sharing in a negative emotion). We first validated a set of sentences designed to elicit empathy, ensuring that they elicited the correct affective empathy responses in a separate experiment (see Section 3.2.1). That is, we expected low empathy with neutral valence for neutral sentences and high empathy with positive or negative valence for positive and negative sentences, respectively (corresponding to positive and negative empathy). These contextual sentences described positive, neutral or negative events happening to other individuals (e.g. "Her newborn was saved/fed/killed yesterday afternoon."). We then presented each sentence during the EEG experiment, followed by a direct or averted gaze image of the person described. Participants were then asked to indicate how much they empathized with that individual, defined as sharing that individual's emotion. ERPs were recorded relative to the face image onset. We predicted that during the negative and positive trials, participants would empathize more with individuals displaying direct than averted gaze while during neutral trials, gaze direction would have less or no impact on participants' responses.

The inclusion of both positive and negative affective empathy conditions was important given the recent research suggesting they are distinct constructs. While both empathy types are positively associated with social competence (Sallquist, 2009) and prosocial behaviour (Telle & Pfister, 2016), some special populations (e.g. Social Anxiety Disorder; Morrison et al., 2016) appear to have specific deficits in only one type of affective empathy. Positive and negative affective empathy also have unique neural correlates (see Morelli et al. 2015a, for a review). While both are associated with prefrontal cortex activation (Light et al., 2009; Mobbs et al., 2009; Morelli et al. 2015b), positive empathy is associated with neural correlates of positive affect (Sallquist et al., 2009), including the ventral striatum (Mobbs et al., 2009) and negative empathy is associated with neural correlates of negative affect, including the anterior insula and dorsal anterior cingulate cortex (Morelli et al., 2015).

As participants knew that they had to make an empathy judgement on each trial, the ERPs time-locked to the face images allowed us to track the time course of the interaction between the valence of the sentence context, the participant's corresponding affective empathy response, and the visual processing of eye gaze. Recent ERP findings suggest that eye-gaze might be processed as early as 100-140ms after face onset (Burra et al., 2018; Schmitz et al., 2012), making it plausible that eye-gaze processing could interact with early or late ERPs associated with experiencing empathy. These ERPs (see Coll, 2018 for a review) include the N100 (50-120ms; see Section 1.4.1) and N200 (200-350ms; see Section 1.4.2) over frontal sites, and the P300 (300-500ms; see Section 1.4.4) and Late Positive Potential (LPP, 500-800ms; see Section 1.4.5) over centroparietal sites. The interpretations of these ERPs are informed by theories of affective empathy, which involve early automatic processes during which an emotional state is elicited in an observer, and then later top down processes (e.g. Decety & Lamm, 2006; Preston and de Wall, 2002) before conscious experience. The earlier N100 and N200 are thought to reflect the initial automatic activation of emotion areas elicited by the perception of emotional stimuli (Fan & Han, 2008) that contribute to a later "emotional sharing" response. Conversely, the later P300 and LPP components are more commonly found to be task sensitive, and may reflect a cognitive evaluation of the situation which is subject to top-down regulation (Decety et al., 2010; see Decety and Lamm, 2006; Fan & Han, 2008; and Gonzalez-Liencres et al., 2013, for more discussion). The association between these ERP components and empathy originates primarily from studies which have focused on empathy judgements made in response to the perception of nociceptive stimulation in others (e.g. hands being cut by scissors or trapped under a cabinet door) in comparison to neutral stimulations (e.g. hands just next to the scissors or atop the cabinet door). However, some have claimed that the N100 (Groen et al., 2013), N200 (Balconi &

Canavesio, 2016; Groen et al., 2013) and LPP (Balconi & Canavesio, 2016; Choi & Watanuki, 2014; Groen et al., 2013) also relate to trait empathy as measured by self-report questionnaires.

We used the same mass univariate ERP technique as in Study 1 to perform an exploratory whole scalp analysis and to then focus on the N100, N200, P300 and LPP, along with the emotion-sensitive Early Posterior Negativity (EPN; Section 1.4.3) and the face-sensitive N170 (Section 1.3.2). The use of this technique was particularly important given that other ERP analysis techniques less robust to type I and type II error have been suggested to be linked to the inconsistencies in both the eye-gaze (see Section 1.3.2) and empathy (see Coll, 2018) literatures. Below, we start by reporting the empathy sentence validation study before moving on to the ERP study on empathy and gaze processing.

3.2 Methods

3.2.1 Online Sentence Validation Study

3.2.1.1 Participants

This study was approved by the University of Waterloo (UW) Research Ethics Board, and 76 UW students with normal or corrected-to-normal vision participated for course credit. Seven participants were excluded for leaving more than ten percent (48) of the 480 questions blank, leaving a final sample of 69 participants (36 female, M *= 19.88 years,* SE *= .24). Thirty-three participants (16 female; 17 male) were randomly assigned to the male pronoun group and 36 (20 female; 16 male) to the female pronoun group as described below. Participant ethnicity in the final sample varied (Caucasian: n = 23; Chinese:* n *= 17, Other Asian Groups:* n *= 15; East Indian:* n *= 4; Aboriginal:* n *= 2, Middle Eastern:* n *= 2, Other* n *= 6).*

3.2.1.2 Sentence Construction

Sentences that varied in the amount of empathy they elicit were created for later use in the EEG-Eye tracking study. Eighty overall *sentence themes* were created, with a positive, negative and neutral variation of each, created by altering key words in the sentence (e.g. “his pet dog was saved/killed/fed yesterday”). The neutral sentences were designed to carry content as neutral as possible, so that participants would not feel much empathy for the individuals described in them.

These would act as baseline low-empathy sentences. The positive and negative sentences were designed to elicit more empathy, varying in valence. All sentences contained eleven syllables and wherever possible, sentence structure for each of these valence variations was kept identical. Some sentences were adapted from those used by Hudson (2018). This resulted in 80 sentences for each valence category, for a total of 240 sentences.

3.2.1.3 Study Design and Data Analysis

To keep the study length under an hour and a half, one study version was created with male pronouns used at the beginning of the sentences, and another version was created with female pronouns (e.g. “he/she was hugged by his/her mom after the meal”). Participants were randomly assigned to one of the two study versions, with random sentence presentation order.

Participants rated each sentence on how much empathy they felt for the individual described in the sentence using a 9-point Likert scale. A rating of 1 meant very little empathy and a rating of 9 meant extreme empathy. Empathy was defined as sharing of another's emotional state, while being aware that the other person is the source of the emotion (de Vignemont & Singer, 2006). Participants also rated the valence of the emotion elicited by the sentence, where a rating of 1 meant very negative and a rating of 9 meant very positive. Participants rated 238.55 (*SE* =.25) sentences on average.

Ratings of the male and female pronoun versions of each sentence were combined for data analysis. For each of the 80 sentence themes, there were positive, negative and neutral variations, and ratings of empathy were averaged across participants for each of these variations (Table 1). Ratings of the valence of the emotion elicited by each sentence were averaged in the same manner.

The key purpose of this validation was to find the sentence themes in which the positive and negative variations elicited significantly more empathy than the neutral variations. Toward this end, an “overall empathy score” was calculated to quantify how much more empathy was elicited by the positive and negative variations relative to the neutral baseline[6]. Here, any score above 0 meant that the positive and negative variations elicited more self-reported empathy than

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[6] Taken by summing the difference between the positive and neutral empathy ratings, and the difference between the negative and neutral empathy ratings ((positive empathy – neutral empathy) + (negative empathy – neutral empathy)). The larger this score, the more empathy participants felt elicited by the positive and negative variations of the sentence theme relative to the neutral variation.

the neutral variation, with the higher the score, the better. Overall, the created sentences were successful: all empathy scores were above 0, with an average score of 3.60. However, we wanted to ensure that we were choosing only the above average sentence themes, so we chose the sentence themes that had an empathy score of 4 or greater. This meant that participants rated the positive and negative variations as eliciting (on average) at least 2 more points on the empathy Likert scale than the neutral variation. This cut-off point corresponded to 29 sentence themes, and for counterbalancing purposes, we rounded to an even number of the top 25 (i.e. excluding approximately the bottom 70% of sentences). All twenty-five selected themes were used in the later EEG-eye tracking study (starred in Table 1), and statistically analyzed below to confirm that 1) the positive and negative sentence variations elicited significantly more empathy than the neutral variation and 2) neutral sentences elicited an intermediate (neutral) emotion, while positive sentences elicited more positive emotion than both negative and neutral sentences, and negative sentences elicited more negative emotion than both neutral and positive sentences.

A positive empathy, negative empathy and neutral empathy average for each participant was created by averaging empathy ratings for the three variations of the selected 25 sentences. A positive valence, negative valence, and neutral valence average for each participant was also created by averaging valence ratings for the variations of the final sentences. Two Analyses of Variance (ANOVA) with a factor of sentence valence (3; positive, neutral, negative) were run, one on the empathy averages and the other on the valence averages. The raw *p*-values for the follow-up comparisons are reported, such that $p<.016$ would reach threshold for significance with Bonferroni correction ($p<.05/3$ for the three comparisons run).

Sentence Theme	Positive Empathy	Positive Valence	Negative Empathy	Negative Valence	Neutral Empathy	Neutral Valence	Overall Empathy Score
***pet dog was saved/fed/killed yesterday afternoon	6.80(.25)	7.42(.22)	7.26(.24)	1.94(.17)	3.90(.26)	5.31(.17)	6.26
***pet cat was found/fed/lost yesterday afternoon	5.99(.25)	6.94(.21)	6.44(.22)	3.13(.20)	3.59(.23)	5.28(.15)	5.25
was just told that he(she) will soon/should go/will not walk again	6.84(.24)	7.91(.18)	7.33(.26)	1.82(.19)	4.93(.25)	5.59(.20)	4.31
***loves/does/hates the job and the boss that he(she) works with	5.62(.26)	7.16(.17)	6.28(.25)	2.87(.19)	3.57(.24)	5.06(.11)	4.76
work environment is very friendly/standard/hostile	5.50(.24)	6.90(.18)	6.01(.24)	2.83(.17)	3.79(.23)	4.87(.07)	3.93
***learned he(she) does not have/has learned now all about/learned he(she) does now have/ the deadly disease	6.93(.25)	7.75(.21)	7.30(.25)	2.75(.32)	4.78(.30)	4.59(.20)	4.67
really loves/knows/hates the way that his(her) body looks	5.59(.26)	7.32(.18)	6.49(.24)	2.54(.17)	4.83(.21)	5.65(.16)	2.42
often thinks that all his(her) children love/know/hate him(her)	5.51(.23)	6.97(.21)	6.30(.26)	2.26(.16)	4.41(.25)	5.31(.18)	2.99
always believes that he(she)/often believes the show/never believes that he(she) could start over	5.37(.26)	5.90(.19)	5.72(.25)	3.32(.18)	4.10(.26)	5.01(.13)	2.89
***partner's life was saved/partner went shopping/partner's life was lost yesterday morning	7.41(.22)	7.87(.20)	7.88(.21)	1.78(.21)	3.49(.24)	5.16(.11)	8.31
mom's life was saved/ book ended/life was lost after a heart attack	7.36(.21)	7.90(.21)	7.63(.24)	1.54(.15)	5.90(.29)	3.10(.23)	3.19
***son's life was saved/son was delayed behind/son's life was lost after a bad car crash	7.30(.22)	7.65(.24)	7.94(.22)	1.57(.17)	5.30(.26)	3.81(.20)	4.64
***was just reunited with/doing housework with/separated from his(her) partner	6.28(.24)	7.26(.18)	6.49(.23)	2.49(.15)	3.94(.26)	5.59(.12)	4.89
***child was reunited with/at his workplace with/separated from him(her) today	6.94(.25)	7.77(.17)	7.16(.25)	1.97(.19)	4.48(.26)	5.98(.14)	5.14
***dog was reunited with/eating her food/taken away from him(her) today	6.72(.24)	7.36(.20)	7.01(.25)	2.38(.19)	4.68(.27)	6.09(.17)	4.37
was rewarded/walking by/disciplined in front of the whole team	5.74(.26)	7.04(.20)	5.98(.26)	3.15(.21)	4.00(.23)	4.84(.10)	3.72
was rewarded/walking by/disciplined in front of the whole school	5.76(.26)	7.18(.19)	6.10(.26)	2.68(.20)	4.00(.27)	4.96(.13)	3.86
was hugged/called/punched by his(her) teammate after the game	4.97(.25)	6.58(.16)	6.00(.21)	2.91(.18)	3.99(.22)	5.43(.11)	2.99
was hugged/called/punched by the coach after the big game	5.17(.25)	6.42(.18)	6.10(.26)	2.51(.19)	4.38(.25)	5.21(.14)	2.51
was hugged/called/slapped by his(her) mom after the meal	5.10(.28)	6.67(.17)	6.55(.24)	2.36(.15)	4.36(.29)	5.81(.16)	2.93
mom embraced/spoke with/punished him(her) after the fundraiser	5.64(.27)	6.41(.25)	5.90(.25)	3.01(.19)	4.04(.23)	5.14(.09)	3.46
won/saw/lost the hardest music competition	5.90(.27)	7.36(.18)	6.00(.24)	3.04(.17)	3.82(.26)	5.18(.13)	4.26
just won/saw/lost the basketball game for his(her) team	5.74(.26)	7.35(.16)	5.68(.24)	3.07(.18)	3.80(.25)	5.32(.12)	3.82
just won/saw/lost the world cup final for his(her) team	5.87(.29)	7.77(.17)	6.22(.28)	2.69(.20)	4.26(.26)	5.86(.17)	3.57
just won/saw/lost the ice skating competition	5.62(.26)	7.22(.17)	5.62(.24)	3.09(.14)	3.71(.23)	5.45(.23)	3.82
***aced his(her)/marked the/failed his(her) very important driving test	5.77(.27)	7.19(.15)	6.28(.23)	3.01(.18)	3.84(.25)	5.22(.13)	4.37
***aced his(her)/marked the/failed his(her) very important physics test	6.26(.27)	7.22(.23)	6.49(.23)	2.77(.17)	3.74(.25)	5.29(.13)	5.27
***aced his(her)/marked the/failed his(her) very difficult psych exam	5.97(.27)	7.49(.18)	6.47(.27)	2.63(.16)	4.03(.27)	4.75(.14)	4.38
***aced his(her)/marked the/failed his(her) very difficult math exam	6.09(.28)	7.49(.18)	6.86(.22)	2.52(.16)	3.73(.25)	5.04(.13)	5.49
just bought/saw/broke an amazing new vehicle	4.94(.28)	6.85(.17)	5.81(.25)	2.99(.17)	4.13(.30)	5.86(.15)	2.49
just won/saw/crashed a fast and expensive new car	4.84(.29)	7.07(.20)	5.86(.26)	2.49(.16)	3.57(.27)	5.22(.17)	3.56
just won/saw/broke a powerful new computer	4.88(.28)	6.86(.16)	5.62(.27)	2.90(.15)	3.81(.27)	5.56(.14)	2.88
just won/saw/missed the award he(she) was working hard for	6.43(.25)	7.57(.15)	6.59(.22)	3.00(.17)	4.81(.17)	5.77(.17)	3.40
fixed his/saw his/broke his old Nintendo and controller	5.25(.23)	6.41(.19)	5.16(.26)	3.67(.18)	4.84(.29)	6.15(.18)	0.73
amazing new/official work/terrible new computer just arrived	4.88(.29)	6.67(.18)	4.01(.24)	3.88(.15)	3.85(.28)	5.75(.15)	1.19
loves/knows/hates the new school he(she) has to enroll in	5.52(.26)	7.16(.17)	6.04(.25)	2.99(.17)	4.29(.25)	5.32(.14)	2.98
loves/knows/hates the cell phone he(she) got for his birthday	5.20(.28)	6.64(.19)	3.42(.27)	3.48(.18)	4.00(.27)	5.44(.12)	0.62
***knows his partner is so in love/not shopping/not in love with him(her)	5.99(.27)	7.68(.17)	7.07(.19)	2.22(.18)	3.93(.24)	5.19(.27)	5.20
was adored/noticed/hated by all of his(her) new classmates	5.19(.27)	7.01(.19)	6.55(.27)	2.15(.17)	4.47(.24)	5.78(.15)	2.80
was accepted to be on/quite interested in/rejected to be on the best team	5.57(.27)	7.15(.20)	6.04(.24)	3.19(.16)	4.00(.25)	5.36(.12)	3.61
***was accepted/also there/rejected at the job interview	6.43(.23)	7.43(.17)	6.53(.24)	2.88(.17)	3.75(.23)	5.04(.09)	5.46
***got accepted by/to read about/rejected by the school he(she) wanted	6.76(.24)	7.56(.16)	6.67(.22)	2.84(.18)	4.07(.24)	5.83(.15)	5.29
just got hired by/read all about/got fired from his(her) all-time dream job	6.03(.29)	7.76(.17)	6.65(.26)	2.12(.17)	4.65(.30)	6.13(.20)	3.38
***partner told him(her) she(he) really does love him(her)/really does love cats/no longer loves him(her)	6.76(.23)	7.44(.24)	7.23(.22)	2.00(.14)	3.96(.27)	5.64(.27)	6.07
***knows right now that his(her) partner is faithful/shopping/cheating	6.03(.26)	7.32(.19)	6.57(.29)	2.26(.22)	3.73(.23)	5.16(.10)	5.14
***insurance will pay for all/needs a code for/will not pay for the treatment	6.41(.25)	7.52(.21)	7.09(.21)	2.44(.18)	4.55(.24)	4.38(.14)	4.40
newborn baby is doing very well/currently asleep/doing very bad	5.96(.28)	7.71(.17)	7.07(.26)	1.91(.15)	4.84(.24)	6.09(.15)	3.35
mom cherishes/remembers/despises the day that he(she) was born	6.26(.26)	7.53(.18)	6.87(.30)	1.74(.18)	5.43(.28)	6.97(.18)	2.27
***partner has decided to marry/drive with/divorce him(her)	6.19(.29)	7.94(.16)	6.74(.24)	2.41(.19)	4.16(.26)	5.75(.13)	4.61
overheard his partner say she's(he's) happy/hungry/lonely	5.83(.26)	7.32(.17)	6.33(.23)	2.78(.16)	4.18(.26)	4.80(.14)	3.80
is excited/beginning/terrified to move out on his(her) own	5.76(.24)	7.07(.18)	6.01(.27)	3.46(.18)	5.77(.26)	6.38(.19)	0.23
life savings quadrupled/we counted/disappeared during the week	5.57(.28)	7.41(.20)	6.37(.26)	2.34(.26)	4.19(.23)	5.21(.13)	3.56
earned the/counted/lost the money for his(her) dream apartment	5.83(.25)	7.26(.17)	6.58(.26)	2.65(.26)	4.65(.25)	5.96(.17)	3.11
fundraised/counted/misplaced money for the homeless shelter	5.83(.26)	7.29(.16)	5.30(.25)	2.94(.17)	4.91(.24)	6.16(.18)	1.31
boss thinks that he(she) is quite intelligent/still undecided/unintelligent	5.52(.27)	6.88(.19)	5.91(.26)	2.81(.16)	4.39(.24)	4.32(.11)	2.65
told his mom that his(her) father is loving/eating/cheating	5.01(.29)	6.85(.19)	6.62(.28)	2.09(.18)	3.84(.27)	5.12(.13)	3.95
just attended his (her) mother's fun party/appointment/funeral	4.48(.24)	6.49(.15)	7.62(.23)	1.84(.19)	4.32(.26)	4.96(.10)	3.46
will definitely get his/lose his/see the dream house soon	5.75(.26)	7.10(.19)	5.59(.27)	3.14(.20)	4.74(.25)	6.38(.18)	1.86
has laughed/read/cried more times today than he(she) can count	5.71(.28)	7.42(.18)	6.67(.22)	2.59(.18)	4.06(.25)	5.28(.18)	4.26

looks back on his past with a lot of joy/quite objectively/with a lot of guilt	5.78(.27)	7.23(.17)	6.14(.26)	2.87(.19)	5.04(.27)	4.83(.16)	1.84
happily relaxed/ate a small dinner/cried hard to himself(herself) after his(her) big game	5.19(.29)	6.44(.19)	6.09(.24)	3.29(.21)	4.09(.26)	5.07(.15)	3.10
class environment is very friendly/standard/hostile	5.25(.24)	7.03(.17)	6.07(.23)	2.93(.18)	4.01(.25)	5.16(.09)	3.30
***cat's life was saved/toy was bought/life was lost yesterday afternoon	6.07(.26)	7.29(.21)	7.00(.25)	2.26(.20)	3.57(.25)	5.45(.13)	5.93
***pet dog was found/fed/lost yesterday afternoon	6.46(.24)	7.55(.19)	6.77(.22)	2.41(.17)	3.94(.24)	5.42(.15)	5.35
loves his(her) class and/goes to class with/hates his(her) class and the students he(she) works with	5.54(.25)	7.04(.17)	5.68(.27)	2.61(.16)	4.10(.25)	5.48(.10)	3.02
daughter's cancer is starting to leave her/class is staring today/is starting to kill her	6.99(.23)	7.75(.19)	7.74(.24)	1.64(.17)	5.99(.26)	3.78(.22)	2.75
believes his(her) marriage is a big success/marriages are a big promise/his(her) marriage is a big failure	5.59(.25)	7.48(.18)	6.04(.28)	2.41(.18)	4.99(.30)	5.74(.21)	1.65
best friend is moving very close to /with some help from/very far from him(her)	5.90(.25)	7.16(.19)	6.81(.24)	2.75(.17)	4.55(.25)	5.59(.18)	3.61
has been feeling more happy/busy/depressed recently	5.94(.22)	7.10(.19)	6.94(.18)	2.72(.20)	5.29(.29)	4.75(.16)	2.30
parents are always/sometimes/never supportive of him(her)	6.39(.26)	7.46(.21)	6.71(.27)	2.49(.23)	5.31(.25)	4.69(.18)	2.48
feels like a superstar/a normal guy(girl)/an imposter living his(her) life	5.16(.26)	6.93(.19)	6.29(.23)	2.80(.19)	4.52(.29)	5.84(.17)	2.41
***close childhood friend just passed by/passed the store/passed away today	6.58(.28)	3.41(.30)	7.55(.23)	1.74(.16)	4.32(.27)	5.68(.19)	5.49
***found an organ match to save/studied organ matches with/ found no organ match to save his(her) sister	6.99(.27)	8.01(.17)	7.41(.24)	2.09(.24)	4.84(.26)	5.20(.19)	4.72
feels he(she) is the cause of their happiness/decision/great sadness	5.58(.25)	6.83(.20)	6.52(.20)	2.52(.18)	5.31(.26)	4.48(.16)	1.48
just found out that the cancer has left him(her)/cancer class began/cancer has left him(her)	7.25(.23)	8.33(.13)	7.56(.23)	1.76(.16)	5.42(.27)	3.78(.18)	3.97
will enjoy seeing/begin to see/now never see his(her) child grow up	5.83(.26)	7.43(.18)	7.39(.25)	1.94(.19)	5.88(.25)	7.22(.18)	1.46
just found out that he(she) is not paralysed/all about paralysis/that he(she) is now paralysed	6.87(.25)	7.97(.19)	7.43(.25)	1.75(.15)	6.30(.30)	2.90(.23)	1.70
has never been in such great shape/really watched/in such bad shape before	5.59(.29)	6.87(.22)	5.91(.24)	3.10(.17)	4.25(.25)	4.75(.16)	3.00
grandfather always remembers his(her) name/does not remember that name/does not remember his(her) name	5.66(.29)	7.00(.19)	6.97(.24)	2.51(.18)	5.70(.29)	3.33(.19)	1.23
***newborn was saved/fed/killed yesterday afternoon	7.28(.23)	7.93(.21)	7.78(.24)	1.41(.13)	3.99(.25)	5.60(.16)	7.08

Table 1. Validation results for each of the original 80 sentence themes, with mean empathy and valence ratings (*SE* in parentheses) averaged across all 69 participants as a function of sentence valence (positive, neutral and negative). The 25 starred sentences were selected for the EEG-Eye tracking experiment. Note: All sentences began with he/she or his/her.

3.2.1.4 Results for the Selected 25 Sentence Themes

3.2.1.4.1 Empathy Ratings

There was a main effect of sentence valence on ratings of affective empathy (Figure 6a), $F(1.50, 102.47) = 152.03$, $MSE = 1.08$, $p < .001$, $\eta_p^2 = .69$. Follow-up paired t-tests indicated that there were significantly higher empathy ratings during the negative condition than both the neutral, $t(68)= 13.417$, $MSE= .22$, $p<.001$, and positive conditions, $t(68)= 4.01$, $MSE= .12$, $p<.001$. There were also significantly higher empathy ratings during the positive condition than during the neutral condition, $t(68)= 13.22$, $MSE= .18$, $p<.001$.

3.2.1.4.2 Valence Ratings

There was a main effect of sentence valence (Figure 6b), $F(1.11,75.32) = 444.99$, $MSE =1.76$, $p <.001$, $\eta_p^2=.87$. Paired t-tests confirmed that the positive condition elicited more positive emotion than both neutral, $t(68)= 18.24$, $MSE= .11$, $p<.001$, and negative conditions, $t(68)= 21.60$, $MSE= .23$, $p<.001$. The negative condition elicited significantly more negative emotion than the neutral condition, $t(68)= -21.42$, $MSE= .13$, $p<.001$.

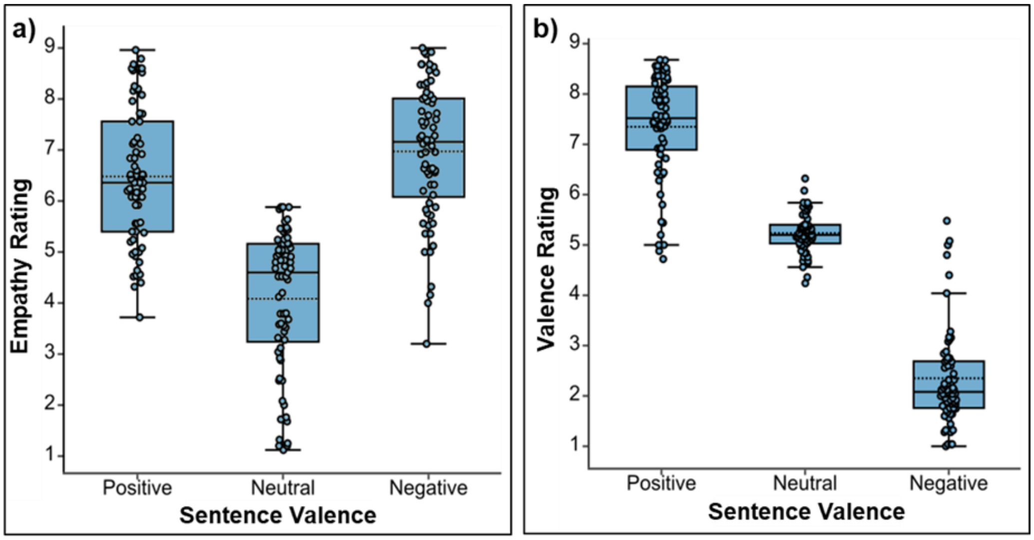

Figure 6. Empathy and valence ratings in the sentence validation study

a) Participants' mean *affective empathy* ratings for the 25 chosen sentence themes in the sentence validation study. **b)** Participants' mean *valence* ratings for the selected sentence themes in the sentence validation study. Each point represents the average from one participant. Boxes indicate participant averages falling between the 25th and 75th percentiles, with the dotted horizontal line representing the mean and the solid horizontal line representing the median.

3.2.2 EEG-Eye-tracking Study

3.2.2.1 Participants

Fifty (50) undergraduate students at the University of Waterloo (UW) participated in this study and received either course credit or \$20 CAD as remuneration. The study was approved by the UW Research Ethics Board, and informed consent was obtained before each individual participated. Five participants were excluded from analysis for failing to complete enough trials, and one for responding with the same answer on each trial, leaving a final sample of 44 (23 female, 21 male; mean age = 20.18 (*SD*=1.56)). All participants were prescreened such that they had corrected-to-normal or normal vision, no neurological or psychological disorders, no current recreational drug use, and had never experienced a loss of consciousness longer than 5 minutes. They also self-reported their ability to recognize both faces and facial expressions as at least a 7/10 on a Likert scale to ensure intact face perception, and had lived in either Canada or the United States for at least 5 years. Participant ethnicity varied (Caucasian: *n*=16, Chinese: *n*=17, Other Asian Groups: *n*=5, Hispanic: *n*=1, East Indian: *n*=2, Korean: *n*=1, Middle Eastern: *n*=1, and Other Not Listed: *n*=1).

3.2.2.2 Face Stimuli

Direct gaze, averted left gaze and averted right gaze images of 10 males and 10 females were selected from the Radboud database (Langer et al., 2010)[7]. Each image was flipped along the vertical axis to create a second set of images, which controlled for any facial asymmetry (Figure 7; e.g. a flipped averted right gaze image became a second averted left gaze image). All individuals were Caucasian and bore a neutral expression. The photos were cropped with the GNU Image Manipulation Program (GIMP 2.8) to display the upper shoulders and head. The SHINE package (Willenbockel et al., 2010) was used to equate images on root mean square contrast (*M* = 0.63, *SD* = 0.0004), and mean pixel intensity (*M* = 0.44, *SD* = 0.0004), and then custom Matlab scripts added the colour information back in for increased ecological validity.

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[7] Identities 1, 10, 12, 15, 19, 23, 24, 25, 27, 30, 31, 32, 33, 36, 37, 38, 49, 56, 58, 61 were used in the study blocks, and identities 07 and 14 were used in the practice trials.

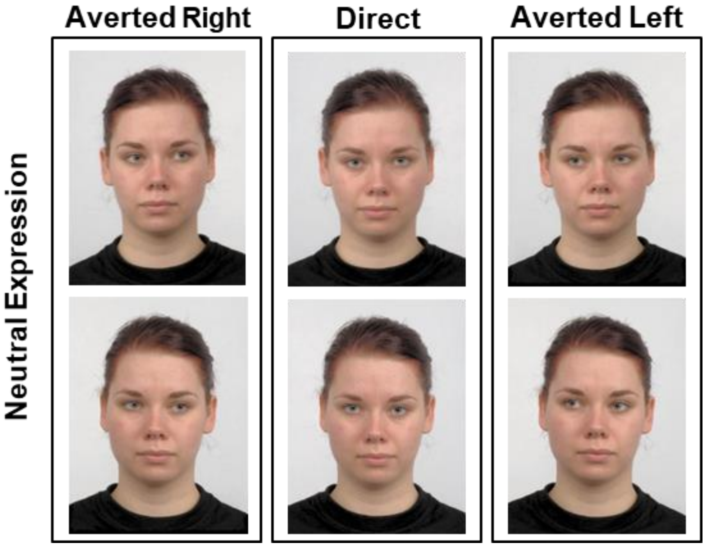

Figure 7. Sample Study 2 face stimuli

Sample averted right, direct and averted left gaze stimuli.

3.2.2.3 Experimental Design

The experimental set-up was identical to that in Study 1, including the testing computer and eye-tracking settings (see Section 2.2.3).

A sample trial progression can be seen in Figure 8. Each trial began with a positive, negative or neutral sentence, designed to elicit positive, negative or no empathy (see Section 3.2.1). A fixation cross followed and participants were required to fixate on the cross (within a radius of 1.92^o) for 300ms to advance the trials. If they failed to meet this requirement, a drift correction occurred and the eye-tracker was re-calibrated. If they met the requirement, they were shown a direct or averted gaze face for 500ms (13.16° horizontal by 17.49° vertical), which they were told was a picture of the person described in the sentence. Critically, the fixation cross was positioned so that participants would be looking between the nasion and the nose when the face was shown to them, ensuring that they were processing the eye-gaze. ERP recording was time-locked to the onset of the face. A 300ms blank screen followed and then two response screens appeared. The first asked participants to rate how much empathy they felt for that individual, using the number keys from 1 (very little empathy) to 9 (extreme empathy). The second asked participants to rate how positive or negative the emotion they were feeling was, from a scale of 1 (very negative) to 9 (very positive).

The experiment was programmed using SR Research’s Experiment Builder 1.10.1385. There were a total of 5 blocks, with 120 trials per block. The combinations of sentence types and gaze directions meant that there were six conditions (positive direct gaze, neutral direct gaze, negative direct gaze, positive averted gaze, neutral averted gaze, negative averted gaze), with 20 trials per condition in a block, and 100 trials per condition over the course of the study. Each of the 20 face identities were shown 6 times in a block, paired with each of the six conditions. An equal number of male and female faces, as well as direct and averted gaze faces (half averted left and half averted right), were shown for each condition and block. The pronouns used in each sentence matched the face gender for that given trial. An effort was made to ensure that similar sentence themes (e.g. about dogs and cats) were not blocked together. Participants were randomly assigned to two versions of the experiment, which were created to vary which faces were presented with which sentence themes. Six practice trials were completed at the start of the experiment.

Following the computer task, participants filled out the Toronto Empathy Questionnaire (TEQ; Spreng et al., 2009), which has been shown to characterize affective empathy better than the widely used IRI scale (Davis, 1983). The TEQ is a sixteen item self-report measure which characterizes empathy as an emotional sharing response (e.g. "When someone else is feeling excited, I tend to get excited too"). It has strong psychometric properties, with a high internal validity and test-retest reliability (Spreng et al., 2009). Scores range from 0-64, with larger scores indicating a higher degree of empathy. All but one participant completed this questionnaire (*n*=43).

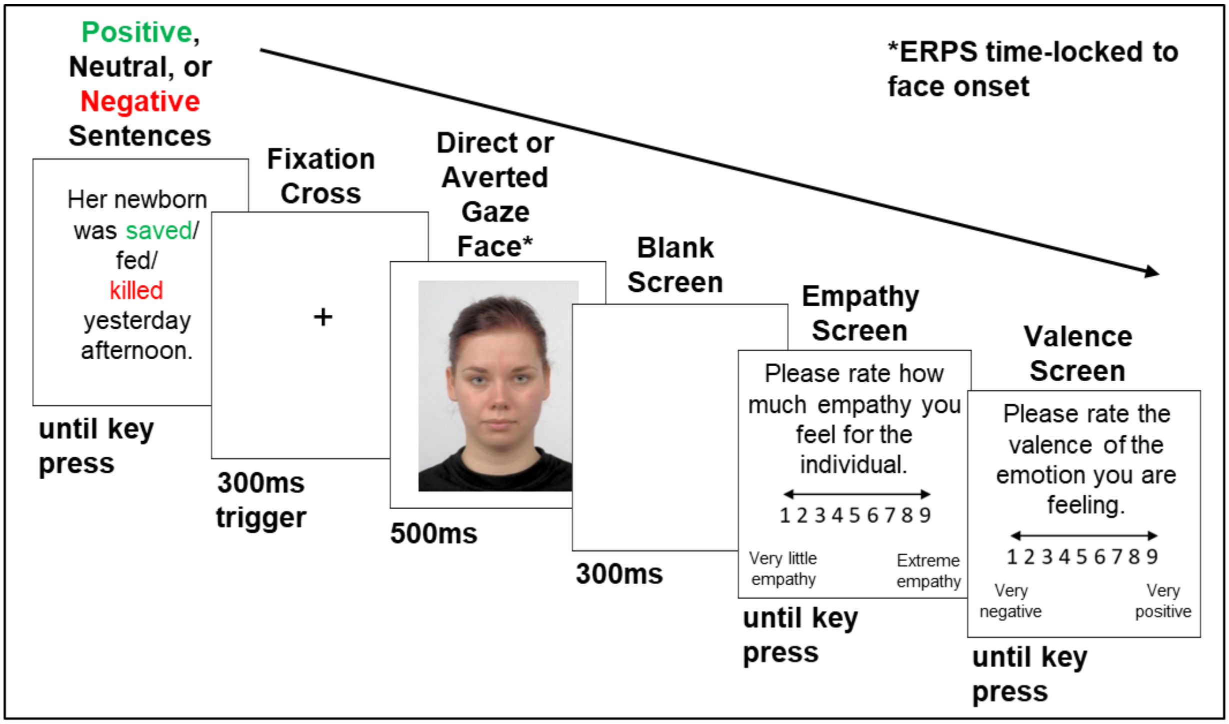

Figure 8. Sample Study 2 trial progression

Illustration of the trial progression with a direct gaze face. ERPs were time-locked to the onset of the face.

3.2.2.4 Electroencephalography Recording

The EEG recording was identical to Study 1 (see Section 2.2.4).

3.2.2.5 Data Preprocessing and Cleaning

The data processing steps were identical to Study 1 (see Section 2.2.5). An average of 5.07 trials (*SD*=11.04) were removed per participant for not reading the sentences and 9.57 trials (SD = 17.67) for failing to maintain fixation on the nasion and eyes for the first 250ms of face presentation. An average of 1.18 (*SE* = 1.67) ICA components were removed per participant. After the cleaning stages were used to remove any additional noisy trials, an average of 59.03 (*SD* = 16.77) trials per condition remained in the final ERP averages.

3.2.2.6 Behavioural Data Analysis

Each participant's mean empathy and valence ratings for each condition were averaged. SPSS 25 was used to run one ANOVA with within-subjects factors of gaze direction (2; direct gaze, averted gaze) and sentence valence (3; positive, negative and neutral) on mean empathy ratings, and another on mean valence ratings. When Mauchly's sphericity test was significant, we reported the Greenhouse-Geisser corrected degrees of freedom. The raw *p*-values are reported below for all follow up paired t-tests, though please note that only those with $p<.016$ would be considered significant with a Bonferonni correction (0.05/3 comparisons).

We also investigated whether participants' self-reported trait empathy (measured by the Toronto Empathy Questionnaire) correlated with how much empathy they reported during the computer task, as a way to probe the truthfulness of empathy ratings during the EEG study. For each participant we used mean empathy ratings in the computer task to calculate a positive ($\text{empathy}_{\text{positive}}$ – $\text{empathy}_{\text{neutral}}$) and a negative ($\text{empathy}_{\text{negative}}$ – $\text{empathy}_{\text{neutral}}$) empathy score. We also used mean valence ratings to calculate a positive ($\text{valence}_{\text{positive}}$ – $\text{valence}_{\text{neutral}}$) and a negative ($\text{valence}_{\text{negative}}$ – $\text{valence}_{\text{neutral}}$) valence score. We ran four correlations to see if these empathy and valence scores were correlated with TEQ scores, using a Bonferroni corrected significance threshold of $p<.0125$ (0.05/4). We reported Spearman correlations when the Shapiro-wilk normality test indicated that these variables were not normally distributed and Pearson correlations when they were.

3.2.2.7 EEG Data Analysis

As in Study 1 (see Section 2.2.7) we used the Factorial Mass Univariate Toolbox (FMUT; Fields, 2017) to analyze our EEG data, with an identical Permutation Based Cluster Mass technique to correct for multiple comparisons. We first performed an exploratory ANOVA on all electrodes and time-points from 50ms post-face to the end of our epoch (800ms). Then, we ran ANOVAs to test our specific a priori time-windows and regions of interest, including ANOVAs on frontocentral sites (Fp1, Fp2, Fpz, AF3, AF4, AFz, F4, F3, F1, F2 and Fz) during the N100 (50-120ms) and the N200 (200-350ms) time-windows, and on parieto-occipital sites (P9, P10, P7, P8, PO7, PO8, PO9, PO10) during the N170 (130-200) and EPN time-windows (200-350ms). We did not run individual ANOVAs on the LPP or P300 because our exploratory analysis had already picked up activity modulated by sentence valence spanning these components. Each omnibus ANOVA included the within-subjects factors of gaze direction (2; direct gaze, averted gaze) and sentence valence (3; positive, negative and neutral).

Follow-up ANOVAs were conducted on significant electrodes and time-windows in the omnibus ANOVAs using Bonferroni corrected alpha levels (i.e. set to 0.016 if there were three follow-up comparisons).

3.3 Results

The FMUT results and behavioural files will be available in the Open Science Framework Repository upon peer-reviewed publication of this study.

3.3.1 Behavioural Results

3.3.1.1 Empathy Ratings

There was a main effect of sentence valence on participants' ratings of empathy (*F*(1.39, 59.93) = 83.37, *MSE* = 211.67, *p* <.001, ηp^2 = .66; Figure 9a). As in the sentence validation study, paired comparisons indicated that the negative condition elicited more empathy than both the neutral (*t*(43)= 10.42, *MSE*= .24, *p*<.001) and positive (*t*(43)= 5.76, *MSE*= .12, *p*<.001) conditions, and that the positive condition elicited more empathy than the neutral condition (*t*(43)= 8.25, *MSE*= .22, *p*<.001).

There was also an interaction between sentence valence and gaze direction (*F*(1.53, 65.83) = 6.12, *MSE* = .166, *p* <.01, ηp^2 = .13; Figure 9a). Paired comparisons indicated that there was no effect of gaze direction on empathy ratings during negative (*t*(43)= -.65, *MSE*= .057, *p*=.52) or neutral conditions (*t*(43)= .62, *MSE*= .039, *p*=.54), but there was an effect of gaze direction during the positive condition (*t*(43)= 2.76, *MSE*= .041, *p*=.008). During the positive condition, participants reported feeling slightly more empathy when the faces displayed direct as opposed to averted gaze.

3.3.1.2 Valence Ratings

There was a main effect of sentence valence on participants' valence ratings (*F*(1.34, 57.77) = 129.22, *MSE* = 345.57, *p* < .001, ηp^2 = .75; Figure 9b). Again, as in the sentence validation study, paired comparisons indicated that participants reported feeling more positive during the positive condition than during the neutral (*t*(43)= 12.08, *MSE*= .13, *p*<.001) and negative (*t*(43)= 12.71, *MSE*= .26, *p*<.001) conditions, as well as feeling more negative during the negative condition than during the neutral condition (*t*(43)= -8.49, *MSE*= .20, *p*<.001). There was also a main effect of gaze direction (*F*(1, 43) = 11.89, *MSE* = .49, *p* =.007, ηp^2 = .22; Figure 9b), driven by participants rating their valence as overall more positive after viewing faces with direct gaze than averted gaze. However this effect was modulated by a weak interaction between sentence valence and gaze direction (*F*(2,86) = 3.51, *MSE*=.053, *p*=.034, ηp^2=.08; Figure 9b). Bonferroni corrected paired comparisons indicated that direct gaze trials were rated as more positive than averted gaze trials for the positive (*t*(43)=3.27, *MSE*=.037, *p*=.002) and neutral (*t*(43)=3.28, *MSE*=.03, *p*=.002) conditions, while there was no effect of gaze in the negative condition (*t*(43)=1.20, *MSE*=.027, *p*=.236).

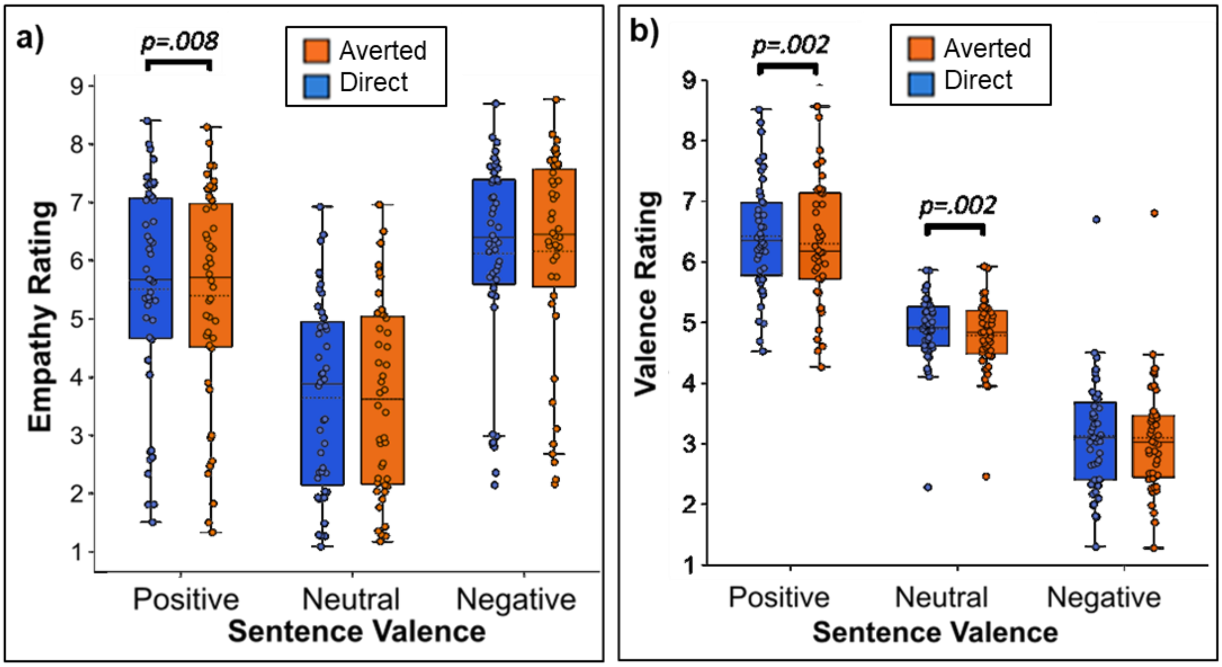

Figure 9. Mean empathy and valence ratings for each condition

a) Average *empathy* ratings for each gaze (averted, direct) and sentence valence condition.
b) Average *valence* ratings for each gaze and sentence valence condition. Boxes indicate data points which fall between the 25th and 75th percentiles. The mean is denoted with a dotted horizontal line and the median with a solid horizontal line. Note: Threshold for significance with the Bonferroni correction is *p*<.016.[8]

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[8] Note: the four outlying points on the valence graph are from the same participant. While this participant answered unusually for the valence question, they had typical responses to the empathy questions and their TEQ score

3.3.1.3 Relation between Behavioural Ratings and Self-reported Trait Empathy

As expected, during the experiment, participants with higher self-reported trait empathy reported experiencing stronger positive and negative empathy than participants with lower trait empathy (positive correlation between TEQ and positive empathy scores; $r_s = .503$, $p<.001$, $N = 43$; and between TEQ and negative empathy scores; $r_s = .502$, $p<.001$, $N = 43$). Participants with higher self-reported trait empathy also reported experiencing stronger positive and negative valence than those with lower trait empathy scores (positive correlation between TEQ scores and positive valence scores; $r_p = .420$, $p=.005$, $N = 43$; and between TEQ scores and negative valence scores; $r_s = -.420$, $p=.005$, $N = 43$). This manipulation check suggests that participants were accurately reporting their emotional states on each trial.

3.3.2 EEG Results

3.3.2.1 Exploratory Analysis Over All Electrodes (50-800ms)

There was a widespread main effect of sentence valence, which was most pronounced over central and parietal sites (Figure 10a; $p=.0018$) from 400-800ms (and thus encompassing the tail end of the P300 and the LPP). Follow-up ANOVAs including the significant electrodes and time-points in the omnibus (IO1, LO1, F7, FT7, FC3, C1, C3, C5, T7, CP1, CP3, TP7, TP9, P1, P3, P5, PO3, PO7, O1, AFz, Cz, CPz, Pz, POz, Iz, AF8, AF4, F6, F4, F2, FT8, FC4, FC2, C4, C6, CP2, P2, P4, P6, PO4; 400-800ms) indicated that this was driven by differences between the negative and neutral conditions (Figure 10b; $p=.00011$) and between the negative and positive conditions (Figure 10c; $p=.0044$) over central and parietal sites. There were more positive ERP amplitudes in the negative condition than in both the neutral and positive conditions, a cluster did form for the difference between the positive and neutral conditions but it did not reach significance with our Bonferroni cut-off (Figure 10d; *ps*>.021). There was no effect of gaze direction (*ps*>.084) or interaction between gaze direction and sentence valence (*ps*>.42).

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indicated that they are likely not psychopathic. While we have kept them in because we believe they had typical empathy responses, we did try running the ERP analyses without this individual and found identical results, with the one exception being that the N200 sentence valence effect became a statistical trend instead of significant.

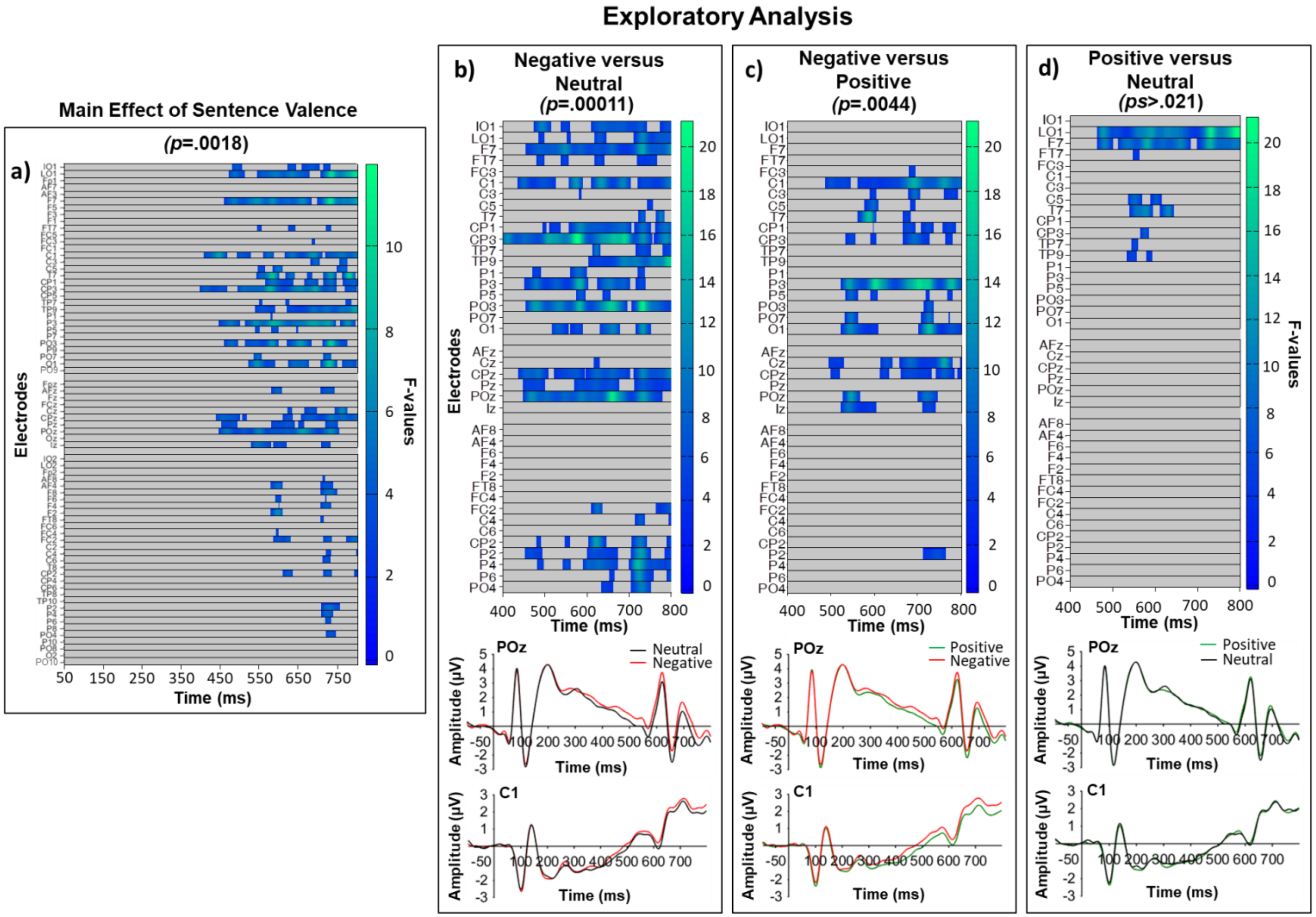

Figure 10. Exploratory analysis sentence valence effect

a) Main effect of sentence valence during our exploratory analysis on all electrodes (from 50-800ms), corrected for multiple comparisons with the Permutation Based Cluster Mass technique (at p <.05 for the omnibus and p<.016 for the paired comparisons). Each electrode included in the analysis is plotted on the y-axes, while the x-axis represents time (post face onset). Coloured sections denote significant F values, as indicated by the colour bar on the right. The differences in the omnibus ANOVA were driven by differences between the **b)** negative and neutral conditions, and the **c)** negative and positive conditions, but not the **d)** positive and neutral conditions. Representative electrodes (POz and C1) are shown for each paired comparison.

3.3.2.2 Frontocentral Sites During the N100 Time-window (50-120ms)

While there was no main effect of sentence valence (no clusters found) or gaze direction (*p*=.74), there was a significant interaction between the two factors (Figure 11a; *p*=.012). Follow-up ANOVAs (from 65-105ms; including electrodes: Fp1, Fp2, Fpz, AF3, AF4, AFz, F4, F3, F1, F2, Fz and using a stronger *p* value threshold of 0.016) revealed that there were main effects of gaze direction in the negative (Figure 11b; *p*=.0014) and positive (Figure 11c; *p*=.0047) conditions, but not in the neutral condition (Figure 11d, no clusters found). In the negative condition, direct gaze elicited less negative ERP amplitudes than averted gaze, while the opposite pattern was seen in the positive condition.

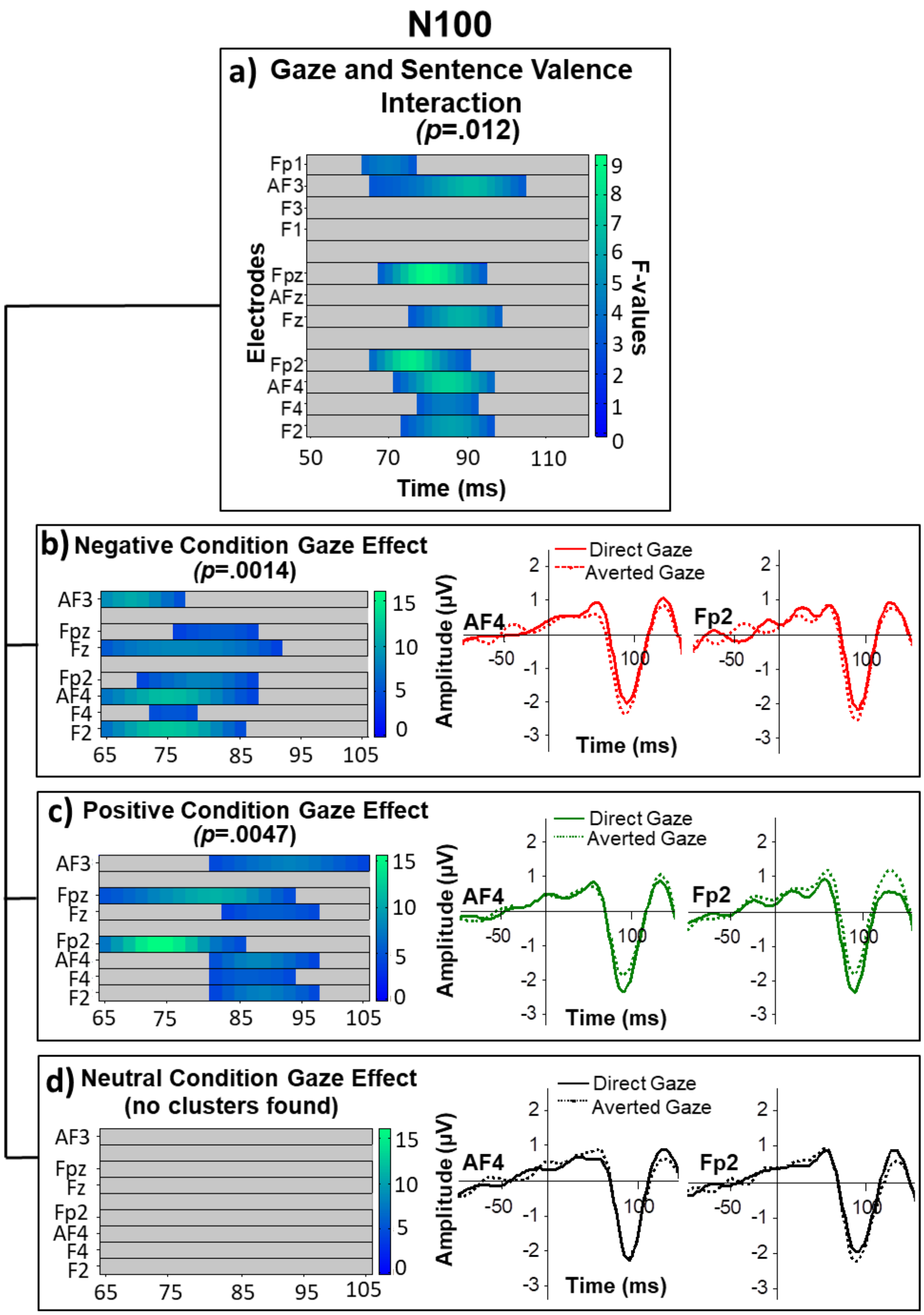

Figure 11. N100 gaze and sentence valence interaction

a) Gaze direction and sentence valence interacted in the N100 time window (50-120ms). Time post-face onset is denoted on the x-axis, and electrodes are listed on the y-axis. Coloured sections correspond to the significant *F* values as indicated by the right-hand colour bar and corrected for multiple comparisons using the Permutation Based Cluster Mass technique (*p* <.05 for the omnibus ANOVA, *p*<.016 for post-hoc paired comparisons). As can be seen on representative electrodes (AF4 and Fp2), there was a significant effect of gaze direction in the **b)** negative and **c)** positive conditions, but not in the **d)** neutral condition.

3.3.2.3 Frontocentral Sites During the N200 Time-window (200-350ms)

There was a main effect of sentence valence (Figure 12a, *p*=.036), which did not interact with gaze direction (no interaction clusters found). Follow-up tests (spanning 290-350ms; including electrodes: Fp2, Fpz, AF3, AF4, AFz, F4, F3, F2, Fz, *p* value threshold of 0.016) indicated that the N200 was larger (more negative) for the neutral condition compared to both the negative (Figure 12b, *p*=.0025) and positive (Figure 12c, *p*=.012) conditions. There was no difference between the positive and negative conditions (Figure 12d, no clusters found). There was no main effect of gaze direction (*p*=.38).

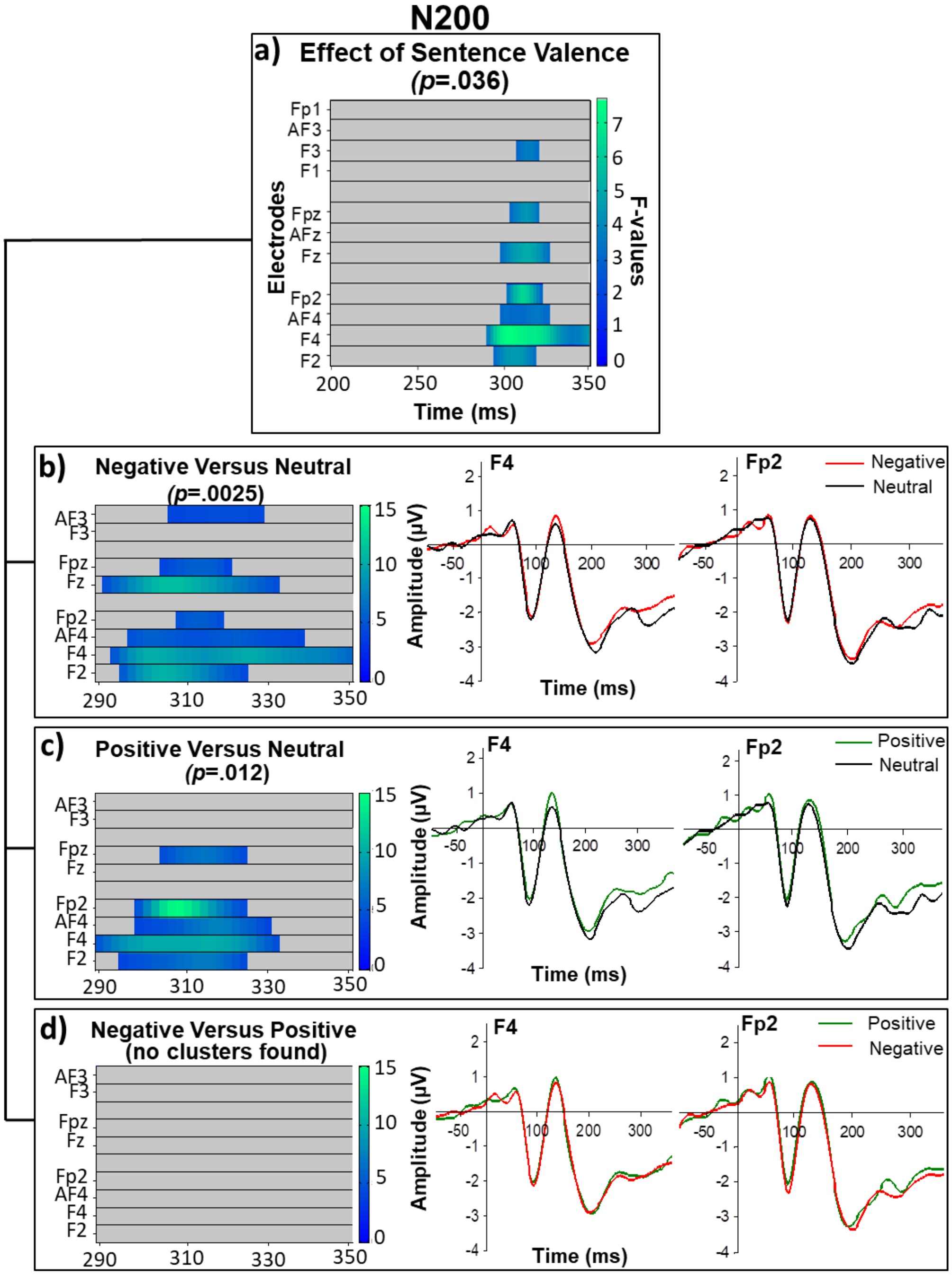

Figure 12. N200 sentence valence effect

a) Sentence valence modulated fronto-central N200 (200-350ms) ERP amplitudes. The Permutation Based Cluster Mass technique was used to correct for multiple comparisons, at *p* <.05 (and at *p*<.016 for the post-hoc comparisons). Electrodes are plotted on the y-axis, and time post-face onset is plotted on the x-axis. Time points and electrodes with significant effects are denoted with coloured blocks, and the magnitude of significance is denoted by colour bar on the right. There were significant differences between the **b)** negative and neutral conditions and the **c)** positive and neutral conditions, but not between the **d)** negative and positive conditions. Representative electrodes (F4 and Fp2) are shown.

3.3.2.4 Parieto-occipital Sites During the N170 Time-window (130-200ms)

There was a right-lateralized main effect of gaze direction from approximately 150-195ms (Figure 13, *p* = .011; P10, P08, PO10), driven by more negative ERP amplitudes for averted gaze than direct gaze. While this effect was picked up during the N170 time-window, it occurred after the N170 peak, on the ascending part toward the P200. There was no main effect of sentence valence (*p* = .33), nor an interaction between sentence valence and gaze direction (*p*=.52).

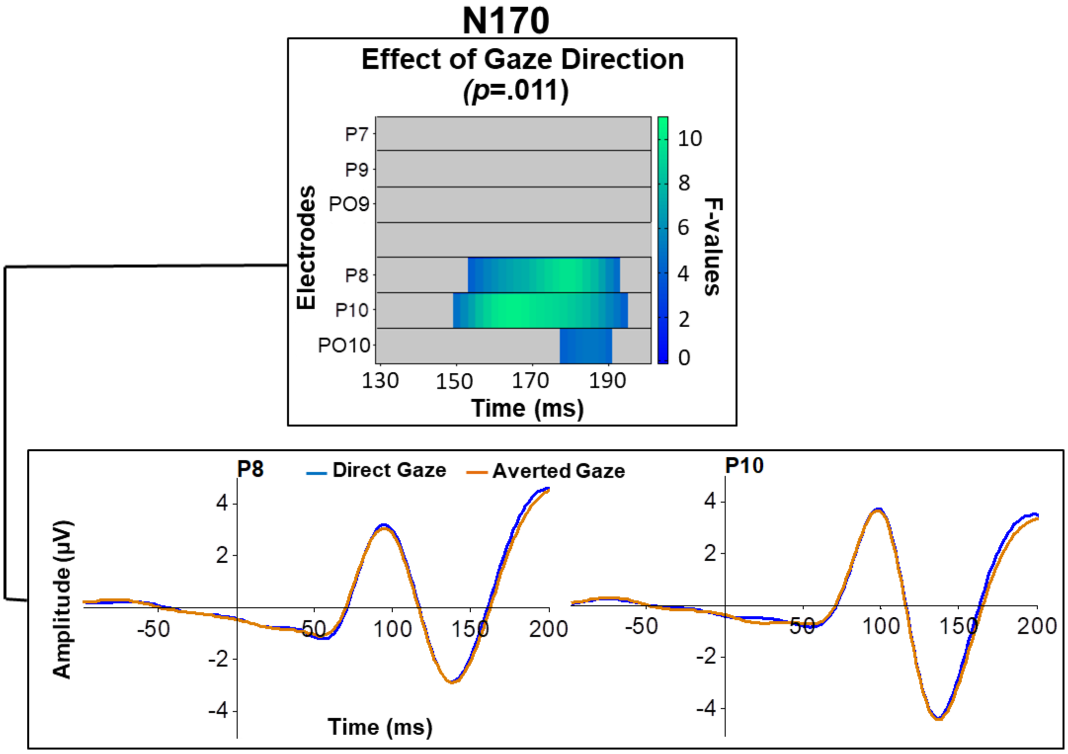

Figure 13. N170 gaze effect

a) An analysis of the N170 time-window (130-200ms) revealed that gaze direction had an effect on the ascending part from the N170 peak toward the P200. Direct gaze was associated with less negative ERP amplitudes, as shown on representative electrodes (P8 and P10). The Permutation Based Cluster Mass technique for multiple comparisons was applied at *p* <.05. Electrodes are indicated on the y-axis, and time post-face onset is indicated on the x-axis. Significant electrodes and time-points are indicated with coloured blocks corresponding to the right-hand colour bar.

3.3.2.5 Parieto-occipital Sites During the EPN Time-window (200-350ms)

There was a main effect of sentence valence restricted to the right hemisphere (Figure 14a, *p*=.036). Follow-up ANOVAs (from 300-350ms, including P8, P10, PO8, *p*<.008) indicated that this was driven by more negative-going ERP amplitudes in the negative condition than in the neutral condition (Figure 14b, *p*=.000020). Although it did not meet our Bonferroni corrected cut-off, there was a similar trend for more negative ERP amplitudes in the positive than in the neutral condition (cluster significance of *p*=.021; Figure 14c). There was no difference between the negative and positive conditions (Figure 14d, no clusters found).

While there was no main effect of gaze direction (*p*=.32), there was an interaction between gaze and sentence valence restricted to the left hemisphere (Figure 15a, *p*=.020). Follow-up comparisons (from 200-275ms, including P7, P9, PO7, *p*<.0083) indicated that there were more positive amplitudes for direct gaze than averted gaze in the positive condition (Figure 15c, *p*=.0050), while there was no difference between direct and averted gaze in the negative (Figure 15b, no clusters found) or neutral (Figure 15d, *p*=.060) conditions. While the interaction occurred during the time window analysed to encompass the EPN, visual inspection of the waveforms indicated that it occurred earlier than the main effect of valence, and was a modulation of the P200 ERP component (Figure 15).

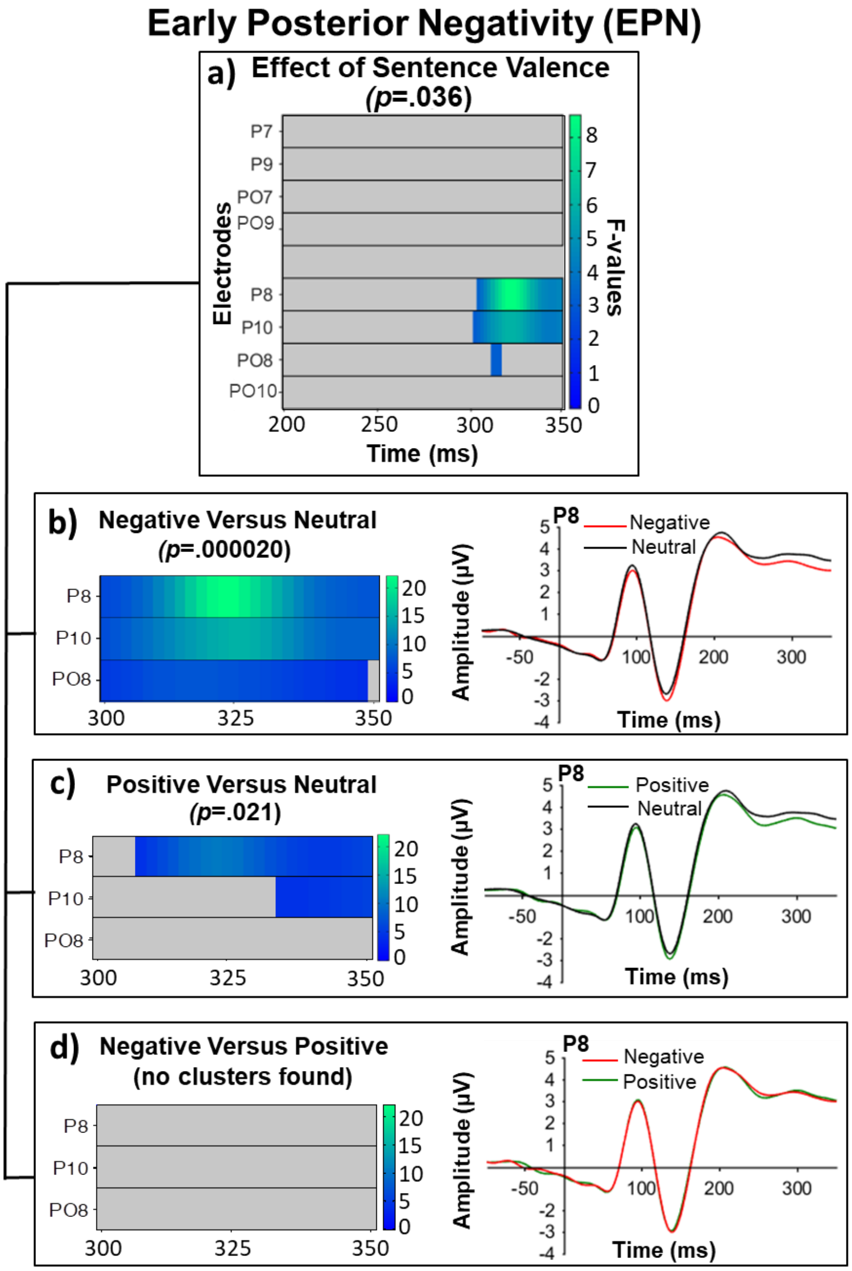

Figure 14. EPN sentence valence effect

a) Sentence valence modulated parieto-occipital ERP amplitudes during a restricted portion of the EPN time-window (significant during 300-350ms) but only on the right hemisphere. Note that all faces had neutral expressions, so the effect was uniquely driven by the valence of the contextual sentence. The Permutation Based Cluster Mass technique was used to correct for multiple comparisons, at p <.05 (with Bonferroni corrected post-hoc comparisons). Each electrode is plotted on the y-axis, with time following the face onset on the x-axis. Coloured sections correspond to significant F values, as denoted by the right hand colour bar. The main effect in the omnibus ANOVA was driven by differences between the **b)** negative and neutral conditions, but not the **c)** positive and neutral or **d)** negative and positive conditions. A representative electrode (P8) is shown.

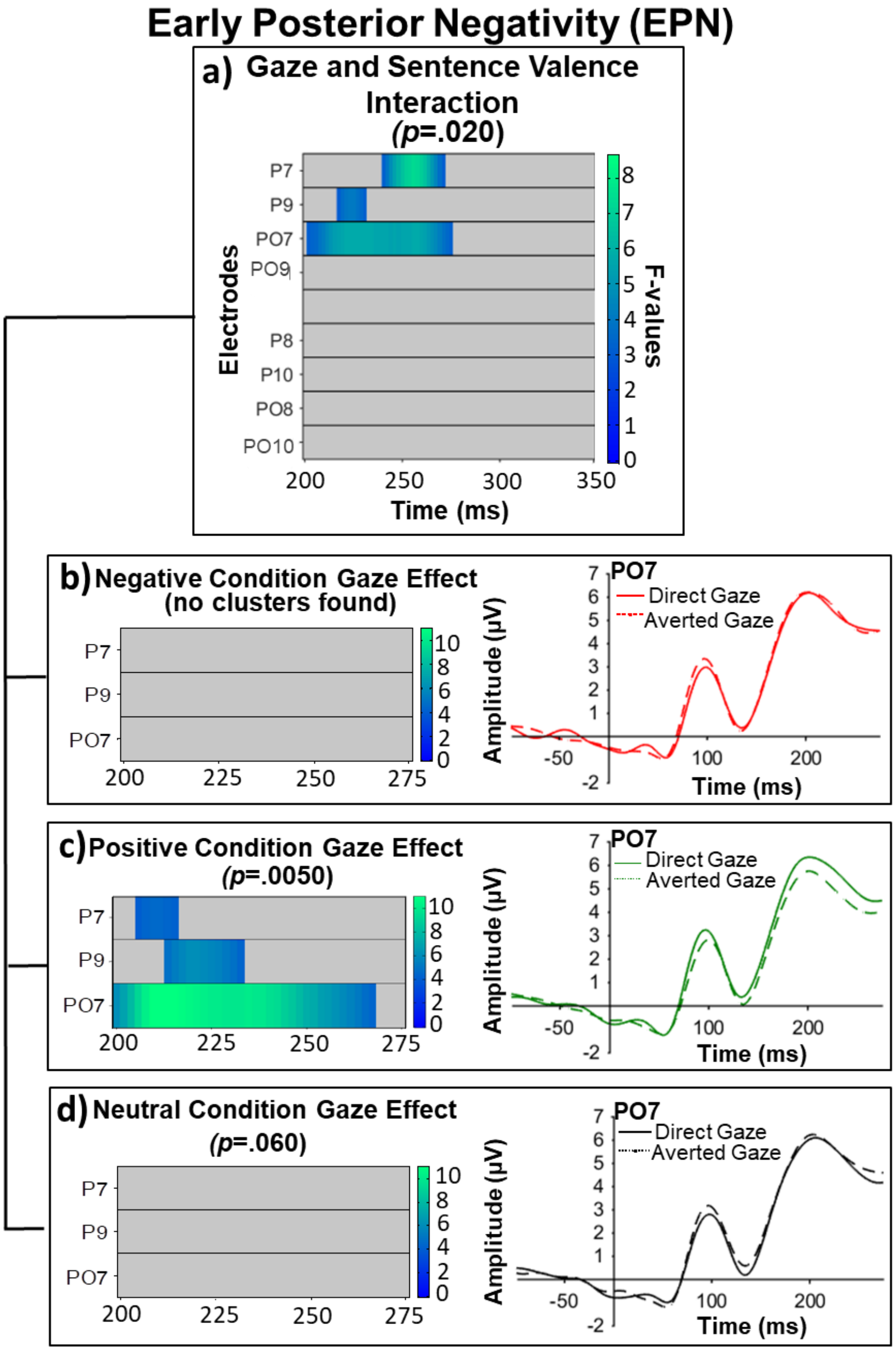

Figure 15. EPN gaze and sentence valence interaction

a) Gaze direction interacted with sentence valence during the portion of the EPN time-window analyzed corresponding to the P2 component (significant between 200-275ms) but only over the left hemisphere. Electrodes are plotted on the y-axis, with time post-face onset on the x-axis. Coloured sections correspond to significant *F* values, as denoted by the right-hand colour bar and corrected for multiple comparisons using the Permutation Based Cluster Mass technique (*p* <.05). Follow up comparisons (Bonferroni corrected) indicated that there was a significant effect of gaze direction in the **c)** positive condition, but not in the **b)** negative or **d)** neutral conditions, as can be seen on a representative electrode (PO7).

3.4 Discussion

There is evidence that eye-gaze perception impacts our emotional state (e.g. Baltazar et al., 2014; Conty et al., 2010; McCrackin & Itier, 2018a; Nichols & Champness, 1971). However, it is still unclear how gaze perception may impact our ability to affectively empathize with the gazer, that is, to share in their emotional state. In the present study, we asked participants to rate how much they affectively empathized with direct and averted gaze individuals who had experienced positive, neutral and negative scenarios. Direct gaze perception appears to be associated with emotional (Baltazar et al., 2014; Conty et al., 2010; McCrackin & Itier, 2018a; Nichols & Champness, 1971) and self-referential (see Conty et al., 2016) processing and with mimicry (Wang et al., 2010), all three of which are supposedly important for experiencing empathy (Lieberman, 2007; Joireman & Hammersla, 2002; Sonnby-Borgström et al. 2003). As such, we predicted that participants would report feeling more affective empathy for individuals displaying direct gaze than averted gaze.

We found that participants reported experiencing slightly more affective empathy for characters with a direct compared to an averted gaze, but only when these characters had experienced positive scenarios. They also reported slightly more positive valence of their empathy for characters with direct compared to averted gaze during positive and neutral trials, but not during negative trials. While these behavioural effects were small, we should emphasize that they were detectable with just 500ms presentations of face images. Several studies have suggested that live actors can increase the cognitive impact of face (Tuefel et al., 2010) or gaze cues (e.g. Hietanen et al., 2008; Pönkänen et al., 2010; 2011), and given the social nature of empathy, the effect we report may be larger with real people and warrants future research.

Our findings add to a growing literature suggesting that the effects of direct gaze perception on various face processing tasks are context specific (Hamilton, 2016). Indeed, while perceiving direct gaze has been previously associated with increased positive valence relative to averted gaze (McCrackin & Itier, 2018a), here we found that direct gaze was not associated with increased positive valence in the negative condition. Against our predictions, direct gaze was also not associated with increased affective empathy in the negative condition, leading us to conclude that direct gaze may only facilitate affective empathy and positive valence ratings in positive contexts.

We believe the present study is one of the first examinations of how the time-course of positive and negative affective empathy may differ (see Morelli et al. 2015a, for a review). We found early (290-350ms) commonality in how they were processed, with both positive and negative trials eliciting less negative ERP amplitudes than neutral trials over the fronto-central N200 component. It is unclear where this frontal activity stems from, but one possibility is the prefrontal cortex, which is associated with both positive and negative affective empathy (Balconi & Vanutelli, 2017; Light et al, 2009; Mobbs et al., 2009; Morelli et al., 2015b). Similar N200 modulation has been theorized to reflect an initial automatic activation of emotion areas (Fan & Han, 2008), potentially through mirror neuron system activation (Gallese & Goldman, 1998). However, this theory stems primarily from nociceptive empathy studies, in which ERPs elicited by pain-inducing stimuli are compared to those elicited by neutral stimuli. The present study's results suggest that N200 modulation occurs for both positive and negative stimuli, and more importantly, can occur in response to the exact same physical stimuli (neutral faces) placed into different affective contexts. However, we should also note that while we found the N200 to be modulated by our empathy task, a recent meta-analysis indicated that the link between the N200 and empathy is unclear (Coll, 2018). More mass univariate analyses are needed to investigate the impact of empathy on frontal sites during this time-window.

We then found divergence between positive and negative trials at later processing stages. The EPN, P300 and LPP components appeared to be modulated specifically by negative affective empathy. Indeed, there were more negative EPN amplitudes during negative trials relative to neutral trials from 300-350ms over the right hemisphere, with no difference between positive and neutral trials (though there was a trend). The EPN is thought to be modulated by emotional stimuli due to attentional or possibly arousal effects (see Section 1.4.3), so this likely reflects enhanced attentional selection for emotional stimuli, which would arguably be adaptive to prioritize. While the EPN to faces is traditionally modulated by facial expressions (e.g. Itier & Neath-Tavares, 2017; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Rellecke et al., 2012; Schact and Sommer, 2009; Schupp et al., 2004b; Schupp et al., 2006), it should be emphasized that all of the face stimuli here were neutral. The only change across trials was the context provided before the face, which aligns with recent research demonstrating that the EPN to neutral faces (Klein et al., 2015; McCrackin & Itier, 2018a; Wieser et al., 2014; Wieser & Moscovitch, 2015) and emotional faces (Aguado et al., 2019; Dieguez-Risco et al., 2013; 2015) can be modulated by affective context. This suggests that the EPN is a more flexible attentional selection process than initially assumed.

There were also more positive ERP amplitudes over frontal, central and centroparietal sites during negative trials relative to both neutral and positive trials from 400-800ms, spanning the end of the P300 and LPP components. In contrast to the EPN, modulation of the LPP is thought to reflect the cognitive appraisal of the emotional stimuli (see Section 1.4.5). Although the LPP enhancement for negative trials could reflect differences in negative versus positive affective empathy, perhaps due to activation of emotion centres, this possibility is unlikely given the lack of amplitude difference between positive and neutral trials. Alternatively, these later stages of processing might reflect the experience of empathic concern, which is a facet of empathy distinct from affective sharing (Decety et al. 2015). Decety et al. (2015) found that the LPP amplitude difference between pain-inducing and neutral stimuli was positively correlated with trait empathy and negatively correlated with psychopathic traits during their empathic concern task but not during their affective sharing task. Thus, it is possible that these later components may reflect processing related to empathic concern, which would likely be present in our negative condition, but not in our positive one. Moreover, although our behavioural data indicated that negative trials did elicit slightly more affective empathy than positive trials, positive trials also elicited more empathy than neutral trials, ruling out the possibility that these larger LPP amplitudes for negative trials be solely due to the magnitude of empathy as opposed to its valence.

We also found more support for the association between eye-gaze and positive empathy at the neural level. The frontal N100 ERP component is believed to be modulated by an automatic activation of frontal emotion areas in an observer (Fan & Han, 2008). Accordingly, gaze direction did not modulate the N100 during neutral (i.e. low empathy) trials, but did so during the trials designed to elicit empathy. During positive trials, direct gaze elicited more negative N100 amplitudes than averted gaze, while the opposite was seen during negative trials, with direct gaze eliciting less negative amplitudes than averted gaze. Again, our visual stimuli were all neutral faces, as opposed to the traditional nociceptive stimuli used by Fan and Han (2008). In our paradigm, there was nothing innately emotional about the stimuli themselves. During the time of visual presentation in the present study, the emotional context had already been instated, and this may have acted to prime the frontal activation that we observed here, perhaps through top-down modulation. This early instatement of the emotional context may also explain why the frontal activation that we report is earlier (65-105ms) than the frontal activation reported by Fan and Han (2008; 140-180ms). However, as for the N200, these N100 results should be replicated with robust statistics.

We also found that gaze direction modulated later ERP amplitudes during only positive trials over the left hemisphere, with more negative amplitudes for averted than direct gaze. While this modulation was detected during our EPN analysis, its timing corresponded to the P200 component. Similarly, we found a main effect of gaze during the N170 analysis, which was found after the N170 peak, on the ascending part toward the P200 on the right hemisphere. It is possible that this earlier main effect of eye-gaze is related to the processing of the gaze-cue itself, before the later interaction between eye-gaze and valence. The later P200 gaze modulation during only positive trials may be related to the unique behavioural interaction between gaze direction and positive empathy ratings. The P200 is the fifth most commonly analysed ERP component in paradigms designed to evoke empathy (Coll et al., 2018). It has shown previous modulation by empathy (Coll et al., 2018) and appears to be modulated more during an affective sharing task than during an empathic concern task (Decety et al., 2015)[9]. Previous research has shown that the P200 is more positive in response to pleasant stimuli, but not negative stimuli (see Olofsson et al., 2008 for a review), which aligns with our finding of more positive ERP amplitudes for direct gaze than averted gaze during positive contexts. The P200 also occurs at approximately the same time as the frontal N200 (Olofsson et al., 2008), so it is possible that the neural generators of these components are part of a larger interactive network responsive to the emotional feeling triggered by affective empathy and by direct gaze.

Both our behavioural and ERP findings provide support for the idea that direct gaze and positive empathy may functionally overlap, and it is important to consider what the mechanism behind this overlap may be. We initially hypothesized that because direct gaze is associated with self-referential processing (Conty et al., 2016; Hamilton, 2016; Kampe et al., 2003; Pönkänen et al. 2011;), it may facilitate an individual’s ability to affectively empathise by allowing them to better simulate the emotion within themselves (Joireman & Hammersla, 2002; Lieberman, 2007 but see Boyraz & Waits, 2015 for null results). However, this theory does not seem to hold in

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[9] Note: While the P200 measured by Coll et al., (2018) and Decety et al. (2015) occurred during the same approximate time-window as the one in this study, there were differences in the locations where each component was measured.

view of the result that direct gaze facilitated positive, but not negative, empathy. We also hypothesized that direct gaze might facilitate empathy due to shared activation of emotional processing areas. This hypothesis shows more promise due to the link between direct gaze and reward system activation (see Hietanen 2018 for a review). Increased ventral striatum activation is not seen for negative empathy and seems unique to positive empathy (Mobbs et al., 2009). The ventral striatum is also implicated in positive affect and reward processing (Cardinal et al., 2002; de la Fuente-Fernández et al. 2002; Schreuders et al. 2018), and is activated when perceiving direct gaze (Kampe et al., 2001; Strick et al., 2008). The interaction between gaze and trial valence on the P200 component was also left-lateralized, and left lateralization of positive emotions (see Machado & Cantilino, 2017 for a review) and positive empathy (Balconi & Vanutelli, 2017) has been previously observed. We therefore suggest that direct gaze processing and positive empathy functionally overlap due to shared neural correlates involved in the experience of positive emotion.

In conclusion, we found support for the idea that positive and negative empathy elicit different behavioural and neural correlates. Positive and negative trials were processed similarly at the early N200 processing stage, while only negative trials modulated the EPN, P300 and LPP components. The early N200 may reflect the activation of emotion areas during affective sharing, while the later differences may be driven by the empathic concern specific to negative trials. Negative and positive empathy were associated with differential processing of direct and averted gaze before and during the N100 time window, which may reflect top-down modulations linked to the affective sharing component of empathy. Positive empathy was also associated with differential processing of eye-gaze during the P200 time window, which might relate to the finding that participants reported feeling slightly more positive empathy after perceiving direct gaze. These results suggest that perceived gaze direction impacts our ability to share in another's emotional state, highlighting the importance of studying empathy in the context of faces.

Chapter 4: Eye-gaze processing during affective theory of mind judgements[10]

4.1 Introduction

It has long been observed that we look to the eyes when engaging in theory of mind (Baron-Cohen & Cross, 1992), the act of making inferences about another person's mental state, also referred to as "mentalizing". Indeed, the interpretation of eye-gaze is a component of current theories about how everyday theory of mind works (e.g. Baron-Cohen & Cross, 1992; Readinger, 2002). Some of the most compelling evidence for the link between eye-gaze processing and theory of mind is that there is altered eye-gaze processing in special populations like autism spectrum disorder (Lajiness-O'Neill et al, 2014; Pelphrey et al., 2005; Senju et al. 2002; 2005; 2009a), schizophrenia (Akiyama, et al. 2008; Kington et al., 2000; Kohler et al., 2008) and social anxiety disorder (Weeks et al., 2013; Wieser et al. 2009), all of which have altered theory of mind (Baron-cohen, 1997; Baron-cohen et al. 1995; 1997; Bora et al. 2009; Cui et al., 2017; Hezel & McNally, 2014; Mathersul et al. 2013; Sprong et al., 2007). Two studies have also observed that there is similar brain activity elicited in eye-gaze processing studies as there is in theory of mind studies, leading to the idea that gaze processing recruits the same neural networks as making mental state inferences (Calder et al., 2002; Conty et al., 2007). However, this hypothesis has never been directly tested within the same participants, which would be necessary to support this claim. Whether eye-gaze processing and theory of mind processing are functionally linked thus remains unclear. Finding a link between the two in neurotypical individuals would be an important step towards better understanding patient populations.

One reason why it has been difficult to come up with a comprehensive theory linking eye-gaze to theory of mind is that theory of mind is a complex construct. First, there appears to be a meaningful difference between affective theory of mind, the ability to make inferences about emotional states, and cognitive theory of mind, the ability to make inferences about beliefs and motivations that do not involve emotion. In support for this distinction, the neural correlates of cognitive and affective theory of mind have been shown to be somewhat dissociable (e.g. Bodden et al. 2013; Kalbe at al. 2010; Shamay-Tsoory et al., 2007a; 2007b), and special

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[10] A version of this chapter is in preparation for submission to an international journal in the field.

populations can show impairments in one type of theory of mind, but not the other. For example, there appears to be specifically impaired affective theory of mind in schizophrenia (Shamay-Tsoory et al. 2007b) and cognitive theory of mind in Alzheimer's disease (Poletti et al. 2012). The first step is thus to determine whether eye-gaze processing is linked to affective theory of mind, cognitive theory of mind, or both.

In the present study we focus specifically on the link between eye-gaze processing and affective theory of mind because there is evidence to suggest that individuals' eye gaze behavior changes depending on their affective state (e.g. Allard & Kensinger, 2018; Demeyer et al., 2017; Isaacowitz & Choi, 2011; Isaacowitz et al., 2008; Kim et al., 2018; Kleinke 1986; Natale, 1977; Wadlinger, & Isaacowitz, 2006), and because gaze behavior acts to regulate emotions (see Isaacowitz et al. 2006 for a review). This research suggests that eye-gaze cues have predictive validity for emotional state, such that if patterns of eye-gaze behavior were observed over time, they could be used to help predict the gazer's emotions. While much of this research has not been done in the context of social interactions, an older review by Kleinke (1986) provides some excellent insights on how eye-gaze towards a partner changes to regulate interactions (e.g. as a function of intimacy, control, and affection). In particular, individuals who have undergone a negative mood induction make less eye-contact than those who have undergone a neutral or positive mood induction (Natale, 1977). If we are sensitive to this pattern of gaze behavior, we may implicitly determine that someone who is gazing away is feeling more negative than someone gazing at us. Eye-gaze cues may also help us predict emotional state because direct gaze facilitates discrimination of happy and angry facial expressions (see Study 1; Adams & Kleck, 2003; 2005; Sander 2007). While emotion discrimination is largely based on physical facial cues (e.g. a smile suggests joy) and can be completed without actually inferring a mind behind the expression, it may act as a stepping stone to facilitate more abstract forms of affective theory of mind (Clark et al., 2008).

Furthermore, the impact that direct gaze has on an observer's emotional state (see Section 1.1.2; Hietanen, 2018 for a review) may affect theory of mind judgements, given that an observer may use their own emotional state to make inferences about how others are feeling (Demers & Koven, 2015). For example, Demers and Koven (2015) demonstrated that affective theory of mind is impaired in those with alexithymia who have trouble attending to their own emotional state. Finally, as empathy and affective theory of mind have many common neural correlates (Sebastian et al., 2012), the interaction between direct gaze processing and positive empathy (see Study 2) may extend to affective theory of mind.

The present study tested the hypothesis that eye-gaze processing impacts inferences about how positive or aroused other people are feeling. Given that positive emotions can result from direct gaze perception (Hietanen, 2018 for a review; Study 2; Kampe et al., 2001; McCrackin & Itier, 2018a; Strick et al., 2008) and are associated with displaying increased direct gaze (Natale, 1977), we predicted that individuals would infer that someone with direct gaze was feeling more positive than someone with averted gaze. Conversely, averted gaze may be associated with experiencing negative emotion. We presented participants with pictures of direct and averted gaze faces with neutral expressions. These faces were primed with the sentences from Study 2, which described the individuals in positive, negative or neutral scenarios. Participants were then asked to rate each individual's emotional valence and arousal. We investigated whether the direction of eye-gaze would impact participants' affective theory of mind estimates, and the time course of these cognitive processes using ERPs time-locked to the face.

As in Studies 1 and 2, we performed both exploratory and hypothesis driven mass univariate analyses, selecting *a priori* time-windows based on previous ERP research on eye-gaze and emotional processing, as the processes that modulate these ERP components are also likely involved in affective theory of mind. These included the early face-sensitive N170 (see Section 1.3.2), the emotion-sensitive Early Posterior Negativity (EPN; Section 1.4.3), the frontal N100 (Section 1.4.1) and N200 (Section 1.4.2), and the centroparietal P300 (Section 1.4.4) and the Late Positive Potential (LPP; Section 1.4.5).

We predicted that the earlier N100 or N200 components would be modulated by sentence valence as the N200 was in Study 2. Specifically, given the theory that the N100 and N200 reflect the activation of frontal emotion areas (Fan & Han, 2008), we predicted that there would be an amplitude difference between emotional trials and neutral ones (though the direction of this difference was hard to predict given past mixed findings; Coll, 2018). However, we also predicted that eye-gaze would modulate the response of frontocentral areas to emotional stimuli. This would result in a sentence valence and gaze direction interaction, similar to the N100 gaze and sentence valence interaction in Study 2 and to the N200 gaze and task interaction in Study 1.

As the N100 and N200 are components with hypothesized frontocentral generators (e.g. Carretie et al., 2004), and frontocentral brain areas have been implicated in both theory of mind and eye-gaze processing (Calder et al., 2002; Conty et al., 2007), we thought that the difference in amplitude between direct versus averted gaze faces in the emotional trials (i.e. replicating Study 2)might be even bigger in an affective theory of mind paradigm.

We also predicted that the later P300 and LPP would be modulated by sentence valence, as they were in Study 2. Furthermore, the P300 and LPP are thought to reflect cognitive evaluation and top-down regulation of emotional processes before conscious awareness (Decety et al., 2010; see Decety and Lamm, 2006; Fan & Han, 2008; and Gonzalez-Liencres et al., 2013, for more discussion). As such, we predicted that these later components may be more sensitive to any learned contingencies between a person's gaze behavior and their affective state. Therefore, an interaction between gaze and trial valence may occur at these later time-windows during an affective theory of mind task, even though there was no interaction on these components in the empathy task (Study 2).

4.2. Methods

4.2.1 Participants

Fifty [50] University of Waterloo (UW) undergraduates participated in the study. Ten participants were excluded for not completing the study (*n*=3), eye-tracking and technical issues (*n*=3), not reading a majority of trial sentences (*n*=1), for having too few trials per condition after EEG cleaning (*n*=2), and for falling asleep during the study (*n*=1). This left a final sample of 40 participants (21 female, 19 male*; mean age* = 19.55; *SD* = 1.80) in our analyses. Participants reported in a prescreen questionnaire that they had normal or corrected-to-normal vision and self-rated their face identity and expression recognition as at least a 7/10 on a Likert scale to minimize the chances of having face-processing impairments. Participants also reported living in Canada or the United States for the past five years, no recreational drug use, and no previous loss of consciousness lasting over 5 minutes. (Caucasian: *n*=16, Chinese: *n*=4, Other Asian Groups: *n*=7, East Indian: *n*=2, Korean: *n*=2, Middle Eastern: *n*=2, Hispanic: *n*=1, Native Canadian: *n*=1, and Other Not Listed: *n*=5).

Informed consent was provided before participating, and course credit was granted upon study completion. The UW Research Ethics Board approved this study.

4.2.2 Face Stimuli

The face stimuli used were identical to Study 2 (see Section 3.2.2.2).

4.2.3 Sentence Stimuli

The sentences selected for the EEG-eye-tracking study reported in Study 2 (see Section 3.2.1) were also used here.

4.2.4 Experimental Design

The experimental set-up, including the testing computer and eye-tracker settings, was identical to that in Studies 1 and 2 (see Section 2.2.3).

Figure 16 depicts the trial progression, which was identical to that of Study 2 (see Section 3.2.2.3) up until the point when the participant was asked to respond. In this study, a first rating screen asked participants to indicate how positive or negative the individual felt (rated from 1/very negative to 9/very positive), and the second asked participants to indicate how affectively aroused the individual was (from 1/very unaroused to 9/very aroused). Valence and arousal were defined for the participant in the study instructions, and participants had unlimited time to indicate their answer with a number key press. Trial randomization, counterbalancing, and the number of trials per condition were identical to Study 2 (see Section 3.2.2.3).

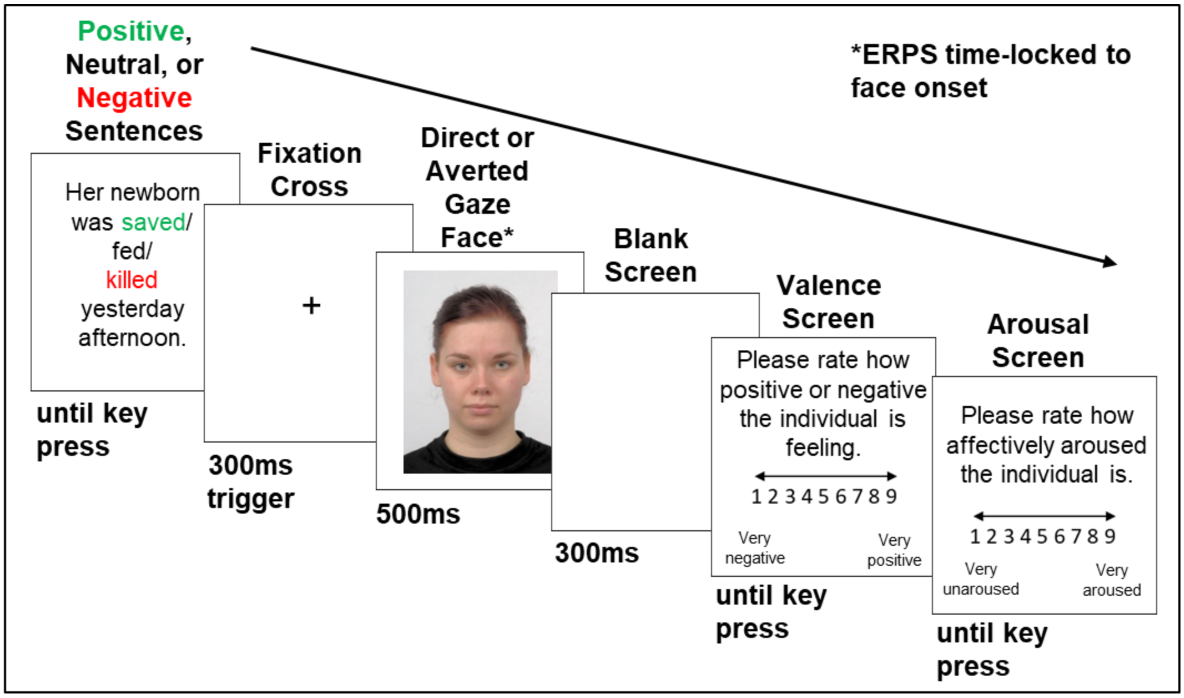

Figure 16. Sample Study 3 trial progression

Trial progression illustrated with a direct gaze trial.

4.2.5 Electroencephalography Recording

The EEG recording was identical to Studies 1 and 2 (see Section 2.2.4).

4.2.6 Data Preprocessing and Cleaning

The data processing steps were identical to Studies 1 and 2 (see Section 2.2.5). An average of 5.65 trials (*SD* = 7.92) were removed per participant for not reading the sentences, and 13.38 trials (*SD* = 25.28) for failing to maintain fixation on the nasion and eyes for the first 250ms of face presentation. On average, 1.95 (*SD*= 1.16) ICA components were removed per participant. After the cleaning stages were used to remove additional noisy trials, an average of 60.48 trials (*SD* = 15.39) per condition remained in the final ERP averages.

4.2.7 Behavioural Data Analysis

The mean valence and arousal ratings for each condition were averaged for every participant. One ANOVA was run with within-subjects factors of sentence valence (3; positive, negative; neutral) and gaze direction (2; direct, averted) on mean valence ratings, and another on mean arousal ratings. SPSS 25 was used to run the analyses and greenhouse-Geisser corrected degrees of freedom are reported below when Mauchly's sphericity test was significant. We report the raw *p*-values for follow up paired comparisons below, with a significance threshold set at the Bonferroni corrected p-value of $p<.016$ (0.05/3 comparisons).

4.2.8 EEG Data Analysis

Our use of the Factorial Mass Univariate Toolbox (FMUT; Fields, 2017) and the Permutation Based Cluster Mass correction for multiple comparisons was identical to Studies 1 and 2 (see Section 2.2.7). Each omnibus ANOVA included the within-subjects factors of gaze direction (2; direct gaze, averted gaze) and sentence valence (3; positive, negative and neutral). An exploratory ANOVA was performed on all electrodes and time-points from 50ms to 800ms post-face onset. Then, ANOVAs testing our specific a priori time-windows and electrode locations were run. This included the frontocentral N100 (50-120ms) and N200 (200-300ms), both at Fp1, Fp2, Fpz, AF3, AF4, AFz, F4, F3, F1, F2 and Fz. It also included the parieto-occipital N170 (130-300ms) and EPN (200-350ms), both at P9, P10, PO9, PO10, P7, and P8. Follow-up ANOVAs ($p<.016$) were conducted on the electrodes and time-windows that were significant in the omnibus ANOVAs. As the exploratory analysis revealed P300 and LPP related activity, these components were not analyzed further.

4.3 Results

The behavioural data and FMUT results files will be available in the Open Science Framework Repository upon peer-reviewed publication of this study.

4.3.1 Behavioural Results

4.3.1.1 Valence Ratings

There was a main effect of sentence valence on ratings of how positive or negative participants believed the individual was feeling ($F(1.06, 41.48) = 78.56$, $MSE = 3.03$, $p <.001$, $\eta p^2 = .67$; Figure 17a). Bonferroni corrected paired comparisons indicated that participants rated the individual's emotional valence as higher when seen in the context of positive relative to neutral ($t(39)= 7.95$, $MSE= .13$, $p<.001$) and negative ($t(39)= 8.98$, $MSE= .28$, $p<.001$) sentences, and when seen in the context of neutral relative to negative ($t(39)= 9.11$, $MSE= .16$, $p<.001$) sentences.

There was also a main effect of gaze direction ($F(1, 39) = 52.07$, $MSE = .076$, $p < .001$, $\eta p^2 = .57$; Figure 17a), where participants gave faces with direct gaze a slightly higher valence rating than faces with averted gaze. There was no interaction between gaze direction and sentence valence on participants' valence ratings ($F(2, 78) = 1.59$, $MSE = .020$, $p = .21$, $\eta p^2 = .039$).

4.3.1.2 Arousal Ratings

There was a main effect of sentence valence on ratings of how emotionally aroused participants believed the individual was ($F(1.64, 63.86) = 22.65$, $MSE = 1.91$, $p < .001$, $\eta p^2 = .37$; Figure 17b). Bonferroni corrected paired comparisons indicated that participants rated individuals' emotional arousal as higher when seen in the context of positive ($t(39)= 4.81$, $MSE= .18$, $p<.001$) and negative ($t(39)= 5.47$, $MSE= .24$, $p<.001$) relative to neutral sentences, and in the context of negative relative to positive sentences ($t(39)= 2.71$, $MSE= .17$, $p=.010$).

There was no main effect of gaze direction ($F(1,39) = 1.44$, $MSE = .13$, $p =.24$, $\eta p^2 = .036$), but there was an interaction between gaze direction and sentence valence ($F(2, 78) = 6.00$, $MSE = .044$, $p = .004$, $\eta p^2 = .13$; Figure 17b). Bonferroni corrected paired comparisons comparing direct and averted gaze in each sentence valence condition indicated that there was no effect of gaze during the positive ($t(39)= .72$, $MSE= .07$, $p=.48$) and neutral conditions ($t(39)= -.69$, $MSE= .054$, $p=.49$). However, there was an effect of gaze during the negative condition ($t(39)= -3.32$, $MSE= .053$, $p=.002$), with higher arousal ratings for negative faces with averted gaze than with direct gaze.

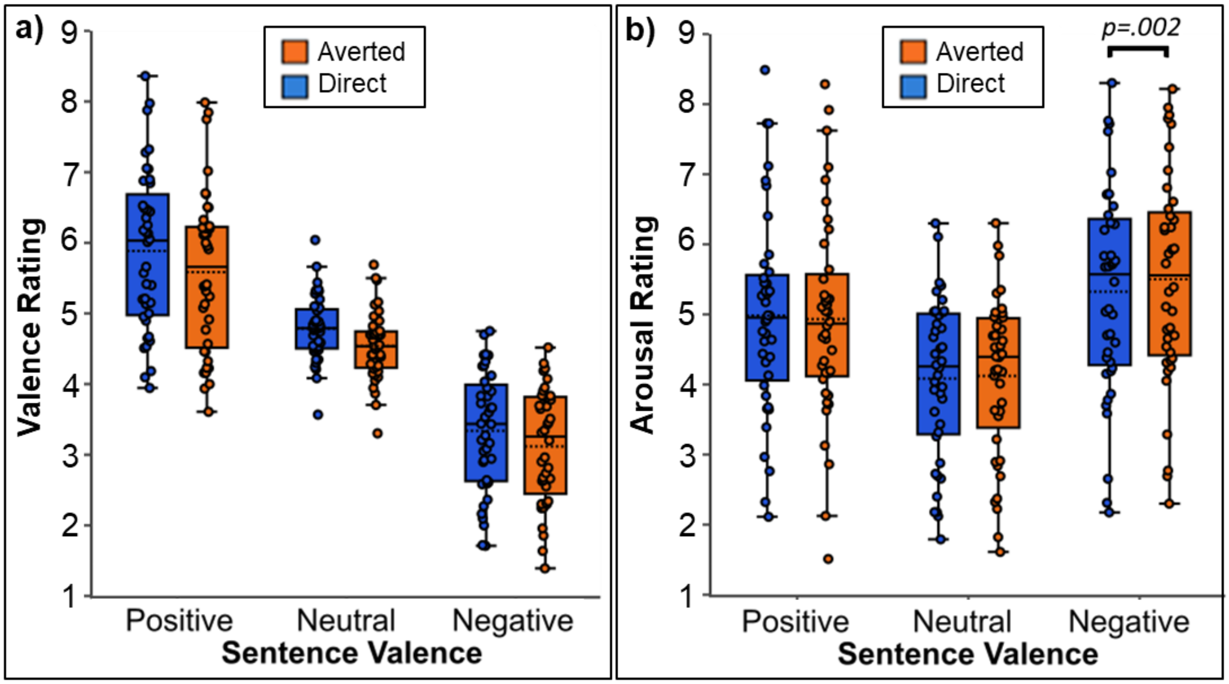

Figure 17. Mean valence and arousal ratings for each condition

a) Average ratings of how positive or negative the individual was likely feeling (from 1/very negative to 9/very positive) for each gaze and sentence valence condition. Note the slightly higher ratings for direct than averted gaze conditions across sentence valence conditions.
b) Average ratings of how affectively aroused the individual was likely feeling (from 1/very unaroused to 9/very aroused) for each gaze and sentence valence condition. The mean and median for each condition are indicated with dotted and solid lines respectively. Data points which fall between the 25th and 75th percentiles are shown within the boxes.

4.3.2 EEG Results

4.3.2.1 Exploratory Analysis Over All Electrodes (50-800ms)

There was a main effect of sentence valence from 405-800ms (encompassing the P300 end and the LPP). It was a widespread cluster (IO1, LO1, Fp1, AF7, F7, F3, FT7, C3, C5, CP1, CP3, TP7, TP9, P1, P3, PO3, PO7, CB1, O1, Fz, FCz, Cz, CPz, Pz, POz, C2, FC2, C4, CP2, P2, P4, P6, PO4, O2), strongest over central and parietal sites (*p*=.0035; Figure 18a). Follow-up ANOVAs were performed to compare valence conditions and included the significant electrodes and time-points (i.e. 405-800ms) from the omnibus effect. A significant cluster indicated that there was a difference between the negative and neutral (*p*=.00010; Figure 18b) trials, while there was no difference between negative and positive trials (Figure 18c; cluster *p*s >=.75).

Another significant cluster indicated that there was a difference between positive and neutral (Figure 18d; *p*=.00085) conditions. Both positive and negative trials had more positive amplitudes than neutral trials over posterior sites.

There was also an interaction between gaze and sentence valence from 540-800ms (*p*=.040; Figure 19a). The interaction cluster was strongest over centroparietal sites despite being widespread (C1, P1, P3, PO7, O1, CPz, Cz, Oz, Iz, C2, FC4, P2, P4, CP4, PO4, P10, O2, PO8). Follow-up ANOVAs compared how direct and averted gaze were processed in each valence condition, including the significant electrodes and time-points (i.e. 540-800ms) from the omnibus interaction. While with a strict Bonferroni cut-off of *p*<.016 (0.05/3 for the three follow up comparisons from the omnibus exploratory analysis), only the neutral gaze difference cluster would be considered significant, clusters did form for each valence condition and a clear pattern emerged. Over centroparietal sites, direct gaze elicited less positive amplitudes than averted gaze in the neutral condition (Figure 19b; *p*=.0078), but more positive amplitudes than averted gaze in both the negative (Figure 19c; two clusters; *p*=.051 and .062) and positive (Figure 19d; *p*=.012) conditions.

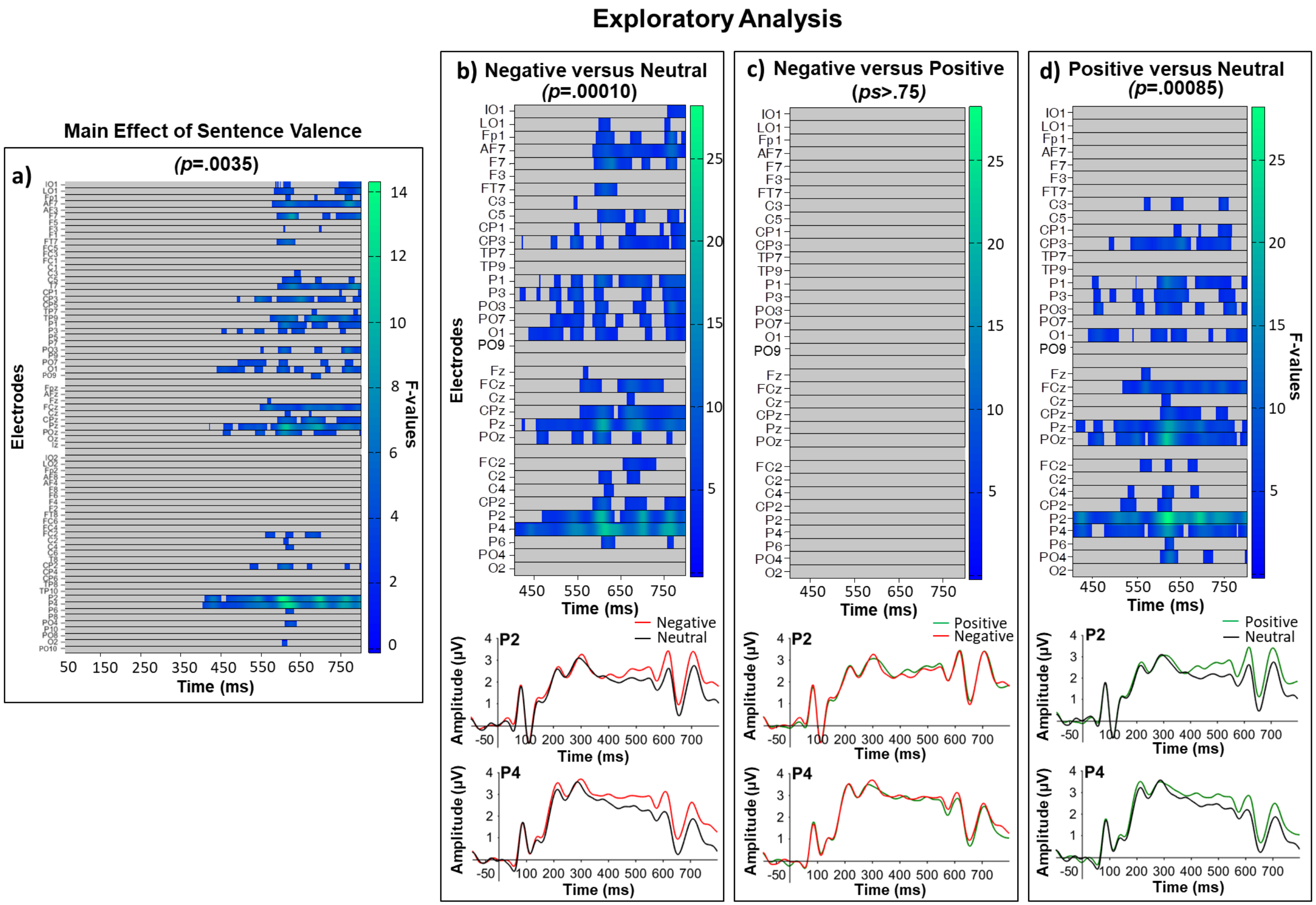

Figure 18. Exploratory analysis sentence valence effect

a) Sentence valence modulated ERP amplitudes during our exploratory analysis over all electrodes and time-points (from 50-800ms). Familywise error rate was controlled for with the Permutation Based Cluster Mass technique (at p <.05 for the omnibus and p<.016 for the follow-up paired comparisons). X-axes denote time following face onset, while y-axes denotes electrodes. Coloured sections depict the F values in each cluster, with the right colour bar as a legend. The overall p-value for each cluster is listed. The negative condition was significantly different from the **b)** neutral condition but not the **c)** positive condition (clusters not pictured as they did not approach significance), while the positive condition was significantly different from the **d)** neutral condition. Representative electrodes (P2 and P4) illustrate the direction of effects.

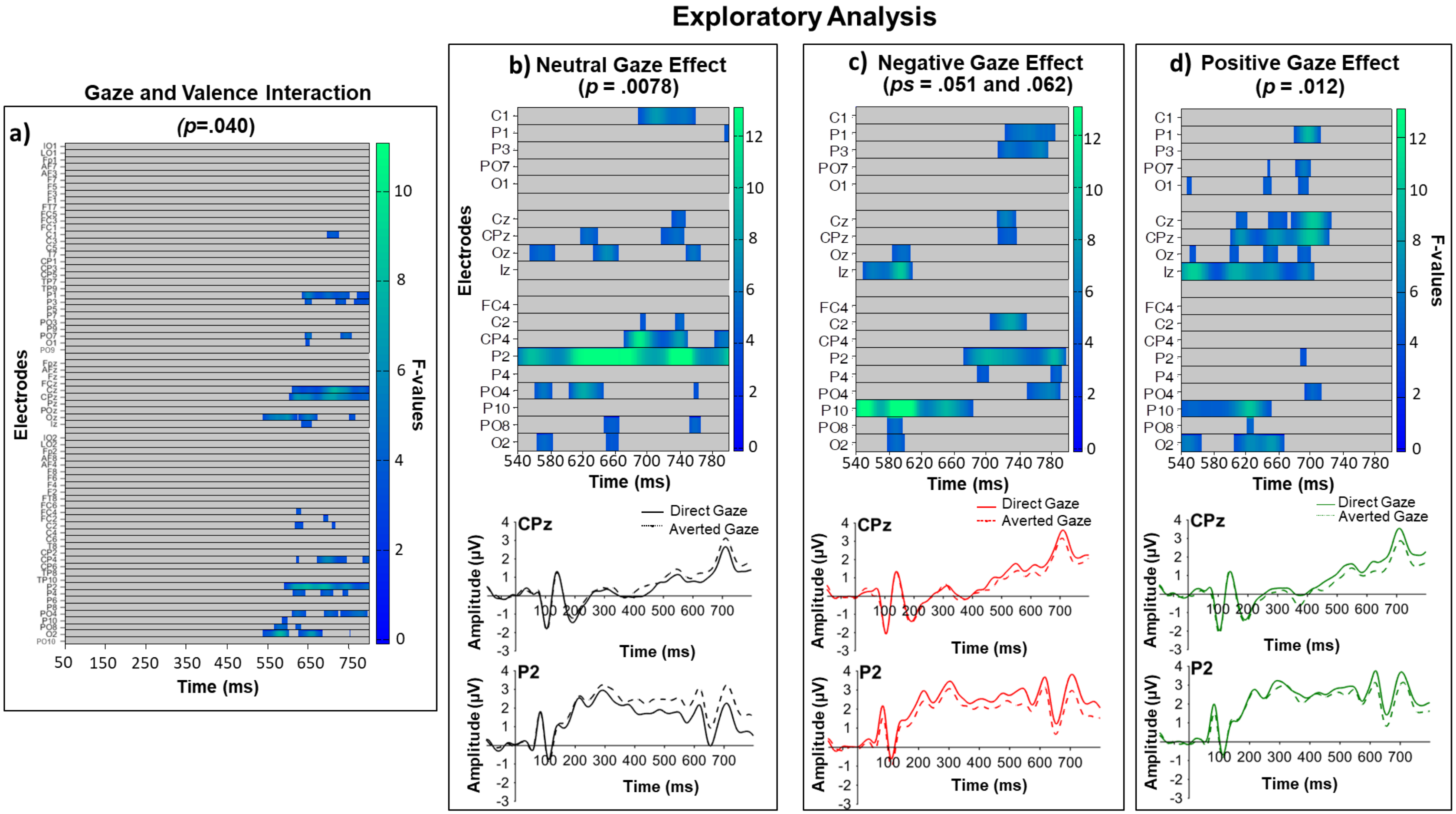

Figure 19. Exploratory analysis gaze and sentence valence interaction

a) Our exploratory analysis over all electrodes and time-points (from 50-800ms) revealed that gaze direction interacted with sentence valence to effect ERP amplitudes. The Permutation Based Cluster Mass technique controlled for type I error (at p <.05 for the omnibus and a Bonferroni corrected p<.0016 threshold for the paired comparisons). Electrode names are plotted on the y-axes, and time-points following face presentation are plotted on the x-axes. Coloured sections denote the magnitude of the F values at the electrode and time-point in each cluster, and the cluster p-values are provided. Representative electrodes where the omnibus interaction was strong (CPz and P2) demonstrate that during **a)** neutral trials, direct gaze resulted in less positive ERP amplitudes than averted gaze, while the opposite trend was seen during **c)** negative trials (note that two trending clusters are pictured here) and **d)** positive trials.

4.3.2.2 Frontocentral Sites During the N100 Time-window (50-120ms)

The N100 analysis yielded no significant main effects or interactions (cluster *ps*>= 0.499570.)

4.3.2.3 Frontocentral Sites During the N200 Time-window (200-350ms)

There was a main effect of sentence valence on the N200 over right, left and central frontal sites (Figure 20a; *p*=.00083; AF3, F3, F1, AFz, AF4, F4, F2). Follow-up ANOVAs (*p* threshold = 0.016) comparing the valence conditions for those significant time-points (215-350ms) and electrodes produced a significant cluster for the positive vs. neutral comparison (*p*=.0018; Figure 20b). There was also a cluster for the negative vs. neutral comparison (*p*=.022; Figure 20a), but this was not significant with our cutoff. Both negative and positive trials had more positive ERPs over frontal sites. Negative and positive trials were not significantly different from each other (cluster *p*s>= 0.67; Figure 20c).

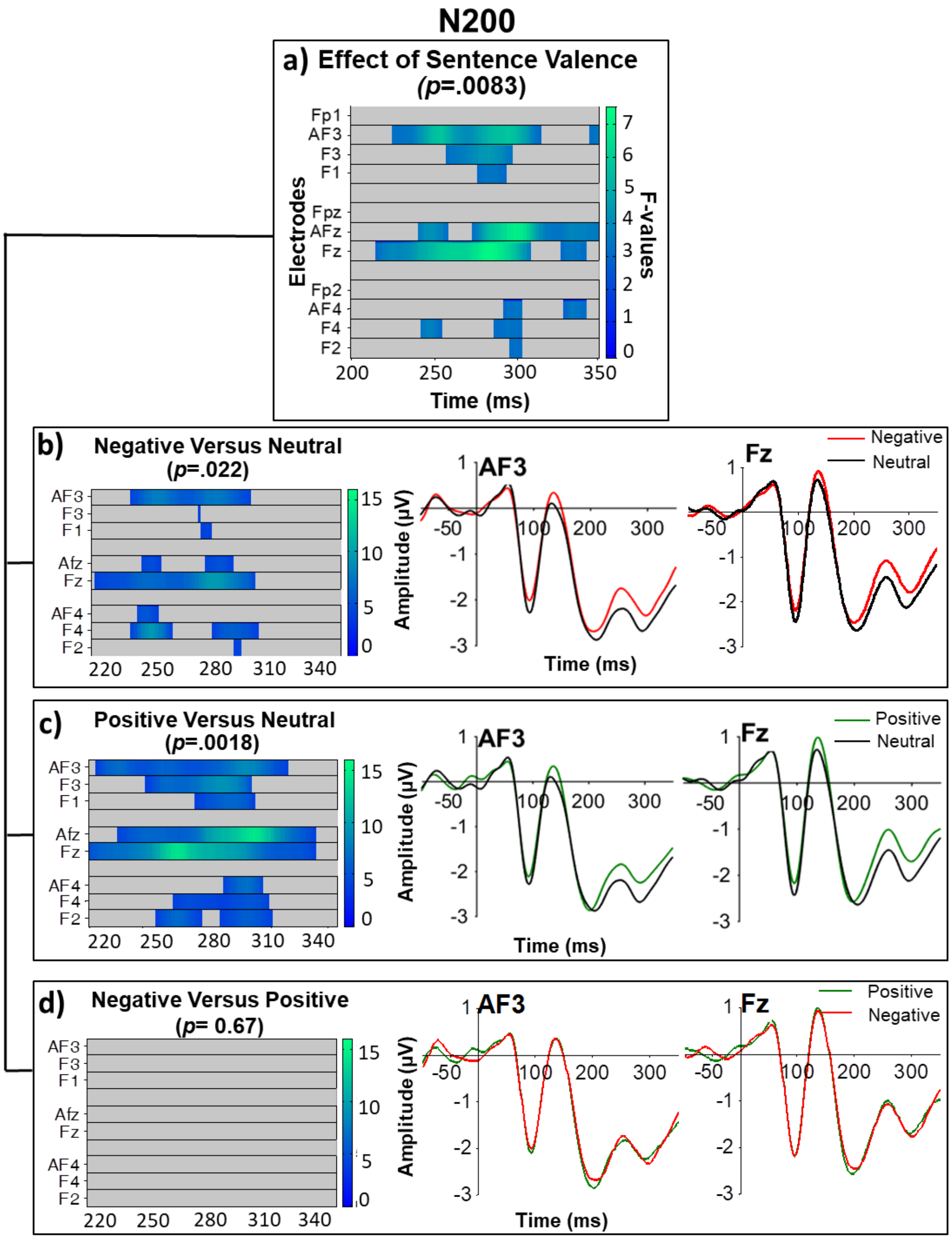

Figure 20. N200 sentence valence effect

a) Sentence valence modulated frontal ERP amplitudes during the N200 analysis (200-350ms). Electrode names are plotted on the y-axes, with time following the face onset on x-axes. The Permutation Based Cluster Mass technique corrected for multiple comparisons, at *p* <.05 (and at *p*<.016 for the three post-hoc comparisons). Coloured sections depict the *F* values in each cluster, as denoted by the right hand colour bar, and the *p*-value for each cluster is listed (no cluster formed for the negative versus positive comparison). The main effect in the omnibus ANOVA was driven by a trending difference between the **b)** negative and neutral condition, and a significant difference between the **c)** positive and neutral conditions. There was no difference between the **d)** negative and positive conditions (cluster not pictured as it did not approach significance). AF3 and Fz are representative electrodes showing that both negative and positive trials resulted in less negative N200 than neutral trials.

4.3.2.4 Parieto-occipital Sites During the N170 Time-window (130-300ms)

There were no significant effects or interactions on the N170 (cluster *ps* >=.28).

4.3.2.5 Parieto-occipital Sites During the EPN Time-window (200-350ms)

There was a main effect of sentence valence on the tail part of the EPN and end of the P200, clustered over the right hemisphere (Figure 21a; *p*=.050; P10, P8, PO8, PO10). Follow-up ANOVAs on the significant electrodes and time-points (265-310ms) indicated that negative trials had more negative ERPs than neutral trials (Figure 21b; *p*=.00061) with a similar cluster for positive trials that did not meet our Bonferroni corrected significance cut-off (Figure 21c; *p*=.017). No cluster formed for the negative versus positive comparison, and thus they were not significantly different (Figure 21d).

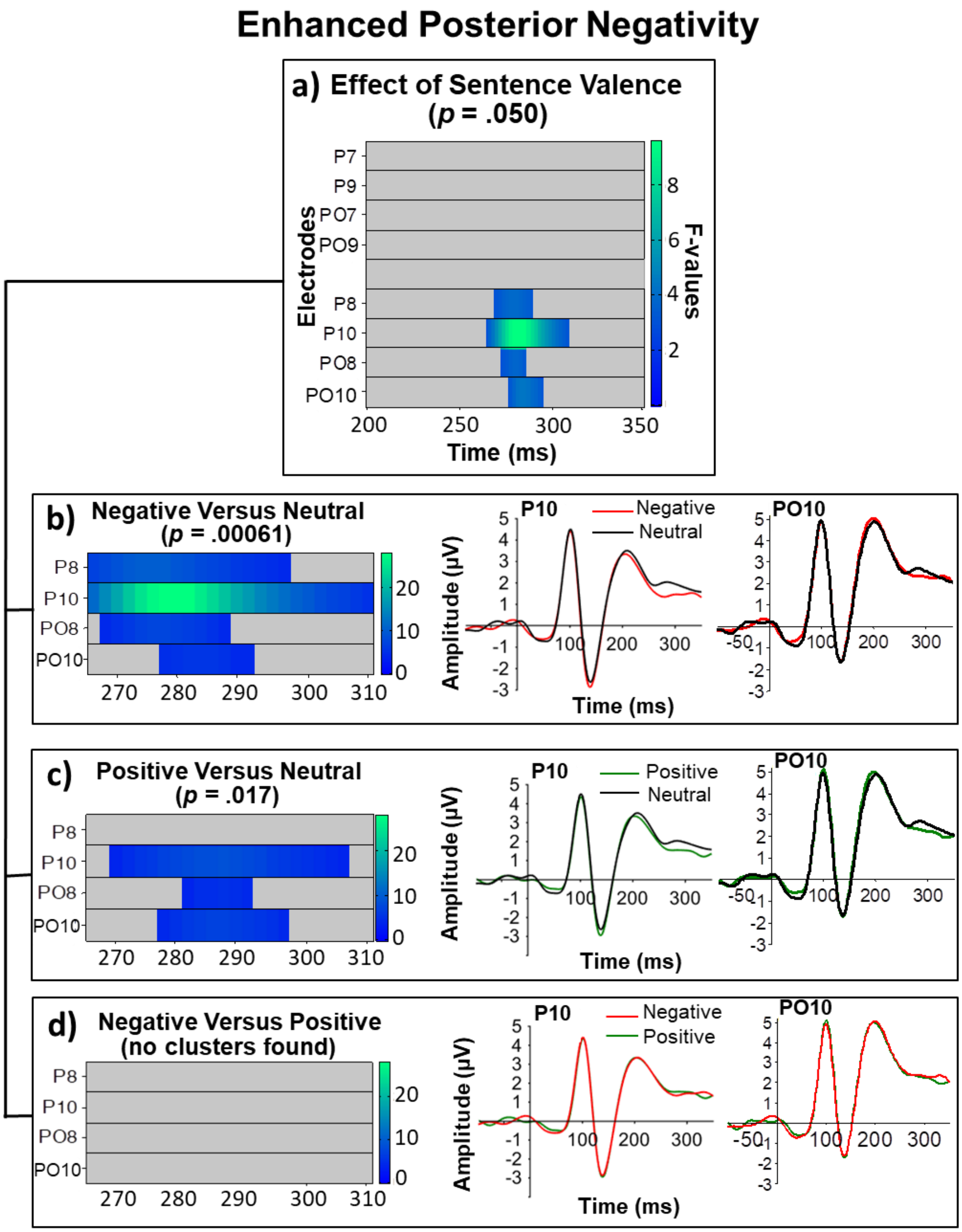

Figure 21. EPN sentence valence effect

a) Sentence valence modulated the EPN and tail end of the P200 in a right-lateralized manner. Multiple comparisons were corrected for using the Permutation Based Cluster Mass technique, at p <.05 (and at p<.016 for the follow-up comparisons). Electrode names are shown on y-axes, and time-points post-face onset are shown on the x-axes. Clustered time-points and electrodes are coloured, with the colour shade corresponding to the magnitude of *F*-values shown on the right-hand bar. Follow up comparisons indicated that there was a significant difference between the **b)** negative and neutral conditions, and a trending difference between the **c)** positive and neutral conditions. There was no difference between the **d)** negative and positive conditions. Two representative electrodes (P10 and PO10) demonstrate that negative and positive trials produced more negative ERP amplitudes than neutral trials between 265-310ms.

4.4 Discussion

The eyes convey some of the most important social cues (see Cañigueral & Hamilton 2019; George & Conty, 2008; Itier & Batty, 2009), and the interpretation of eye-gaze is incorporated into many current theories about how we infer the mental states of others (Readinger, 2002). Despite this, there is actually very little evidence of a direct link between direct and averted gaze processing and affective theory of mind, our ability to infer the emotions of others. We presented participants with sentences describing individuals in positive, negative or neutral scenarios, followed by direct or averted gaze pictures of the individuals' faces. Participants made affective theory of mind judgements about each person, and we investigated whether the face's gaze direction would impact those judgements, and event-related potential (ERP) markers of affective processing.

Despite the fact that paying attention to the eye-gaze was not required for participants to complete the task, gaze direction did impact affective theory of mind judgements. Participants consistently rated that direct gaze individuals were feeling slightly more positive than averted gaze individuals, regardless of whether the sentence context was positive, negative, or neutral. They also rated that individuals with averted gaze were experiencing more arousal, but this was specific to negative contexts only. We believe this is one of the first demonstrations that direct and averted gaze processing can impact perception of the gazer's positive affect and arousal. Critically, while other studies have shown that direct gaze perception can facilitate discrimination of positive (happy) facial expressions (Study 1; Adams & Kleck, 2003; 2005; Sander 2007), the faces here were neutral, carrying no affective content themselves. Discrimination of facial expressions may be a stepping stone towards affective theory of mind (Clark et al. 2008), but it does not require making a mental state inference. Here, direct gaze impacted perceptions of how a positive, negative, or neutral situation would affect an individual's mood, which is a better test of the link between gaze processing and affective theory of mind.

There are a couple potential explanations as to why perceived gaze direction impacted affective theory of mind. One theory is that observers use their own emotional state as a guide when inferring the emotional state of others (Demers & Koven, 2015); if the observer is feeling more positive, perhaps this biases their affective theory of mind ratings to also be more positive. Perception of direct gaze has been shown to produce increased positive affect (McCrackin &

Itier, 2018a), positive empathy (Study 2) and reward processing (Kampe et al., 2001; Strick et al., 2008) within the observer. While this aligns with our finding that participants rated direct gaze individuals as more positive, it does not fit with the arousal ratings results. Individuals in negative contexts were perceived to be more affectively aroused if they displayed averted gaze, while it is perception of direct gaze that has been consistently linked to increased arousal in an observer (Conty et al., 2010; Helminen et al., 2011; Nichols & Champness, 1971;), including for faces primed by both positive and negative contextual sentences (McCrackin & Itier, 2018a).

Another theory which may better explain the data stems from research suggesting that individuals change their eye gaze behavior as a function of their affective state (Allard & Kensinger, 2018; Demeyer et al., 2017; Isaacowitz et al., 2008; Isaacowitz & Choi, 2011; Kim, Seo, & Laine, 2018; Kleinke 1986; Natale, 1977; Wadlinger, & Isaacowitz, 2006) to regulate their emotions (see Isaacowitz et al. 2006 for a review). While the relationship between eye-gaze and affective state may not be something that we are always consciously aware of, we engage in so many social interactions that we likely pick up these associations over time. If these associations are learned, incorporating eye-gaze cues into affective theory of mind judgements would offer some predictive validity and allow for more accurate judgements. For example, we found that faces with direct gaze were rated as feeling more positive, and there is some data to suggest that individuals who are feeling more positive make more eye-contact (Natale, 1977).

While participants completed the task, we captured ERPs time-locked to the face onset and associated with affective processing. This allowed us to investigate whether gaze direction impacted these ERPs. It also allowed for a comparison of the results to those of Study 2, in which the same sentences and faces were presented, but where participants completed an affective empathy task instead of an affective theory of mind task. First, we found that there were more negative N200 amplitudes for neutral faces in neutral contexts than in positive and negative contexts, though it should be noted that the negative-neutral comparison did not meet our Bonferroni cut-off (p=.022 with a cutoff of p<.016). It has been proposed that the frontal N200 reflects initial activation of emotion areas during emotional contagion, perhaps through a system of mirror neurons (Fan & Han, 2008). The present study and Study 2 suggest that the N200 in response to neutral faces can be modulated by the emotional context provided by sentence primes. This is evidence that a physical affective cue is not needed to modulate the N200, as there was nothing inherently emotional about the faces themselves. The implication of this finding is that the N200 is likely a more flexible process than initially thought, allowing the prioritization of emotional stimuli of varying types.

We also found that during the EPN time-window (265-310ms), negative trials produced more negative ERPs than neutral trials, with a similar trend for positive compared to neutral trials (although that did not meet our cut-off). These results mirror the EPN findings we reported in the empathy study (Study 2), suggesting that the activity during this time-window is largely task independent. This is not too surprising, given that the EPN has been shown to be modulated during many types of tasks by both positive and negative stimuli, including facial expressions (Itier & Neath-Tavares, 2017; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Schupp et al., 2004b), verbal stimuli (Herbert et al. 2008; Kissler et al. 2009; Schact & Sommer, 2009) and pictures (Schupp et al., 2004a). These results support the assumption that the EPN reflects attentional prioritization of emotional stimuli, regardless of whether the stimuli contain inherent emotion content (e.g. a facial emotion) or are presented within an emotional context.

Contextual valence also impacted ERP amplitudes from 405-800ms over frontal, central and centroparietal sites, spanning the end of the P300 and LPP components. This valence effect was almost identical in timing and distribution as the valence effect that we found in Study 2, with one key difference. In the empathy study, negative trials differed from both neutral and positive trials (which were similar), while here, both negative and positive trials (which were similar) differed from neutral trials. While group differences could be a factor, specificity for negative trials during an empathy task but not during an affective theory of mind task may reflect the type of emotional evaluation involved. In the empathy task, we proposed that specificity for negative trials may reflect empathic concern for the protagonist in the situation. The present affective theory of mind task simply required inferring emotional state, so there was likely less empathic concern for the individual than in the empathy task.

Contrary to our predictions, there was no sentence valence by gaze direction interaction on either the N100 or N200 in the present study. This lack of effect is at odds with the interaction between eye-gaze processing and task demands that we previously found during the N200 (Study1) and between gaze processing and sentence valence during the N100 in an affective empathy task (Study 2). We had hypothesized that these frontal gaze effects may be due to shared orbitofrontal cortex or inferior frontal gyrus activation between emotional contagion (see Shamay-Tsoory et al., 2009 for a review) and the processing of eye-gaze and facial expressions (Dapretto et al. 2006). Critically, since these areas are implicated in higher order social cognition and theory of mind, we had predicted that eye-gaze effects on theory of mind processing may occur there. However, we instead found a later eye-gaze and sentence valence interaction over centroparietal sites (which was not seen in Study 2). Gaze direction was processed differently during positive and negative trials than during neutral trials from 540-800ms, spanning the LPP. Specifically, during neutral trials, direct gaze elicited more negative amplitudes than averted gaze trials, while the opposite pattern was observed for both positive and negative trials (note that for negative trials this was a statistical trend). While not in a frontal location, we believe this later time-window may still reflect elaborative processing related to affective theory of mind, likely including cognitive evaluation of the emotional state of the other person. As this later time-window is also likely more sensitive to top-down modulation, these effects may also reflect the cognitive evaluation of any learned contingencies between a person's gaze behavior and their affective state. For example, if an individual is consciously or unconsciously drawing on their past experience with eye-gaze and affect while making theory of mind inferences, this would likely show up at a later time-window instead of earlier windows thought to reflect more spontaneous processing. This idea is expanded upon in the general discussion below.

In summary, the present research provides preliminary evidence that eye-gaze processing does impact affective theory of mind. Eye-gaze processing and neural measures of affective processing interact from 540-800ms over centroparietal and parieto-occipital sites. At the behavioural level, direct gaze is associated with the inference of increased positive affect regardless of the situational context, while averted gaze is associated with the inference of increased arousal during negative scenarios.

Chapter 5: General Discussion

We use the eye-gaze of others to make social inferences that inform our interactions with them. Not only do direct and averted eye-gaze provide information about the gazer, but they also have unique attentional (see Section 1.1.1) and emotional (see Section 1.1.2) effects on the observer. However, the social impact and neural processing of direct and averted gaze are by no means clear-cut. As discussed in previous studies (Latinus et al., 2015; Puce et al., 2015), not only do methodological factors like EEG reference site make it hard to compare results from each study, but it seems that several factors can impact eye-gaze responses (also see daSilva et al., 2015, 2016 for similar discussions about how different methodological factors impact ERPs to teeth and emotional expressions), including the type of task performed (e.g. Burra et al., 2018; Hoffman & Haxby, 2000; Hooker et al., 2003; Latinus et al., 2015) and low level visual features of the stimuli such as dynamic changes in luminance and contrast (see Puce et al., 2015 for a review). The studies included in this thesis (all using the same recording equipment and the same average reference) investigated eye-gaze processing during different socioemotional tasks with an emphasis on three main goals.

The first goal was to investigate how perception of eye-gaze would impact participants' behavioral responses in each task. I investigated whether direct and averted gaze perception would differentially affect performance within the same participants as they discriminated emotion from facial expressions, attention from eye-gaze, and gender (Study 1). I then investigated the impact of direct and averted eye-gaze perception on positive and negative affective empathy for the gazer (Study 2), and on affective theory of mind judgements about the gazer (Study 3). The second goal was to track the time-course of eye-gaze processing using ERPs time-locked to the onset of each face. Using a mass univariate analysis technique, I investigated whether direct and averted gaze perception would interact with the neural processing associated with each task. Along with the face-sensitive N170, I focused on ERP markers sensitive to emotional processing (see Section 1.4), which were likely to be modulated by the emotional cues specific to each task. Finally, the third goal was to compare the modulation of these ERPs across tasks irrespective of eye-gaze effects, which was particularly important because the time-course of affective empathy and affective theory of mind are relatively new areas of exploration. In this final chapter, the results from each study will be discussed with reference to our current understanding of eye-gaze processing. The potential social implications of the results for both neurotypical and clinical populations will be explored.

5.1 The Behavioural Impact of Direct and Averted Eye-gaze

The first aim of this thesis was to better understand if, and how, direct and averted gaze differentially impact behavior during the aforementioned social tasks. Relative to direct gaze, averted gaze perception was associated with more accurate attention discrimination from eye-gaze (Study 1). It was also associated with affective theory of mind judgements that the gazer was more aroused, though this was specific to gazers described as experiencing negative situations (Study 3). In contrast, relative to averted gaze, direct gaze perception was associated with more accurate emotion discrimination (Study 1), increased ratings of positive empathy for the gazer (Study 2), and affective theory of mind judgements that the gazer was feeling more positive (Study 3).

While it is important to be aware of the limitations of between-group comparisons and the generalizability from lab studies to real life, the behavioural results of these studies provide initial evidence that direct and averted gaze perception affects important socioemotional abilities that we use every day. If neurotypical individuals are impacted by eye-gaze during these social tasks, then altered eye-gaze processing in clinical populations may be contributing to associated differences in social interactions. This idea is explored further in Section 5.5. The results also provide further evidence that the exact same direct and averted gaze stimuli are processed differently depending on the type of task being performed. Not only was this reflected by the different behavioural effects of direct and averted gaze during each task, but direct and averted gaze were associated with unique neural correlates during each task.

5.2 The Time-course of Direct and Averted Eye-gaze Perception

5.2.1 No Effect of Eye-gaze on N170 Amplitude in the Present Studies

The majority of previous investigations of the time-course of direct and averted gaze processing have focused on the N170 ERP component, as it displays sensitivity to faces compared to other object categories (Bentin et al., 1996; Eimer, 2000; George et al., 1996). These studies (e.g. Burra et al., 2017; Conty et al., 2007; Itier et al., 2007; Latinus et al., 2015;

Puce et al., 2000; Pönkänen et al., 2010; Rossi et al., 2015; Schweinberger et al., 2007; Taylor et al., 2001; Watanabe et al., 2002; 2006) have found mixed results, though some moderating factors have been proposed (see Section 1.3.2). The N170 analyses in the present studies revealed no main effects of gaze direction, nor any interactions between gaze direction and either task demands (Study 1) or the valence of preceding contextual sentences (Studies 2 and 3). Although there was a main effect of eye-gaze detected during the N170 analysis in Study 2, an examination of the waveforms revealed that this effect really occurred after the N170 peak, during the start of the P200 thought to reflect a different process than the structural encoding of the face that the N170 has been commonly associated with (Bentin et al., 1996; Eimer, 2000; George et al., 1996). I come back to this in the next section.

There are a few potential explanations as to why there were no N170 eye-gaze effects in the present studies. First, the N170 gaze effect has been proposed to be due to changes in luminance and contrast that occur during the perception of dynamic gaze stimuli (e.g. Conty et al. 2007; see Puce et al. 2015 for a review). The lack of N170 effects here would fit with this idea, given that all direct and averted gaze comparisons were between static images. Interestingly, the N170 gaze effect to dynamic stimuli appears to be modulated by the social significance of the task participants are performing (Latinus, 2015), and it is unclear if any N170 effect in response to static gaze images may be similarly impacted by task. However, this does not seem too likely, as in the three studies here, participants completed five different tasks with no N170 gaze effects. However, one could also argue that, with the exception of the gender categorization task, each task used in the present study was at least as socially involved as the tasks used by Latinus (2015) and Conty (2007) in that they involved indicating if a gazer was attending to them or to something else, or more complex social tasks like emotion discrimination, affective theory of mind or empathy. Given that the N170 effect to dynamic images seems to be reduced for more social tasks, potentially due to increased gain of early visual processing (Puce et al. 2015), any N170 effect to static images here could have been similarly reduced.

Another alternative is the possibility that previously reported N170 eye-gaze effects to static face stimuli are type I errors driven by the type of ERP analysis being performed. Researchers are becoming increasingly aware that traditional ERP analysis practices can inflate type I error (see Section 1.5). One main distinction between the current studies and other studies on eye-gaze processing is that the present studies used a mass univariate analysis, which is more resistant to this type of error. Other methodological parameters may also have played a key role. In the present thesis, eye-tracking was used to enforce fixation to the eye-region during face presentation. If participants looked elsewhere before the N170 time-window had elapsed (i.e. before 250ms to be conservative), that trial was removed. This fixation control was added in response to a growing body of research demonstrating that the N170 amplitude varies depending on which face area is fixated, with the largest N170 following eye-fixation (de Lissa et al., 2014; Itier & Preston, 2018; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Nemrodov et al., 2014; Parkington & Itier, 2018). To the best of my knowledge, previous studies have not controlled participant gaze fixation. If the participants in these studies systematically looked at different face parts during different eye-gaze conditions, this fixation difference may have created the false appearance of eye-gaze effects. For example, there is evidence suggesting that direct gaze faces are looked at more often than averted gaze faces (e.g. Batki et al., 2000; Farroni et al. 2002; Palancia & Itier, 2012; Senju & Johnson, 2009b). If participants look at the eye-region of direct gaze faces more than they look at the eye-region of averted gaze faces, this may make the N170 appear enhanced in response to direct gaze faces.

Finally, an interesting alternative to explore is that there may be a lot of individual variation in N170 eye-gaze effects, which would make detection of these effects highly dependent on the participant group. For example, the N170 peak latency can span anywhere from 130-200ms between individuals. Past ERP analyses that were run on the average N170 time-window may have missed effects if many individuals fell outside of that window. Furthermore, mass univariate analyses may be particularly prone to masking effects that have a lot of natural latency variation, as they run ANOVAs on each window time-point instead of on the average amplitude across the whole time-window. The idea that there may be significant individual differences in eye-gaze processing is explored further below in Section 5.6.

With these possibilities in mind, the present thesis found no support for the idea that gaze direction of static stimuli impacts the N170, which is thought to reflect the structural encoding of face features (Bentin et al., 1996; Eimer, 2000; George et al., 1996). However, direct and averted eye-gaze did impact both early and late ERPs and some of these ERPs occurred before the N170, which is traditionally assumed to be the first "face sensitive" component (Bentin et al., 1996; Eimer, 2000; George et al., 1996). Instead of this classic marker of face perception, the ERPs that gaze modulated are actually more commonly associated with emotional processing. Accordingly, there were interactions between eye-gaze processing and different task conditions that varied in emotional valence.

In the next two sections, I summarize early (i.e. 100-200ms post face presentation) and late (> 200ms post-face) interactions between eye-gaze and different task conditions and speculate about what each type of activity may reflect. The distinction between early and late interactions is based on the general understanding that early and late ERPs likely reflect different types of processes. Theories about earlier ERPs like the N100, N200 and P200 propose that these reflect a selection process that prioritizes important information, including emotional stimuli, which are motivationally relevant (see Hajcak et al. 2010; Olofsson et al. 2008; and Schupp, 2006 for reviews). In contrast, later ERPs are typically proposed to reflect processes involved in elaborative cognitive appraisal of the stimulus.

5.2.2 Early Gaze Interactions: N100, N200 and P200

The earliest components modulated by eye-gaze were the N100, N200 and P200. In Study 1, eye-gaze processing during the N200 varied depending on which discrimination task participants were performing. In Study 2, eye-gaze processing during the N100 and P200 varied as a function of the emotional context presented before the face. The N100 was only modulated by eye-gaze during trials designed to elicit empathy (i.e. positive and negative, but not neutral, trials), while the P200 was only modulated by eye-gaze during positive contexts, designed to elicit positive affective empathy.

While the N100, N200, and P200 are three unique ERP components, there are comparable theories about what the emotional modulation of each component reflects. Both the N100 and N200 are measured over identical sites, and are thought to reflect activation of frontocentral emotion areas when emotional stimuli are perceived (Fan & Han, 2008). While the gaze and task interaction occurred on the N200 (Study 1), and the gaze and sentence valence interaction occurred on the N100 (Study 2), it seems likely that both interactions reflect the same type of response to emotional stimuli. The earlier timing of the N100 interaction in Study 2 may be because the emotional part of the trials (i.e. the context) was presented before the face was seen, allowing for more processing time. In contrast, the emotional content in Study 1 came from the face itself, as this study was the only one that used emotional instead of neutral faces. This may have resulted in a longer time for frontocentral sites to integrate both eye-gaze and the emotional information from the face, resulting in an interaction on the N200 instead of the N100. Finally, while the P200 is measured over posterior sites instead of frontocentral ones, its time-course does overlap with the N200 (Olofsson et al., 2008), which makes it quite possible that the neural generators of the P200, N200 and N100 are interactive components of a broader network (see Section 5.3 for speculation about what areas could be involved in this network). There is evidence that these components behave similarly in response to emotional stimuli. For example, both the P200 (Paulmann & Pell, 2009) and N200 (Balconi & Canavesio, 2016) are modulated by facial expressions compared to neutral ones, and in a review of affective processing, Olofsson et al. (2008) grouped the N200 and P200, observing that they are similarly sensitive to arousal and valence (e.g. Amrhein et al., 2004; Carretie et al., 2004; Cuthbert et al., 2000; Olofsson and Polich, 2007).

5.2.3 Late Gaze Interaction: Late Positive Potential

While most eye-gaze interactions occurred during early time-windows, there was an interaction between sentence valence and eye-gaze processing on the LPP during the affective theory of mind task (Study 3). Gaze direction was processed differently during emotional trials than during neutral trials from 540-800ms. Being a later component that is unaffected by low-level stimulus characteristics (e.g. size: De Cesarei & Codispoti, 2006; complexity: Bradley, et al., 2007), the LPP is thought to reflect the cognitive appraisal of emotional content and meaning (see Section 1.4.5; Schupp et al. 2006, Hajcak et al. 2010, and Olofsson et al. 2008 for reviews). This appraisal process is elaborative and long-lasting, and likely more closely linked to conscious awareness than earlier components.

While it is possible that the centroparietal LPP modulation may be linked to modulation of the frontocentral N100 and N200 or the P200, the LPP was the only component found to be sensitive to a gaze and sentence valence interaction in Study 3. This is evidence that the LPP interaction reflects a distinct process from the frontal network that I've proposed, at least during an affective theory of mind task. Below, I have integrated the field's current understanding of eye-gaze processing with the current studies' ERP and behavioural and gaze effects in order to speculate about potential links between these proposed networks and the attentional and emotional impact of eye-gaze.

5.3 Integrating neural and behavioural data: emotional eye-gaze effects on the observer and on observer judgements of the gazer

As reviewed in Section 1.1.2, there is a long history linking direct gaze perception to emotional processing. There is a body of research showing that direct gaze perception impacts an observer's emotional state, including increasing arousal (Conty et al., 2010; Helminen et al., 2011; Hietanen et al., 2008; McCrackin & Itier, 2018a; Myllyneva and Hietanen, 2015; Nichols & Champness, 1971; Pönkänen et al., 2011) and the experience of positive emotion (see Hietanen, 2018 for a review). I have theorized that the N100, N200, and P200 components are part of an interactive frontocentral network whose activity increases in response to emotional stimuli. While eye-gaze is not typically considered to be inherently emotional, it appears to some degree to "share a signal" with the processing of emotional stimuli, by modulating this network. If eye-gaze does modulate early responses to emotional stimuli, this may set off downstream effects responsible for the many previous reports of observers experiencing a conscious emotional impact of eye-gaze perception (see Section 1.1.2). The time-course of these emotional eye-contact effects on the observer is an area that has received little attention, but I believe the N100, N200 and P200 are strong candidates for exploration. While Study 2 was the only study here in which the observer was asked about their own emotional state, there did appear to be a link between the emotional response to eye-gaze and both N100 and P200 amplitudes. Specifically, the P200 was modulated by eye-gaze only in positive trials, and behaviorally, eye-gaze only impacted participant's affective empathy in positive conditions.

Recently, Hietanen (2018) offered predictions about which brain areas may be responsible for affective eye-contact effects. While it should be acknowledged that ERPs have poor spatial discrimination, I have speculated that the ERP effects here are driven by involvement of frontocentral areas. Key candidates include the orbitofrontal cortex, which has been implicated in eye-gaze processing (Calder et al., 2002; Conty et al. 2007), emotional processing (Dixon et al., 2017), and higher order theory of mind tasks (Amodio & Frith, 2006; Calder et al., 2002; Conty et al., 2007) and the inferior frontal gyrus, implicated in eye-gaze processing (Hooker et al. 2003), emotional contagion (Shamay-Tsoory et al. 2009 for a review) and the processing of facial expressions (Dapretto et al. 2006). I have also speculated that the P200 may specifically be linked to the activation of the reward network by direct gaze (e.g. Cavallo et al., 2015, Conty et al. 2007; Kampe et al. 2001; Ethofer et al. 2011) as research has shown that the P200 is more positive in response to pleasant stimuli, but not negative stimuli (Olofsson et al., 2008 for a review). However, it is important to acknowledge that these areas are likely nodes within a network of areas, many of which are undetectable with electroencephalography, which is mostly sensitive to activity on the cortical surface. These other areas might include subcortical structures implicated in both emotional and eye-gaze processing like the amygdala (Burra et al. 2013; George et al., 2001; Hooker et al., 2003; Kawashima et al., 1999; Wicker et al., 2003), ventral striatum (Kampe et al. 2001), or the anterior insula (Cavallo et al., 2015; Ethofer et al. 2011) deeper within the neocortex. Previous work has shown that eye-gaze processing has both cortical and subcortical pathways (see Burra, Mares and Senju, 2019 for a review), and it may be the fast, subcortical route that is responsible for the early eye-gaze effects reported here. In particular, the subcortical route involves the amygdala (e.g. Burra et al. 2013), which has direct connections to the orbitofrontal cortex (e.g. Lichtenberg et al. 2017), an area that I've proposed may be involved in the early frontal effects.

A second body of research on eye-gaze and emotional processing has demonstrated that direct gaze perception impacts emotional evaluations of the gazer. For example, individuals who make more eye-contact are considered more attractive (Ewing, 2010; Conway et al., 2008; Mason et al., 2005; Palancia & Itier, 2012) and likeable (Mason et al., 2005; Kuzmanovic et al., 2009) than those who make less eye-contact. Eye-gaze effects on the observer may be functionally linked to the impact of eye-gaze on evaluations of the gazer. For example, one may feel more positive when viewing direct gaze, which could lead to more positive attributions of the individual displaying direct gaze. However, as I argued in the discussion of Study 3 (Section 4.4), it seemed that participants were not using their own emotional state as a cue to help them make affective theory of mind judgements. Indeed, direct gaze faces were not associated with higher arousal ratings in all conditions, despite much previous literature showing that direct gaze increases an observer's arousal (e.g. Conty et al., 2010; Helminen et al., 2011; Hietanen et al., 2008; Nichols & Champness, 1971; Myllyneva & Hietanen, 2015; Pönkänen et al., 2011; Porter et al., 2006) regardless of whether the context is positive or negative (McCrackin & Itier, 2018a). If individuals do not always integrate their own emotional state with eye-gaze information while making inferences about the gazer, there may be two distinct patterns of gaze effects: emotional effects of direct gaze within the observer, and emotional appraisals of the gazer.

Distinct effects would likely require that there be distinguishable neural correlates. In Study 3, there were no detected early frontocentral eye-gaze effects, but a late eye-gaze and task interaction was picked up on the centroparietal LPP (spanning 540-800ms). Gaze direction was processed differently during emotional trials (more positive for direct gaze than averted gaze) than during neutral trials (more negative for direct gaze) and impacted participants' affective theory of mind ratings about the gazer. A few other studies have similarly found late eye-gaze effects on centroparietal sites, typically spanning from approximately 300-600ms (Burra et al., 2018; Carrick et al., 2007; Conty et al., 2007; Itier et al., 2007; Myllyneva & Hietanen; 2015). These have been interpreted to reflect P300 modulation, which is commonly considered to be the early portion of the LPP (Olofsson et al. 2008; Schupp et al. 2006). Recently, others have offered similar theories that P300 eye-gaze effects reflect cognitive evaluation of gaze linked to a higher level of social cognition than gaze effects on attentional or structural encoding processes (Burra et al. 2018; Carrick et al. 2007). These effects may be linked to cognitive evaluations of the gazer. One study that supports this idea found that participants' P300 amplitudes (and their arousal) were only enhanced by direct gaze perception when they believed the gazer could see them (Myllyneva & Hietanen, 2015), which may be because seeing a real person led to the kinds of cognitive evaluations that occur during social interactions. While Study 3 used pictures and not real actors and still found eye-gaze to modulate the tail end of the P300, this study required participants to make the same cognitive evaluations (i.e. affective theory of mind judgements) as if the gazers were real. This may have put participants into a social mode of processing and evaluation that would not otherwise be present when looking at a picture.

It is possible that P300 and LPP gaze sensitivity may be due to activity from more posterior components of the theory of mind network, like the superior temporal sulcus, which is also sensitive to gaze direction (Allison, Puce, & McCarthy, 2000; Calder et al. 2007; Hoffman & Haxby, 2000; Puce & Perrett, 2003; Numenmaa & Calder, 2009). However, the lack of involvement of frontal areas in gaze perception was not something that I hypothesized in an affective theory of mind task. If anything, I presumed that this would be where an interaction between eye-gaze and the sentence valence would occur, given that frontocentral areas are thought to be heavily involved in theory of mind. However, it is not that these frontal areas were inactive during the theory of mind task, as reviewed below. Rather, the activity of these areas was not detectably modulated by eye-gaze during that task.

5.4 Time-course of Affective Processing Irrespective of Eye-gaze Effects

While perception of eye-gaze modulated some of the analyzed ERPs associated with emotional processing, there were also general task effects irrespective of gaze direction. As reviewed in Section 1.4, our understanding of ERP components is evolving, and understanding how they are modulated by different tasks brings us a step closer to understanding what processes they reflect (see Amodio et al., 2014; Hajcak et al. 2010; Olofsson et al. 2008; and Schupp, 2006 for reviews). As Amodio et al. (2014) discuss, ERPs associated with emotional processing are likely modulated by many types of emotional tasks. While there has been much research investigating the processing of emotional stimuli including words, scenes or emotional expressions, there has been much less investigating more complex socioemotional processes like affective theory of mind and empathy. In an attempt to better understand what kinds of activity are elicited by each task, I draw parallels below between the general task effects on each ERP component in each study. As Studies 2 and 3 displayed identical emotional priming sentences and faces, any differences between activities elicited in each Study is likely driven by task demands.

5.4.1 The Frontal N100 and N200 as Emotional Response Processes

N100 and N200 modulation has been theorized to reflect an initial automatic activation of emotion areas (Fan & Han, 2008), potentially through mirror neuron system activation (Gallese & Goldman, 1998). In support for this theory, there was no main effect of task on the N200 in Study 1. This is likely because each task contained the same emotional faces, and thus the neural substrates driving the N100 and N200 were equally active during each one. In contrast to Study 1, Studies 2 and 3 did have both neutral and emotional conditions, and accordingly there were main effects of sentence valence on the N200. In both studies, positive and negative trials elicited less negative ERP amplitudes than neutral trials (though the negative-neutral difference was not quite significant in Study 3 with the Bonferroni correction).

Those results suggest that N200 modulation occurs in response to both positive and negative stimuli, and the affective content can come from either priming sentences or faces with emotional expressions. This point is important given that these components have typically been studied in response to stimuli that are themselves emotional, like emotion words (Kanske, &

Kotz, 2010; Zhang et al. 2019), facial expressions of emotion (Balconi & Canavesio, 2016) and images of body parts in painful situations (Coll, 2018 for a review). These components are seemingly responsive to more abstract forms of emotional processing as well, including the semantic context under which neutral stimuli are perceived. Furthermore, while a recent meta-analysis indicated that the link between the N100, N200 and empathy is unclear (Coll, 2018), our results suggest that the N100 and N200 can be modulated by emotional stimuli in a wide range of tasks, including by stimuli that elicit both positive and negative affective empathy.

5.4.2 The Early Posterior Negativity as an Attentional Selection Process

The EPN is believed to be part of an attentional selection process that enhances processing of emotionally arousing stimuli (Junghöfer et al., 2001; Schupp et al., 2004b). Similar to the N200, there was no difference in the EPN amplitude elicited during each task in Study 1. Again, it seems likely that this is because in Study 1, each task involved looking at the same emotional faces, and there was no neutral condition. There was a main effect of sentence valence on the EPN in both Studies 2 and 3, where the EPN was enhanced (i.e. more negative) for faces seen in negative relative to neutral contexts, and there were statistical trends suggesting the EPN was also enhanced for faces in positive relative to neutral contexts.

These results align with the common finding that EPN is enhanced for both negative and positive stimuli relative to neutral stimuli (e.g., Herbert et al. 2008; Kissler et al. 2009; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Rellecke, Sommer, & Schacht, 2012; Sato et al., 2001; Schupp et al., 2006), and sometimes for negative relative to positive stimuli (Rellecke et al., 2011; 2013; Schupp et al 2004a). While this typically includes negative or positive facial expressions relative to neutral expressions (Itier & Neath-Tavares, 2017; Neath & Itier, 2015; Neath-Tavares & Itier, 2016; Schupp et al., 2004b; Rellecke, Sommer, & Schacht, 2012), Studies 2 and 3 add to a list of recent studies demonstrating that the EPN can be modulated in response to the exact same neutral faces placed into different affective contexts with priming sentences (McCrackin & Itier, 2018a; Wieser et al. 2014; but see Klein et al., 2015 for null results). If the EPN truly does reflect an attentional selection process (Junghöfer et al., 2001; Schupp et al., 2004b), then the present results suggest that the mechanism driving this enhancement does not require direct visual perception of emotional stimuli. Rather, the process is flexible enough to respond to affective priming, which is likely adaptive as it would enable response to a wider range of emotional events. As the EPN effects were nearly identical between the affective empathy task (Study 2) and the affective theory of mind task (Study 3), this selection process seems to be relatively independent of task demands. This idea supports the theory that the EPN is too early to reflect the actual cognitive appraisal of emotional content, which would have differed between the two tasks.

5.4.3 The P300 and Late Positive Potential as Cognitive Appraisal Processes

The P300 and LPP are measured over similar centro-parietal sites and it is commonly thought that the LPP is really an extension of the processes associated with the P300 (Olofsson et al. 2008; Schupp et al. 2006). As they occur relatively late in the processing stream, these components are theorized to reflect elaborative stimulus appraisal instead of earlier attentional selection effects (Olofsson et al. 2008; Schupp et al. 2006). Accordingly, differences between tasks emerged during these later time-windows, as they presumably require different types of cognitive appraisal. In Study 1, there was a main effect of task condition from 400-800ms, and this timing was where main effects of sentence valence occurred in Studies 2 and 3. However, in Study 2, negative trials differed from both neutral and positive trials whereas in Study 3, both negative and positive trials differed from neutral trials. I theorized that specificity for negative trials during an empathy task but not during an affective theory of mind task may reflect what kind of emotional evaluation is being done (see Section 4.4). In particular, during negative trials in the empathy task, participants may have engaged in other types of cognitive appraisal like evaluating their empathic concern for participants, which is believed to be a distinct facet of empathy (Decety et al. 2015). Critically, this would likely occur less during positive trials, in which there would be no concern for the individual described.

5.5 Implications for Neurotypical and Clinical Social Interactions

While the participants included in this thesis were neurotypical, understanding how eye-gaze impacts neurotypical socioemotional functioning can help improve our understanding of clinical populations. Indeed, while much eye-gaze research is performed with neurotypical participants out of convenience, it is motivated by the observation that many clinical populations with social impairment also have altered eye-gaze processing. It is tempting to assume there is a direct link between social impairment and eye-gaze processing, but this has yet to be determined for many areas of socioemotional functioning. The studies included in the present thesis are some of the first to use experimental manipulations to focus on the link between eye-gaze processing and affective empathy, affective theory of mind, attention discrimination, and emotion discrimination. Different combinations of these areas are impaired in special populations with altered eye-gaze processing, including autism, schizophrenia, social anxiety disorder, and psychopathy. While one must be careful not to make causal claims, the experimental manipulations here are another step towards determining if there may be a direct link.

In Study 1, perceiving direct gaze facilitated emotion discrimination and perceiving averted gaze facilitated attention discrimination. This is in line with the assumption that the eye-gaze avoidance characteristic of autism spectrum disorder (e.g. Pelphrey et al., 2002; Senju & Johnson, 2009a; Senju et al. 2002; 2005; 2009) may be contributing to impairments in emotion discrimination (Clark et al., 2008; Humphreys et al., 2007) and joint attention (Bruinsma et al., 2004). In Study 2, perceiving direct gaze was associated with increased positive empathy for the gazer. Attention to the eyes has been shown to be reduced in populations with altered affective empathy, including psychopathy (e.g. Dadds et al., 2008; 2012; Gillespe et al., 2015) but also social anxiety disorder, which preliminary evidence suggests may be associated with impaired affective empathy specifically for positive emotions (Morrison et al., 2016). This later finding is particularly interesting given that only positive empathy was facilitated by direct gaze perception in Study 2. If the relationship between eye-gaze perception, emotion discrimination, and affective empathy extends to real-life contexts, avoiding the eye-region will prevent this facilitation from occurring. The present ERP findings also provide a potential mechanism to explain how emotion discrimination and affective empathy might be impacted by eye-gaze avoidance. Avoiding the eyes may result in less N100, N200, and P200 modulation, potentially reflecting less modulation of frontocentral areas that process both gaze and emotion. If this is the case, behavioural therapies which encourage exploration of the eye-region may prove valuable.

In Study 3, information from eye-gaze was incorporated into theory of mind judgements. People with direct gaze were presumed to feel more positive, and those with averted gaze in negative situations were presumed to feel more affective arousal. As individuals' gaze behavior has been shown to vary as a function of mood, I theorized that gaze processing may impact affective theory of mind because of learned associations between gaze behavior and affective state. This theory of learned associations also offers one potential explanation as to why altered eye-gaze processing in disorders like autism spectrum disorder (Lajiness-O'Neill et al, 2014; Pelphrey et al., 2005; Senju et al. 2002; 2005; 2009; Senju & Johnson, 2009a), schizophrenia (Akiyama, et al. 2008; Kington et al., 2000; Kohler et al., 2008) and social anxiety disorder (Weeks et al., 2013; Wieser et al. 2009) may be associated with affective theory of mind impairments (Baron-cohen, 1997; Baron-cohen et al. 1995; 1997; Bora, Yucel, & Pantelis, 2009; Cui et al., 2017; Hezel & McNally, 2014; Sprong et al., 2007). The eye-gaze avoidance characteristic of these disorders would prevent utilization of eye-gaze cues when making affective theory of mind judgements. Furthermore, if someone avoids looking at the eyes during their developmental trajectory, they may not learn the associations between gaze behavior and affect to the same degree. These learned associations theoretically modulate later ERPs (P300 and LPP) presumed to reflect the cognitive appraisal of emotional content. While this is an interesting theory, much more research is needed to verify it, both on how eye-gaze behavior varies within social interactions as a function of mood, and on how affective theory of mind attributions align with the gaze behavior that occurs.

5.6 Limitations and Future Areas for Investigation

Throughout this final chapter, I have identified some limitations of the current research and will expand on them here. First, it is important to acknowledge the limitations of the ERP technique in general, and the specific analyses run in this thesis. Event-related potentials have excellent temporal resolution, but they lack good spatial resolution, so any discussion of potential neural generators is speculation. Furthermore, they predominantly pick up the activity on the cortical surface, when the neural generators likely include networks with a mixture of cortical and subcortical areas. The results from these studies are therefore better interpreted within the context of related functional neuroimaging work that has been done and hopefully future work can address these questions with complementary techniques. For example, magnetoencephalography (MEG) or functional magnetic resonance imaging (fMRI) could help localize the generators of the activity observed here. Furthermore, within the EEG technique, time-frequency analysis is another interesting area to explore. For example, some have recently reported increased gamma band power in response to a gaze aversion from eye-contact (Caruana et al. 2014) or to direct gaze shifts relative to averted gaze shifts (Rossi et al. 2014). Changes in beta band power have also been observed in response to direct versus averted gaze shifts, with the direction of effects varying depending on the time post stimulus (Rossi et al. 2014).

The use of a mass-univariate technique here was chosen to help prevent type I error, which has been acknowledged as a problem resulting from the use of traditional ERP analysis techniques. However, it is possible that being more conservative with type I error has also introduced some type II error. I ran exploratory analyses over all electrodes and time-points in each study to attempt to reduce type II error, but given that these analyses involve numerous comparisons across many time-points, when the multiple comparisons correction is applied, there is not much power. Effects would have to be fairly large and widespread to be detected using this technique, as was the eye-gaze and sentence valence interaction detected with my exploratory analysis in Study 3. This type of analysis also currently has no associated method to assess effect size or confidence intervals (Fields & Kuperberg, 2018), beyond rudimentary tactics like assuming smaller *p*-values reflect larger effects.

Another main limitation is that by averaging behavioral data and ERP data at the group level for analysis, there is no assessment of the individual variation in responses between participants. As can be seen from examination of the individual data points on the behavioural graphs in each study, there was a lot of variation in how participants responded. This is not surprising given that different life experiences likely change the way in which eye-gaze is interpreted and processed, and different orientations of neural generators may change the locations and timing of ERP interactions. If differences in eye-gaze processing are great enough to impact the results of ERP analyses, some of the between group differences I have assumed to be driven by unique task demands in each study may really be driven by participant differences in each sample. Regardless, an assessment of individual variation in responses to eye-gaze while completing socioemotional tasks is an exciting area for future research. As most of the research on eye-gaze is motivated by the everyday social impact that it can have, understanding what is happening at the individual level, in both neurotypical and clinical populations is a critical next step.

Finally, understanding the everyday social impact of eye-gaze perception also requires that tasks are used which adequately simulate real life scenarios. The research in this thesis was performed in a laboratory setting with face stimuli, and so generalizability could be an issue.

First, these studies assume that participants understood task instructions and responded truthfully, which may be a false assumption. Second, recent studies have demonstrated that some eye-gaze effects are dependent on the observer believing that they are being observed (e.g. Pönkänen et al. 2010; 2011), which cannot be obtained with face images. There are many methodological challenges involved when doing ERP studies with live actors, but with advancements in ERP cleaning and recording techniques (see Puce & Hämäläinen, 2017 for a review), the use of live actors is an exciting future area to explore.

Part of increasing the ecological validity of the stimuli also includes lower level manipulations like displaying dynamic gaze movements and expressions akin to what would be experienced in real life. Indeed, while it is important to note that any interactions between eye-gaze and task processing here cannot be attributed to differences in the physical stimuli (as the direct and averted gaze faces were identical for each task condition), one recent theory suggests that the N170 response to dynamic eye-gaze reflects a response to low level contrast and luminance changes in the eye-region (see Puce et al. 2015). While these lower level effects may appear to be less directly relevant to questions about higher level social cognition, one should not rule out the possibility that they are inter-related. For example, recent work suggests that the N170 eye-gaze effect to dynamic gaze stimuli is also modulated by the social significance of the task being performed (see Latinus et al. 2015 and Section 1.3.2). There is thus a very real possibility that not only the N170, but other ERPs analyzed here may display different patterns of activity in response to dynamic face cues.

5.7 Conclusions

The impact of eye-gaze on different socioemotional processes is unclear, despite there being many apparent clinical links between altered eye-gaze processing and social functioning. Furthermore, the time-course of eye-gaze processing and how it may vary depending on the task being performed is still unknown. The studies in this thesis investigated eye-gaze processing during different socioemotional tasks including emotion, attention and gender discrimination (Study 1), affective empathy (Study 2), and affective theory of mind (Study 3). Direct and averted gaze differentially impacted performance in all of these tasks, except gender discrimination, demonstrating that eye-gaze likely impacts many aspects of everyday social functioning. These results provide preliminary experimental support for the idea that altered eye-gaze processing in clinical populations like autism spectrum disorder, social anxiety disorder, schizophrenia, and psychopathy may be contributing to social impairment.

Event-related potentials associated with face perception and emotional processing were used to track the time-course of eye-gaze processing and its interaction with the tasks. The N170 was unaffected by eye-gaze, suggesting that gaze direction does not impact the structural encoding of the face for static gaze images. In contrast, both early and late ERPs sensitive to emotional processing were modulated by gaze direction. The results suggest that the early N100, N200 and P200 components may be part of a frontocentral network of emotion areas responsible for the emotional impact of eye-gaze perception on the observer. A later network including the LPP and the tail end of the P300 may reflect the involvement of eye-gaze in the cognitive evaluation of the gazer.

Finally, the present studies are some of the first to report the modulation of ERPs during an affective empathy task (Study 2) and during an affective theory of mind task (Study 3). While completing both of these tasks, the N200 and EPN appear to represent flexible processes which prioritize the processing of emotional information, regardless of whether it is semantic (e.g. a priming sentence), or physical (e.g. an emotional picture) in nature. The tail end of the P300 and the LPP appear to reflect the cognitive appraisal of emotional stimuli, instead of earlier attentional selection processes.

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