

MODULATION OF LATERALISED RESPONSES TO PRIMARY AFFECT

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DECLARATION

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ABSTRACT

Do we use one cerebral hemisphere or both to process positive and negative emotions? Is it more physiologically economical for the brain to initiate responses to both types of primary affect from a unilateral locus, or does our readiness to react to emotional stimuli depend on the differential contribution of each hemisphere based on the approach or avoidance behaviours positive and negative affect elicit? This thesis is concerned with these questions that have so far remained unanswered even though they form a key part of emotional perception research. The behavioural literature has provided evidence for both unilaterally (right hemisphere) and bilaterally derived responses to different types of emotional stimuli, with the directionality of response patterns changing depending on stimulus type and task demands. The neuroimaging literature has addressed whether there is a functional need for the lateralised processing of basic emotional stimuli by mapping subcortical and cortical emotional attention networks, specific to different variants of only negative affect (i.e. fear, sadness). How this subcortically originating lateralisation manifests into observable behaviour however still remains to be established. This research therefore posits that hemispheric lateralisation may be a modulated process, and aims to explore how this modulation guides the directionality of our behavioural responses to primary affect. The thesis introduces a novel methodology that provides the first evidence of the modulation of emotional lateralisation by establishing a behavioural paradigm that can effectively investigate hemispheric lateralisation through measures of response efficiency. The thesis further investigates whether subcortically originating lateralisation may be inferred through its resulting behavioural response, by examining visual field asymmetries in responses to positive and negative affect through nasally and temporally viewed stimuli. Additionally, the thesis considers the modulating properties of contextual emotion-enhancing features of facial expressions such as direct vs. averted gaze and the presence of looming sounds on behavioural responses to negative affect, and also investigates whether individual variability in anxiety levels translates into lateralised responses to affect. Findings from the present thesis suggest that lateralisation is not a sustained, static phenomenon, but in fact a dynamic, modulated process that depends on subtle stimulus-contextual elements to subsequently translate into observable response.

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1 CHAPTER 1: GENERAL INTRODUCTION

1.1. THEORETICAL BACKGROUND & OVERVIEW

In 1884, William James submitted a paper to the then-philosophical journal *Mind* asking why one would run when faced with a wild bear; do we run because we're afraid of what will happen if we don't, or are we afraid because we're running? The present thesis poses a similar question: to clarify what happens during the stages from stimulus to feeling, and identify the processes that modulate and facilitate this timeline of events that come in between. What is it that dictates and guides the way in which we perceive and respond to the most basic and evolutionarily ingrained of emotions? The way in which we perceive our environment and function within it is for the most part dictated by our ability to correctly identify, as well as to efficiently respond to emotional information.

Efficiency in the way we cognitively process affect is essential to our survival; accurate detection and classification of environmental emotional stimuli enables us to detect and respond to potential threat as well as regulating our behaviour and enabling our social interactions. Emotional perception has been extensively researched in the cognitive, social and developmental psychological neuroscience domains since the late 19th Century with no sign of decreasing in momentum as methodological techniques advance. Emotional perception research has not however been without theoretical, conceptual, and methodological issues; across studies, the reporting of conflicting evidence for elements of emotional processing spanning their definition, classification and categorisation, and how emotions are processed and responded to from perception to resulting observable behaviour, has become somewhat of a trademark of emotion research. This chapter will introduce the underlying theoretical issues informing emotional perception research, present the evidence so far, and outline the theoretical framework forming the rationale on which the present thesis is based.

1.2 DEFINITIONS OF AFFECT AND LATERALITY

Perhaps one of the most controversial topics in the field of emotion research has been that of a suggested differential hemispheric contribution, or lateralisation, specific to the nature of emotional information processed. A large body of evidence supports the hypothesis of a valence-specific lateralisation (e.g. Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995; Reuter-Lorenz, & Davidson, 1981; Ahern & Schwartz, 1979; Ross, 1977), which has however been at the forefront of considerable debate as an equally large body of evidence has conversely suggested that all aspects of emotional processing may be attributed solely to right hemisphere specialisation (e.g. Borod & Caron, 1980; Borod et al., 1998; Devinsky, 2000; Dimberg & Petterson, 2000; Ladavas, Umiltà, & Ricci-Bitti, 1980; Tucker, 1981).

The valence hypothesis suggests that each of the two hemispheres becomes preferentially engaged depending on the phenomenological nature of emotional environmental stimuli we are exposed to (Ross, Homan, & Buck, 1994; Schwartz, Ahern, & Brown, 1979). Emotions that are perceived to be negative or threatening are suggested to be preferentially processed by the right hemisphere, while the left hemisphere engages with the processing of positive emotional stimuli (Ross et al., 1994). The alternative, right hemisphere dominance hypothesis suggests that all emotional information regardless of valence is unilaterally processed by the right hemisphere; the underlying rationale in favour of unilateral hemispheric emotional processing suggests that if a function does not need to be represented bilaterally in the morphology of the human body (i.e. such as having a left and right arm and leg), then it is more evolutionarily economical to group all neural connections for said function close together (Rolls, 1990, 2005).

The theoretical foundations of this debate might be perhaps better understood through historical attempts at defining, categorising and classifying the concept of emotions. In the 19th century, William James conceptualised emotions as being physiological changes occurring in the self following exposure to an arousing stimulus (LeDoux, 2000). James's definition suggested that the term 'emotion' represents a timeline of perceptual and action events, starting from the exposure to an arousing stimulus (usually threatening), and resulting in the emotional subjective experience itself – in other words, the feeling (LeDoux, 2012).

One resulting categorisation of emotions is based on the assumption that they are individual subjective states concerned with maintaining the life of an organism, and as such are comprised of a number of attributes relating to instinctual, innate behaviours (Damasio et al., 2000). Individual emotional states are thence categorised into primary-basic, secondary-social, and background emotions according to their phenomenology. Specifically, primary emotions (i.e. fear, anger, sadness, surprise, disgust, happiness) are shared by numerous animal species and are grounded in ontologically ancient instinctual behaviours closely connected with ensuring survival. Secondary (a.k.a. social) emotions (i.e. guilt, pride, empathy, embarrassment, jealousy) are grounded in experience of social interactions, by implying the presence of a social audience and do not share the same direct link to survival as primary emotions. Lastly, background emotions (i.e. wellbeing, malaise, calmness, tension) are connected to organisms' current individual physiological states and might act as mediators, modulators, or inhibitors of behaviour (Damasio et al., 2000; LeDoux, 2000).

The dichotomisation of emotions into positive and negative is predominantly concerned with primary/basic affect, and links its strong instinct-based attributes to both a basis on an organism's homeostatic regulation (Damasio et al., 2000), and on the prompting of cognitive plans for action (Rolls, 1990, 2005). In behaviouristic terms, positive and negative emotions relate to whether the environmental stimuli causing them are perceived as possible rewards or possible punishers (Rolls, 2005), with rewards comprising anything that an organism that will act towards obtaining (approach), and punishers being anything that an organism will act to avoid (avoidance).

The grouping of emotions into primary, secondary, background as well as into positive/negative has also been established on the identification of neuroanatomically discrete emotional systems, thought to be specific to different types of basic affect - a type of localised, emotional map comprising subcortical structures in the limbic system and midline mesencephalic structures (Panksepp, 2004, 2005; Panksepp & Zellner, 2004). This map includes a dopamine-facilitated appetitive motivation seeking system, located in the ventral tegmental area and nucleus accumbens, and thought to promote learning, exploratory searching as well as facilitating goal-directed activities; a fear system which mediates flight and general anxious feelings and connects the amygdala, the bed nucleus of the stria

terminalis, and the periaqueductal grey of the mesencephalon; a rage system which courses parallel to the fear system's circuitry from the medial amygdala to the periaqueductal grey and facilitates aggressive acts and feelings; a system associated with separation-distress and panic reactions connecting the periaqueductal grey matter with more rostral brain areas that triggers separation-distress feelings and mediates panic reactions; regions associated with erotic desire in basal forebrain and hypothalamic structures connecting them down to the periaqueductal grey and which are associated mainly with erotic feelings; a care system which facilitates maternal/paternal nurturing feelings; and lastly a play system which is associated with youthful rough-and-tumble play and laughter, which is primarily relevant to positive affect (Panksepp, 2004, 2005).

Specifically relevant to the positive/negative emotion grouping are bottom-up and top-down perceptual processing networks (Derryberry & Tucker, 1992). For example, when considering top-down hierarchical cognitive organisation combined with Panksepp's more instinctual emotion-mapping system, one observes some overlap. Specifically, descending neuronal connections allow the cortex to regulate emotional functions of the limbic system and brainstem, while also controlling finer peripheral responses (Derryberry & Tucker, 1992). This system includes several circuits of low-level effectors which process and regulate the endocrine, autonomic and motor systems, and its projections contribute to specific elements of emotional expressions (i.e. vocalisations, gestures), as well as to the coordination of eye movements and postures involved in approach-avoidance behaviours (Derryberry & Tucker, 1992; Harrison, 2015). The bottom-up organisational system encompasses connections from the limbic system and brainstem to the cortex, with four ascending and neurochemically-distinct systems relevant to emotional processing: noradrenergic projections stemming from the locus coeruleus, serotonergic projections from the dorsal and medial raphe nuclei, dopaminergic projections from the ventral tegmental area, and cholinergic projections from the nucleus basalis (de Gelder, van Honk, & Tamietto, 2011; Derryberry & Tucker, 1992; Harrison, 2015; Pessoa & Adolphs, 2010).

Given the discrete anatomical and functional systems relating to positive and negative types of primary affect, lateralisation research has attempted to link the contralateral physiology of the human visual and musculoskeletal systems to the preferential engagement of either left or right hemispheric engagement, based on the

nature of an emotional stimulus (positive vs. negative). However, thus far lateralisation of emotional physiology and its expression in behaviour remains uncertain. The following sections will outline reasons for the continuing uncertainty by considering the evidence for a functional need for lateralisation, and by addressing current research.

1.3 REVIEW OF EVIDENCE FOR THE LATERALISATION OF PRIMARY AFFECT

1.3.1 BEHAVIOURAL LATERALISATION LITERATURE

Up to now, a number of studies have examined the lateralised versus right-hemisphere dominant processing of primary affect, with conflicting evidence reported in the literature. For example, some behavioural studies report on the overall right-hemisphere processing for positive and negative, visual and auditory emotional stimuli (e.g. Borod & Caron, 1980; Borod et al., 1998; Borod, Koff, & White, 1983; Campbell et al., 1990; Hugdahl, Iversen, & Johnsen, 1993; Ladavas et al., 1980; Ley & Bryden, 1979; McLaren & Bryson, 1987; Safer, 1981), while other reports suggest emotion-specific right-biased lateralisation which is less prominent for positive affect (e.g. Dimond, Farrington, & Johnson, 1976; Ehrlichman & Halpern, 1988; Ley & Bryden, 1979; Sackeim, Gur, & Saucy, 1978; Sackeim & Gur, 1978). Other work reports negative emotion-specific laterality effects, with no converse lateralisation for positive emotions (Best, Womer, & Queen, 1994; Bryden, Free, Gagné, & Groff, 1991; Mandal et al., 1999), while several research reports suggest that positive emotions are preferentially processed by the left hemisphere, while negative affect is processed by the right hemisphere, as inferred by visual field asymmetries during visual presentation of emotional stimuli such as faces and words (Lane et al., 1997; Moretti, Charlton, & Taylor, 1996; Reuter-Lorenz et al., 1990; Reuter-Lorenz, & Davidson, 1981; Schwartz et al., 1979; Van Strien & Valstar, 2004; Van Strien & Van Beek, 2000) (see Table 1 on the following pages for a summary of a selection of behavioural studies emotional laterality).

| Study | Subjects | Task Description & Key Comparisons | Results | Laterality |
|------------------------------------|---|--|--|-----------------------------------|
| Borod & Caron, 1980 | Left vs Right handers | Subjects asked to perform (pose) pleasant vs unpleasant facial expressions | Overall left side of face (i.e. RH) dominant in posed expressions / no effect of handedness | RH across emotions |
| Borod et al, 1998 | Right-brain damaged group, left-brain damaged group, normal control group (all right-handers) | Battery of identification and discrimination emotional perception tasks of facial, prosodic, and lexical emotion, where each perception task used three positive (happiness, interest, and pleasant surprise) and five negative (sadness, fear, anger, disgust, and unpleasant surprise) emotions | Support for RH processing from significant main effects of group but no significant Group × Emotion interactions. | RH across emotions |
| Borod, Koff & White, 1983 | Right-handed normal adults (18 male, 19 female) | Subjects asked to pose facial expressions under two conditions (verbal prompts, and visual imagery). Measures of facial asymmetry and expression intensity. | Left side of face (i.e. RH) showed increased expression intensity regardless of condition and regardless of gender. | RH across emotions |
| Hughdahl, Iversen, Johnsen, 1993 | 70 right-handed normal adults (50% male) | Unilateral presentation (right vs left visual field) of positive, negative and neutral facial expressions. Collected response times and accuracy scores. | Overall RH was more accurate and quicker in responding to emotional stimuli, with positive expressions eliciting quicker responses overall. | RH across emotions |
| Ladavas et al, 1980 | 24 right-handed normal adults (50% male) | Unilateral presentation (right vs left visual field) of positive, negative and neutral faces. | LVF (i.e. RH) responses quicker and more accurate overall, regardless of emotion | RH across emotions |
| Ley & Bryden, 1979 | 20 right-handed normal adults | Unilateral presentation (right vs left visual field) of cartoon drawings of a five-scale emotional expression spectrum ranging from extremely positive to extremely negative in an emotion recognition task. | Significant LVF superiority in accuracy of emotion recognition, independent of type of emotion (positive or negative). | RH across emotions |
| McLaren & Bryson, 1987 | 24 right-handed normal adults | Bilateral presentation of face pairs, (positive and neutral or negative and neutral) in an emotion identification task. | LVF (i.e. RH)-presented emotional faces elicited higher accuracy, regardless of nature of emotion | RH across emotions |
| Dimond, Farrington & Johnson, 1976 | 20 right-handed normal adults, split in two groups. | Showing of short film on either the LVF or RVF via the use of a specially constructed contact lens. Three films used; one positive, one neutral, and one negative. Each subject group was assigned to either LVF presentation only, or RVF presentation only. Following display of films, subjects were asked to rate the films for emotiveness. | Significant difference for the RVF group (i.e. LH) for increased rating and judgement of negative films, with no difference found in the LVF group, and no effects for the positive and neutral films. | LH for negative |
| Sackeim, Gur & Saucy, 1978 | 86 subjects (57 male), right-handed | Photographs of facial expressions and their mirror reversals were split down the midline, creating right-side and left-side composites. | Left-side negative emotion composites and right-side positive emotion composites were judged as higher in emotional intensity. | RH for negative / LH for positive |

| | | | | |
|-----------------------------------|--|--|--|-------------------------------------|
| | | Composites from angry and happy paired with neutral half-faces were displayed to the subjects, and subjects were asked to make a judgement on the emotionality of the faces. | | |
| Best, Womer & Queen, 1994 | 46 subjects, all right-handed | Chimeric faces composed of half-neutral and half-emotional infant facial expressions (expressions were of infant cries and infant smiles to represent positive and negative distinction) were shown in a free-viewing task. Subjects were asked to rate the emotionality of the photographs. | Overall RH-bias for negative (cries), and bilateral sensitivity for positive (smiles). | RH for negative |
| Bryden, Free, Gagne & Groff, 1991 | 20 subjects (left and right handers) | Dichotic listening task, where two dichotically competing words were spoken (one in a neutral tone, one in an affective tone – either positive or negative). Subjects were asked to report whether they perceived the words as emotional or not. | Overall left ear advantage for negative vs. positive tones. | RH for negative |
| Mandal et al 1999 | 60 unilateral cortical lesion patients (30 with right hemisphere damage, 30 with left hemisphere damage) | Emotion recognition task, where subjects were asked to match photographs of four emotional expressions (angry, happy, fearful, sad). | RH damage patients showed significant impairment in overall emotional perception, which was significantly more prominent in relation to negative affect. | RH for negative |
| Moretti, Chariton & Taylor, 1996 | 40 young adults | Emotion recognition task, where subjects viewed photographs of happy or sad facial expressions presented unilaterally (either on the LVF or RVF). Subjects also completed Beck's Depression Inventory as a measure of whether depressiveness effects emotional recognition. | Regardless of depression score, all subjects showed a LVF advantage for sad expressions, and no effect of RVF or happy expressions. | RH for negative |
| Reuter-Lorenz & Davidson, 1980 | 28 young adults, all right-handed | Task involved the bilateral presentation of an emotional (happy or sad) photograph paired with its neutral counterpart per trial. Subjects were asked to identify the visual field in which they thought they saw the emotional photograph in each trial, with the stimuli remaining on display until the subject gave a response. | Quicker response times were elicited for sad faces when presented on the LVF (i.e. RH), and for happy faces when presented on the RVF (i.e. LH). | RH for negative and LH for positive |
| Van Strien & Valstar, 2004 | 54 female students, all right-handed | Emotional Stroop task, whereby subjects were presented unilaterally (LVF vs RVF) emotional (positive vs negative) words written with different colour fonts. Subjects were asked to name the colour of the font, without focusing on the word's semantic | Subjects with higher anxiety showed more incorrect responses for positive words when present on the LVF (i.e. RH). | RH for negative |

| | | | | |
|-----------------------------|--|--|---|-----------------|
| | | meaning. All subjects also completed the Trait anxiety scale. | | |
| Van Strien & Van Beek, 2000 | 16 right-handed (8 males & 8 females) and 16 left-handed (8 males & 8 females) | Subjects completed a forced-choice unilateral (LVF vs RVF) facial expression-rating task, where they were asked to rate the displayed photographs as positive or negative. Correct responses were correlated with handedness and gender. | Female participants rated photographs more positively when displayed on the RVF (i.e. LH), with male participants showing no difference in responses based on visual field. | LH for positive |

Table 1. Summary table outlining task details and findings from a selection of behavioural lateralisation studies that have informed the rationale of the present thesis.

1.3.2 NEUROIMAGING LATERALISATION LITERATURE

More recently, there has been a nearly complete shift of research interest from the behavioural to the neurological domains. This body of work has produced more consistent support for the lateralised processing of basic affect, by observing activation patterns of specific subcortical structures in the basal ganglia and limbic system, which are also known to activate during states of vigilance and alertness. Much of what we know in terms of lateralised subcortical activation patterns in the processing of affect comes from studies on the perception of negative emotional stimuli. For example, neuroimaging studies investigating subcortical activation during emotional perception and response have produced a large body of evidence for fear-specific unilateral activation of specific subcortical structures that are part of the subcortical vigilance/alarm activation network through the amygdala. For example, structures such as the superior colliculus (e.g. Cesarei & Codispoti, 2015; Ellenbogen & Schwartzman, 2009; Vuilleumier, Armony, Driver, & Dolan, 2003), amygdala (e.g. Adolphs, Russell, & Tranel, 1999; Pessoa & Adolphs, 2010; Pessoa, 2010; van der Zwaag, Da Costa, Zürcher, Adams, & Hadjikhani, 2012), substantia innominata (e.g. Mesulam, 1998; Viinikainen et al., 2010; Whalen et al., 1998), and nucleus accumbens (e.g. Carretié et al., 2009; Duncan & Barrett, 2007; Haegelen, Rouaud, Darnault, & Morandi, 2009; Richter-Levin & Akirav, 2003) have been identified as structures mediating the speeded processing of self-relevant, biologically significant, fearful in valence, information. Specifically, this thesis defines self-relevant, or biologically significant emotional stimuli as any stimuli that the organism may perceive as having a direct consequence and impact on their wellbeing. For instance, the nearby sound of a lion's roar may signify the impending arrival of an aggressor, thus prompting a person to flee.

Fearful stimuli have been predominantly used in the neuroimaging literature as the main representation of what constitutes negative affect, with a substantially smaller amount of research utilising angry or sad stimuli. For example, in fear-conditioning studies of the subcortical processing of auditory affect, reports from amygdalar lesion studies have shown both the complete disappearance of fear-specific responses in cases of bilateral lesions (Armony & LeDoux, 2010), or the significant decrease in

fear responses in cases of unilateral partial lesions (Baker & Kim, 2004). The primary emotion of anger has primarily been examined in relation to its effects on other higher-order cognitive functions such as working memory (e.g. Jackson, Linden, & Raymond, 2014; Thomas, Jackson, & Raymond, 2014) and in further relation to personality or mood disorders like anxiety and depression (e.g. Bradley, Mogg, Millar, & White, 1995; Eysenck, Derakshan, Santos, & Calvo, 2007; Mogg, Garner, & Bradley, 2007), and schizophrenia (e.g. Linden et al., 2010; Wolf et al., 2011). It remains unknown as to whether biologically significant angry stimuli would exhibit similar lateralised subcortical activation to that reported during processing of fearful stimuli, as no studies have so far directly compared subcortical engagement between these two types of negative affect during emotional perception. The thesis will address the neuroimaging emotional perception literature in detail in chapters 3 and 4, where it is directly relevant to the rationale of the experiments presented therein.

1.3.3 PRELIMINARY CONCLUSIONS ON LATERALISATION

One possibility for the lack of research interest in examining laterality effects specific to angry stimuli might be the lack of consensus regarding the definitional distinction between positive/negative affect and approach/avoidance affect and resulting behaviour (Wager, Phan, Liberzon, & Taylor, 2003). The two categorisations have since been used interchangeably in emotion research (i.e. in early behavioural studies on lateralisation positive affect has been conceptualised as approach, and negative as avoidance) (Davidson, Jackson, & Kalin, 2000). The conceptualisation that the positive/negative dichotomy might be equated to the approach/avoidance distinction however can be somewhat problematic; why is it that only positive affect should result in approach behaviours? One might argue that negative affect – especially if directly relevant to the organism by signalling the presence of potential threat or danger – might instigate fight behavioural reactions in the fight or flight dilemma by acting as a potent localiser for the location of threat. Fight reactions to anger could therefore also be interpreted as approach behaviours, as one would seek to engage the potential threat instead of always seeking to avoid it.

While studies in the neuroimaging literature on laterality report subliminally perceived negative affect as being preferentially processed (e.g. Liddell et al., 2005), behavioural accounts of emotional face perception report biased processing of positive affect in visual search (e.g. Calvo & Beltrán, 2014; Calvo & Nummenmaa, 2007) and masked emotion tasks (Juth, Lundqvist, Karlsson, & Ohman, 2005; Leppänen & Hietanen, 2004). An underlying conclusion at this point might be that differential whole-hemisphere engagement that is thought to depend on either the positive/negative valence of stimuli, or on the approach/avoidance reactions which emotional information might inform, might be a somewhat crude generalisation. Instead, it is specific cortical regions or subcortical structures and areas within them that have been shown to display distinctly unilateral activation depending on the nature of the emotional stimulus perceived or being responded to (Wager et al., 2003).

Given the close, biologically significant relationship between primary affect and reflexive reactions, it is not surprising that a considerable proportion of lateralisation research focuses on the so-called threat advantage – the suggested preattentive processing of threatening emotional information (Horstmann, 2007; Horstmann & Bauland, 2006). Again, mostly fearful stimuli (e.g. fearful facial expressions) tend to be predominantly used when considering the possibility of processing threatening environmental information before they pass the awareness threshold. For example, support for the threat advantage assumption has been provided from studies using chimeric (i.e. facial expression stimulus which is created by presenting different stimuli, either all-fearful and all-neutral, or all-fearful and all-happy, to the right and left visual field simultaneously) and schematic facial expressions of fearful affect (e.g. Horstmann & Bauland, 2006; Horstmann, 2007; Rafal, Henik, & Smith, 1991), and negatively-valenced words and scenes (e.g. Fox, 2013; Koster, Crombez, Damme, & Verschuere, 2004; Yiend, 2010).

1.3.4 MIGHT LATERALITY PATTERNS BE DEPENDENT ON METHODOLOGY?

In behavioural research on lateralisation, a large number of studies have investigated the potential of preferential engagement of either the left or right hemisphere through a number of behavioural indices (i.e. button-press response

times, saccades latency and direction, physiological measures of arousal, signal detection sensitivity indices/ d' prime). A range of experimental paradigms have also been applied that utilise a variety of primarily visual and spatial attention tasks with equally varied stimulus types, with subsequent results reported differing in the directionality of lateralised observable responses. Application of such methodological variations could have potentially resulted in the resulting variation in patterns of lateralisation. For example, some studies using valenced facial expressions have opted to utilising chimeric stimuli (e.g. Jansari, Tranel, & Adolphs, 2000; Lang, Greenwald, Bradley, & Hamm, 1993), while some opt for photographic facial expression stimuli (e.g. Bradley et al., 1995; Mogg et al., 2007).

Similarly, behavioural lateralisation studies in the visual domain use a multitude of stimulus presentation types. For example, facial expression stimuli have been presented either in an upright (e.g. Horstmann, 2007; Moretti, Charlton, & Taylor, 1996; Reuter-Lorenz, & Davidson, 1981), inverted (e.g. Calvo & Beltrán, 2014; Calvo & Castillo, 2001), or a combination of both layouts (e.g. Horstmann, 2007; Jansari et al., 2000). Gaze direction in negative facial expressions of affect also tends to direct the lateralisation pattern of responses, although in this case laterality appears to depend on the approach/avoidance dichotomy as opposed to a distinction purely based on valence. For example, participants responding to happy facial expressions with gaze directed at them often exhibit motivation to approach behaviours (Adams & Kleck, 2003a; Davidson, Jackson, & Kalin, 2000). Conversely, a distinctly negative affect such as anger with eyes directed to the observer might also be expected to elicit similar motivation to approach behaviours, possibly as a means of intending to engage with the threat (fight instead of flight) (Adams et al., 2003b). The link between approach/avoidance behaviours and laterality is founded on earlier reports of approach/avoidance behaviours suggested as being products of the lateralised engagement of the right and left hemispheres during visual cognitive activities concerning personal and extrapersonal space respectively (Heilman, Chatterjee, & Doty, 1995). In this report, the authors observed right hemisphere activation in visual cognitive activities concerning the space away from the observer's body (avoidance), and left hemisphere activation during visual cognitive activities concerning the space near the observer's body (approach).

Additionally, stimulus onset-offset latencies and participant response time allowances greatly differ across behavioural paradigms. For example, typically visual

search and forced-choice detection tasks allow valenced stimuli to be displayed up until participants provide a response (e.g. Moretti et al., 1996; Reuter-Lorenz et al., 1995; Reuter-Lorenz, & Davidson, 1981), thus resulting in 1 to 3 seconds long response times. Importantly however, reflex-like responses to valenced stimuli (or emotion linked to approach behaviours) are more likely to occur following rapid stimulus display times, as rapid attentional engagement is initiated after 50-100ms-long stimulus display times, with displays of 300ms and longer resulting in full, higher-order attentional engagement (Posner, Rafal, Choate, & Vaughan, 1985). The sheer multitude of emotionally charged environmental stimuli that we are exposed to on a daily basis necessitates the rapid engagement of attentional vigilance, and requires a type of filtering mechanism that can efficiently and accurately distinguish between self-relevant and self-irrelevant information. Facial expressions that convey emotional nuances are possibly amongst the most attentionally significant stimuli we are exposed to, not simply due to their automatic recognisability, but also due to the strong self-preservation relevant signals they might carry. For example, when observing an emotional face, one is able to identify a friend or a foe, while automatically initiating plans for appropriate action. When investigating the perceptual processing properties of primary emotion, facial expressions of affect lend themselves as being ecologically valid and biologically significant stimuli that could possibly also apply to other, non human-specific stimuli of affect such as spiders or snakes. An underlying conclusion, relevant to all different methodologies that have been used in explorations of lateralised processing of primary affect seems to be that the lack of consensus in laterality patterns could be due to inconsistency between methodologies.

1.4 IS THERE A FUNCTIONAL NEED FOR LATERALISATION?

The earliest evidence for lateralised hemispheric contribution comes from clinical studies on abnormal emotional behavioural manifestations resulting from specific psychiatric conditions. In a study of epileptic patients who suffered unilateral lesions, Flor-Henry observed that left-sided lesions resulted in catastrophic emotional reactions (i.e. tears and dysphoria), while right-sided lesions resulted in emotional unawareness and indifference that manifested as a lack of concern and hypomania

(Flor-Henry, 1983). In another example, in an investigation of pathological laughing and crying symptoms in patients with nuclear brainstem lesions, Gainotti and colleagues observed that pathological crying symptomatically occurred in patients with left lateralised lesions, while pathological laughing occurred in patients with right lateralised lesions (Gainotti, Antonucci, Marra, & Paolucci, 2001). Examples from the neuroimaging and neurophysiological literature have also provided support for a differentially distributed, lateralised hemispheric contribution, which is recruited accordingly depending on the nature of the emotion perceived. In the non-psychiatric neuroscience literature, early work in laterality and speech production by Rossi and Rosadini concluded that the two hemispheres incur opposite influences in the tone of emotional speech production, as observed in participants having undergone unilateral hemispheric sedation with sodium amobarbital; the authors noted that the right hemisphere was recruited during organisation of speech expressions of positive affect, while the left hemisphere was recruited during negative emotional speech expression (Rossi & Rosadini, 1967). Further reasoning suggesting a functional need for lateralisation based on the type of emotional stimulus perceived comes from emotional attention research. Specifically, attentional networks in the human brain are fine-tuned to ensuring survival by quickly and correctly identifying relevant information from our environment and filtering secondary, unnecessary stimuli. Depending on the biological relevance of a valenced stimulus, we are able to engage in appropriate action. This reasoning may be derived by linking evidence from the literature on the asymmetrical attentional processing of the space near or far from the body, to the suggested lateralised differential hemispheric engagement for positively and negatively valenced stimuli if one was to assume that positive vs. negative valence might manifest into approach vs. avoidance behaviours. Left/right asymmetries have been linked to attention being directed to near/far interpersonal space; for example, Heilman and colleagues reported that the left hemisphere was preferentially engaged during visual cognitive activities concerning the space close to the body, thus drawing attention close to the personal space. Heilman and colleagues also reported the right hemisphere was preferentially engaged during visual cognitive activities concerning extrapersonal space, therefore drawing attention away from the body (Heilman et al., 1995). It is therefore a possibility that if a valenced stimulus is suggesting actual threat to survival, the most efficient musculoskeletal response will be executed after engaging left-lateralised cerebral

networks linked to action-readiness. Conversely, if a positively valenced stimulus is perceived, right-lateralised hemispheric engagement will allow for action to approach.

1.4.1 MIGHT EMOTIONAL FACIAL EXPRESSIONS ENHANCE THE FUNCTIONAL NEED FOR LATERALITY?

Faces are heavily loaded stimuli regardless of valence; when observing a face, one is able to identify a multitude of socially-relevant cues which are key to human interaction such as for example identity, gender and attractiveness (Morris, Ohman, & Dolan, 1999; Vuilleumier, 2005a). In this light, any face – be that emotionally expressive or not – carries some element of biological significance and relevance, which could in theory mean that all faces irrespective of an emotionally-charged expression could be fast-tracked through the filters of selective attention. However, in the neuroimaging literature, some basic emotions – particularly those pertaining to threat or danger – have repeatedly been reported as preferentially processed as attention is biased towards them (e.g. Ledoux, 2000; Morris et al., 1999; Vuilleumier, 2005a, 2005b), with a similar processing preference for threat also displayed in behavioural studies of emotional processing (Horstmann, 2007; Horstmann & Bauland, 2006). Contrarily, a number of behavioural accounts of emotional face perception report biased and preferential processing of positive affect in visual search and backward masked emotion tasks (e.g. Calvo & Beltrán, 2014; Calvo & Nummenmaa, 2007; Juth, Lundqvist, Karlsson, & Ohman, 2005; Leppänen & Hietanen, 2004). Therefore, it may be the case that the two broad categories of basic emotional expressions (positive and negative) – such that do not require more complex, higher order cognitive disambiguation – impose a stronger bias on attention than non-emotive faces and may also therefore be sped through attentional filters. It may also be the case, that when two opposing types of emotional facial expressions (positive vs. negative) are presented, a form of attentional competition for their speeded processing takes place, the outcome of which depends on the type of experimental task employed; for example, in cases of backwards masking (i.e. Leppänen & Hietanen, 2004) positive affect commands attention, whereas in cases of simpler emotional stimulus detection (i.e. Horstmann & Bauland, 2006) negative faces grab attention.

The sheer multitude of emotionally charged environmental stimuli that we constantly encounter requires a sophisticated filtering mechanism that distinguishes between self-relevant and self-irrelevant information. Based on the outcome of this filtering, the most suitable type of response is selected and initiated, which in turn aids in managing the high attentional demands involved in deciphering, classifying and responding to a stimulus (Compton, 2003; Haxby, Hoffman, & Gobbini, 2000). Similarly, the detection, categorisation, and processing of facial expressions carrying an emotional load is a process which makes equally strong and biologically-relevant attentional demands (Palermo & Rhodes, 2007), suggested as being a product of a complex dynamic network of structures; namely, the amygdala, anterior insula, brainstem, hypothalamus, and orbital and somatosensory cortices (Dailey, Cottrell, Padgett, & Adolphs, 2002). The suggestion of increased biological relevance and hence speeded attentional processing of emotive faces has been confirmed primarily through studies comparing behavioural responses to basic facial affect to those resulting from exposure to phobic stimuli. Specifically, some facial expressions are thought to be processed in a similar way to other highly biologically-relevant stimuli such as spiders or snakes (Palermo & Rhodes, 2007).

What is it however about faces that makes them as effective as phobic stimuli in grabbing attention? The answer may lie in specific physiognomic elements of emotional expressions, which are suggested to be processed independently to others. For example, facial features which are dynamic and changeable and therefore can signal subtle changes in emotional expression have been suggested to be processed differently to other, invariant facial expression features (Adams & Kleck, 2003; Haxby et al., 2000; Palermo & Rhodes, 2007). Specifically, once through the initial encoding stage, dynamic elements of a facial expression such as eyebrows, mouth movement/shape and eye gaze, are processed independently of elements which for instance can aid in determining identity (Demaree, Everhart, Youngstrom, & Harrison, 2005; Haxby et al., 2000). While processing of the dynamic elements of an expression is facilitated by the superior temporal sulcus (Palermo & Rhodes, 2007), processing of elements establishing identity are processed through the lateral fusiform gyrus, via the fusiform face area, and through to anterior temporal regions (Adolphs, 2002; Haxby et al., 2000). Arguably, basic emotional facial expressions are effective, attention-grabbing stimuli that may be equally survival-relevant to the observer as a direct aggressor such as a snake. Given their strong

biological significance the attentional networks mediating our behavioural responses to facial expressions should be the same bottom-up subcortical emotion processing networks that are not only fine-tuned in correctly detecting and establishing relevance of the stimuli, but also are asymmetrically distributed in midline mesencephalic structures. The following section will provide an overview of this asymmetrical attention network distribution, so as to draw parallels with the hypothesised lateralisation of the resulting behavioural response.

1.4.2 MIGHT DISTRIBUTION ASYMMETRIES OF CORTICAL ATTENTION RESULT IN LATERALISED RESPONSES?

The overall asymmetrical distribution of cortical attentional networks has been consistently reported in both neuroimaging/neurophysiological and behavioural literatures. For example, Facoetti and colleagues, found evidence for asymmetrical attentional control when comparing dyslexics to control participants using a covert attentional orienting task (Facoetti, Turatto, Lorusso, & Mascetti, 2001). Use of a covert attentional orientation task allows the attention to shift from one target to the next without implicating eye movements such as those elicited when participants are asked to overtly orient their attention to a target stimulus. As a general rule, covert attention tasks present a cue, followed by a target stimulus. The target may appear either in a valid location (i.e. location previously cued), or an invalid location (i.e. uncued location). This type of task hypothesises that response times will be quicker in valid as opposed to invalid trials. By using such a covert attentional orienting task, and even though the authors reported the presence of attentional orienting in both visual fields for both dyslexic and control participants, they also observed significant differences in response latency in invalid cueing conditions, where dyslexic participant responses were slower than controls for the left visual field as opposed to the right (Facoetti et al., 2001). In another study on the control of visuospatial attention, Spencer and Banich found competing biases from the two hemispheres in the directionality of participants' attention in a bilateral presentation adaptation of the flankers task (Spencer & Banich, 2005). In earlier work by Levine and colleagues, differential hemispheric dominance was observed in a series of perceptual tasks (1987). Specifically, Levine et al reported that during bilateral stimulus presentation in three target location identification tasks using word, face and pictures of chairs as

stimuli, participants showed a left hemisphere advantage for words and a right hemisphere advantage for faces; pictures of chairs did not produce a lateralised effect (Levine, Banich, & Kim, 1987).

Hemispheric asymmetries have also often been reported in studies of spatial attention. Reuter-Lorenz and colleagues had previously reported on the asymmetrical distribution of spatial attention; they found that the spatial distribution of attention is biased in the direction contralateral to the more activated hemisphere, with the rightward bias of the left hemisphere being stronger overall (Reuter-Lorenz et al., 1990). Conversely, in an fMRI study investigating the distribution of the network for spatial attention, Gitelman and colleagues used a spatial attention task that required an equal shift of attention to both left and right visual field, and reported that the significant majority of participants showed right-lateralised hemispheric dominance (Gitelman et al., 1999).

There is evidence to suggest that attention networks are asymmetrically represented across the two hemispheres, in terms of both cortical and subcortical areas and structures. Although often reported as separate, distinct concepts, attention and primary emotional perception are intrinsically linked. For example, the two-step emotional perception model suggested by Haxby and colleagues (Haxby et al., 2000) highlights that the processing of emotional stimuli is functionally connected to subcortical attention networks. This model suggests two cognitive stages involved when perceiving primary affect: encoding/evaluation, and interpretation. During encoding, the self-relevance of emotional information is evaluated by filtering out self-irrelevant information; functionally, this is mediated by an attention/vigilance network well-established in the literature involving structures such as the medial geniculate nucleus, superior colliculus, pulvinar and amygdala (Vuilleumier & Driver, 2007; Vuilleumier, 2005). In the interpretation stage self-relevant emotional stimuli having been preferentially processed over other less relevant information are passed through to selective attention (Adams & Kleck, 2003; Compton, 2003) through a collaboration of both top-down and bottom-up processes (Compton, 2003; Palermo & Rhodes, 2002; 2007). One example for the asymmetrical cortical distribution of attention reports the lateralised engagement of the right and left hemispheres during visual cognitive activities concerning personal and extrapersonal space respectively (Heilman et al., 1995). Specifically, the authors observed right hemisphere activation in visual cognitive activities concerning extrapersonal space (i.e. space away from

the body), and left hemisphere activation during visual cognitive activities concerning personal space (i.e. near the body). In terms of asymmetrical subcortical activation depending on the nature of affective stimuli, there are numerous studies in the neuroimaging literature reporting left lateralisation of the attentional alarm/vigilance network involving the brainstem, amygdala, pulvinar and superior colliculus and ending in projections to somatosensory cortex, occurring during perception and processing of masked negative (typically fearful) stimuli (e.g. de Gelder et al., 2011; Liddell et al., 2005; Tamietto & de Gelder, 2010; Vuilleumier & Driver, 2007).

A proportion of the literature on hemispheric emotional laterality, or on a hemispheric preference to specific emotions (e.g. Carver, 2004; Eder, Hommel, & De Houwer, 2007; Fox, Russo, & Dutton, 2002) has been based on subjective emotional experience data. Hemispheric asymmetries however are not restricted to the subjective, physiological experiencing of emotions; they also extend to emotional perception (Jansari et al., 2000; Reuter-Lorenz, & Davidson, 1981). Using a bilateral presentation paradigm where a neutral facial expression was paired with an ambiguous but visible expression of one of the six primary emotions (happiness, surprise, disgust, fear, or sadness), and by not employing any time constraints on stimulus display time, Jansari and colleagues were able to detect valence-dependent laterality effects, and to further report on an overall increase of accuracy during bilateral stimulus presentation of two emotional facial expressions (Jansari et al., 2000).

In earlier studies looking at the behavioural response to valenced stimuli, paradigms by Reuter-Lorenz and Davidson, and Moretti and colleagues used bilateral presentations of emotional and neutral facial expressions of affect and reported preferential engagement of the left hemisphere for positive facial expressions and preferential engagement of the right hemisphere for negative facial expressions (Moretti, Charlton, & Taylor, 1996; Reuter-Lorenz, & Davidson, 1981). Based on the above-suggested link between cortical asymmetrical distribution of attention and the resulting laterality of behavioural responses, particularly when resulting from valenced stimuli, the following section discusses further links to physiological contralaterality.

1.4.2 MIGHT THE ASYMMETRIC DISTRIBUTION OF CORTICAL EMOTIONAL ATTENTION RELATE TO PHYSIOLOGICAL CONTRALATERALITY?

The asymmetrical distribution of basic attentional emotional processing might be related to the contralateral anatomy of the human visual, visceral and muscular-skeletal systems, when considered as a product of visual field dominance and the subsequent lateralised attentional bias depending on the type of emotion observed. In the human anatomy, the physiological perception and action networks such as vision, conjugate lateral saccades, and face muscles involved in the production of facial expressions and reflexive bodily reactions are contralaterally intertwined. In the vision literature, evidence suggests that parts of the visual periphery are processed asymmetrically by the human eye, in terms of both resolution, and visual hyperacuity (Fahle, 1987). The human visual system is contralaterally represented in the body's morphology (Figure 1), whereby visual input from the left and right visual field passes through to its contralateral primary visual cortical areas (Felten & Shetty, 2011). This asymmetry is also evident in lateral eye movements, whereby voluntary saccades originating from the frontal eye fields cause a strong, rapid deviation of the eyes to the contralateral side that is often accompanied by movement of the head and trunk (Merckelbach, de Jong, & Muris, 1990).

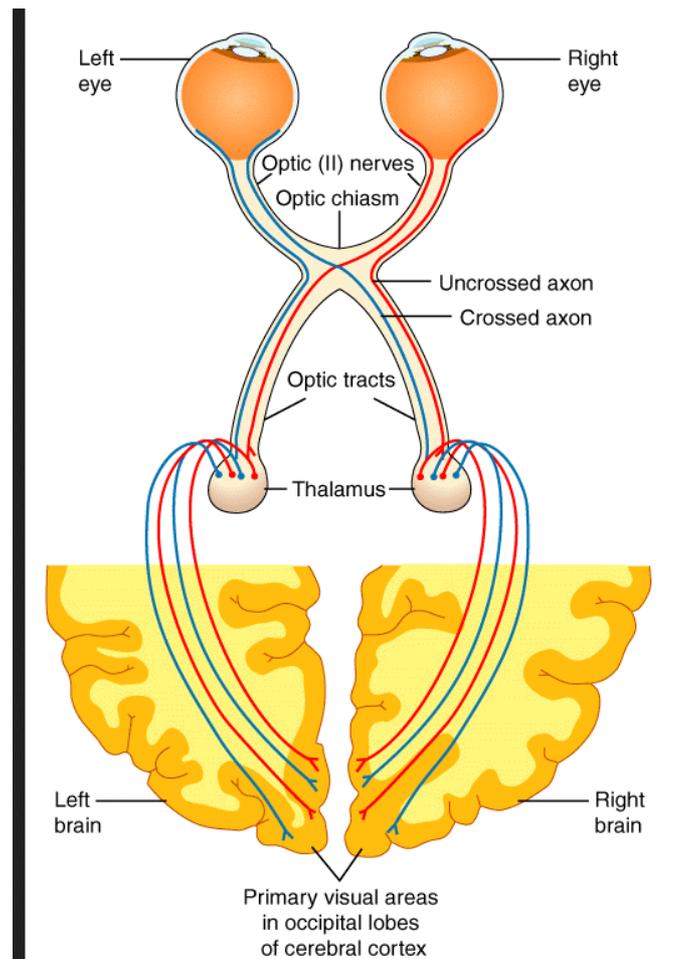


Figure 1. Diagram displaying the contralateral distribution of the human visual system (Figure adapted from Felten & Shetty, 2011).

Projections from the frontal eye fields travel downwards towards the pontine centre for lateral gaze, from where impulses subsequently ascend through the medial longitudinal fasciculus to cranial nerve nuclei responsible for ocular movement. The route of these impulses is nearly fully decussated, with the frontal eye fields of one hemisphere supplying the contralateral ocular nuclei, resulting in contralateral eye movements (Merckelbach et al., 1990). The importance of the medial longitudinal tract involved in the production of conjugate (i.e. combined) lateral eye movements is evidenced by its presence in all vertebrates, as well as it being the first tract to myelinate in humans (Willer, 1977); this implies that it is closely linked to reflex reactions when experiencing environmental emotion-inducing stimuli (Willer, 1977). Similarly, face musculature is contralaterally represented in the human body, which might explain evidence for emotion-specific laterality effects in studies of posed facial expressions reported in the literature (e.g. Yecker et al., 1999). Specifically, when investigating posed facial expressions in right-handed participants, Yecker and

colleagues reported that negative posed facial expressions were more intensely represented in the left hemiface, and positive expressions more intensely represented in the right hemiface (1999).

One observation from the overview of the laterality literature in this section is that lateralisation might address a specific functional need; lateralised activation specific to positive and negative emotions mediated respectively by right/left ocular and musculoskeletal symmetrical cross-laterality needs to occur so that we may be able to respond to basic emotional stimuli that tap into instinctual reflexes as efficiently as possible. Although Rolls had previously argued that a lateralised organisation may not be evolutionarily economical (2002), and although the contralateral nature of basic emotional perception might not be as elegant as the overall interhemispheric communication required for more complex, higher-order cognitive functions (and possibly the processing of secondary/social affect), it does serve the specific – albeit somewhat crude – purpose of maintaining survival by ensuring the most efficient behavioural response is selected and executed.

1.5 SUMMARY AND THESIS OUTLINE

To summarise, emotional lateralisation is evidently a complex automatic process that has historically proven difficult to disentangle. So far, behavioural findings towards directionality of lateralisation appear to be closely linked to the type of methodology, task and stimulus used. Usage of this wide range of methods has resulted in the lack of consensus as to whether lateralisation occurs for all types of basic affect, and difficulties establishing whether some basic affect (i.e. negative) is better suited to engaging and maintaining attention than others. Reports from the neuroimaging literature consistently point towards the lateralised engagement of subcortical structures in the processing of specific types of basic affect. Whilst differential engagement of subcortical structures and activation routes has been well reported, it still remains to be established how this subcortical lateralisation which is thought to tap into an attentional activation network of increased vigilance might translate into observable behaviour.

The main body of evidence from lateralisation research can be interpreted to suggest that elements such as impact of methodology and stimulus parameters, and

impact of participant parameters and individual variability (i.e. personality traits such as anxiety, and psychiatric conditions such as depression or schizophrenia) have had a significant effect on the directionality of behavioural lateralisation patterns reported. Up to date however, there has been little interest in establishing the key factors modulating behavioural lateralisation through using consistent and comparable methodologies. The current thesis addresses this gap by first developing a behavioural paradigm to establish the behavioural manifestation of emotion-specific lateralised processing, then examining whether subcortical lateralisation can be effectively measured in terms of observable behaviour, and finally by adapting this paradigm to incorporate both stimulus valence-enhancing factors, as well as participants' personality traits which have been suggested to modulate this process.

2 CHAPTER 2: MODULATION OF LATERALISED RESPONSES TO PRIMARY AFFECT

2.1 INTRODUCTION

Chapter 1 introduced the core theoretical assumptions that furnish the rationale for the present thesis. To summarise, the thesis investigates the existence and directionality of lateralised emotional processing as defined according to the valence hypothesis (Ahern & Schwartz, 1979). The valence hypothesis suggests that positive stimuli are thought to preferentially engage the left hemisphere and negative stimuli the right hemisphere (Ahern & Schwartz, 1979). Given the contralateral nature of the visual system (Harter, Aine, & Schroeder, 1982), the directionality of cerebral processing suggests that positive stimuli displayed on the right visual field (RVF) are being preferentially processed by the left hemisphere, while negative stimuli on the left visual field (LVF) are preferentially processed by the right hemisphere (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz, and Davidson, 1981). As discussed in chapter 1, studies on emotional lateralisation have consistently resulted in conflicting directionality patterns of laterality and have historically shown poor replicability. Behavioural research on emotional laterality in particular, has seen a wide range of methodologies utilised as well as different types of behavioural data collected, with particular preference for paradigms using participants' subjective emotion categorisation of facial expression stimuli (e.g. Eder, Hommel, & De Houwer, 2007; Fox, Russo, & Dutton, 2002), or alternatively participants' self-reports on emotional state (e.g. Carver, 2004). Variation in experimental methodologies has resulted in a lack of replicability and generalisable findings. As a result, chapter 1 highlighted the need for a generalisable, concrete and reliable behavioural method investigating emotional lateralisation, which could subsequently be used as a basis for further adaptation to include additional factors that have previously been suggested to influence or modulate lateralisation of affect.

To this end, the present chapter aims to lay the groundwork for such a behavioural methodology, by introducing a paradigm that effectively measures lateralised responses towards angry and happy facial expressions of affect. Instead of utilising

tasks that require engagement of higher order and potentially competing cognitive functions such as self-report of emotion (e.g. Carver, 2004) or facial expression emotion categorisation (e.g. Eder, Hommel, & De Houwer, 2007; Fox, Russo, & Dutton, 2002), the experiment developed here utilised a basic target location identification task with target location unpredictable per trial, where the nature of the target emotion stimulus was irrelevant to participant responses. As such, this experiment sought to test the assumption that resulting lateralised participant responses are modulated by the nature of the emotion observed.

2.1.2. IMPACT OF METHODOLOGY ON THE INTERPRETATION OF LATERALISED PROCESSING OF AFFECT

The impact of paradigm design on research accounts of affect-dependent lateralised processing has often been reported as an issue in terms of the validity of response patterns reported (Jansari et al., 2000; Schepman, Rodway, & Geddes, 2012). The following section will address two design elements that might play a pivotal role in terms of which directionality the resulting lateralised behaviour pattern is reported as taking. Specifically, the sections below suggest that the lateralised direction of findings is reliant on the type of emotional stimulus used, often within the same broad category of negative or positive, and on the type of experimental task employed.

2.1.2.1 THE PROBLEM WITH NEGATIVE AFFECT

A considerable proportion of the lateralisation literature has consistently used fearful emotional stimuli as the main representative emotion of the 'negative' spectrum (e.g. Adams et al., 2012; Liddell et al., 2005; Morris, Ohman, & Dolan, 1999; Yang, Zald, & Blake, 2007). Another equally large part of the lateralisation literature regards sadness as the core representation of negative valence (e.g. Du & Martinez, 2013; Reker et al., 2010; Reuter-Lorenz, and Davidson, 1981; Voyer, Bowes, & Soraggi, 2009). Angry emotional stimuli on the other hand – be those schematic, chimeric, or realistic/photographic – have typically been used in visual search paradigms, in order to establish whether negative affect is processed preattentively (Horstmann, 2007;

Horstmann & Bauland, 2006), without placing emphasis on whether or not responses to anger are also derived from distinctly lateralised hemispheric engagement.

Horstmann et al.'s suggestion of a preattentive processing specific to angry/threatening stimuli leads to new, testable hypotheses. Specifically, how might (if at all) this preattentive processing for threat relate to suggestions of a right-lateralised preference for negative affect?

Although angry facial expressions are frequently used stimuli in studies examining a suggested overall preferential cognitive engagement with threatening stimuli (e.g. Horstmann & Bauland, 2006; Marinetti, Mesquita, Yik, Cragwall, & Gallagher, 2012), they have also played an important role in investigations of the effect and implications of cognitively-loaded emotive stimuli on working memory (Jackson, Wolf, Johnston, Raymond, & Linden, 2008; Jackson, Linden, & Raymond, 2014), short-term memory (Jackson et al., 2008; Subramanian, Hindle, Jackson, & Linden, 2010), anxiety and/or depression (Byrne & Eysenck, 1995; Eysenck & Calvo, 1992; Eysenck et al., 2007; Mogg & Bradley, 1999), and schizophrenia (Wolf et al., 2011). Based on this broad range of applications for angry facial expressions, their lack of usage in lateralisation studies directly against an opposite affect such as happiness is surprising.

Instead, the most commonly used facial expressions to depict negative affect remain those of fear. Perhaps the strongest reason encouraging their preferential use in lateralisation studies in particular could be linked to the establishing of a distinctly lateralised subcortical activation network including superior colliculus, pulvinar and amygdala, which has been found to be particularly sensitive to fearful emotional stimuli (Morris et al., 1999; Vuilleumier et al., 2003). With regards to the valence of the facial expression itself, fear lends itself to hypotheses of carrying contextual information relating to the imminent presence of threat towards the observer; as such, fearful facial expressions can be seen to act as triggers for a fight or flight response. It is likely that there is a specific functional need requiring a lateralised subcortical activation pathway which is triggered as a response to fear, and which is closely linked to a state of vigilance or action readiness for the individual. On perception of a fear-laden stimulus, the organism needs to act (or react) efficiently and effectively. By deciphering the nature of the stimulus observed via the subcortical pathway short-cut, the person perceiving the potential threat is able to be goal-directed and action-ready; in other words, they can fight or flee (Corbetta & Shulman, 2002). In conjunction with this subcortical vigilance short-route, Corbetta and Shulman posit a right-lateralised

cortical attentional system via the temporoparietal and inferior frontal cortex which is highly sensitive to detecting salient and relevant environmental information, especially when it is unexpected to the observer (2002); subsequently, this system also assists the selection of an appropriate response towards it.

One design-related caveat in studies reporting a fear-sensitive subcortical vigilance route is that fearful faces are rarely directly compared against other emotions in terms of whether responses to other affect (such as anger, happiness or sadness) also stem from the activation of equally sensitive, lateralised subcortical networks. This caveat stretches to behavioural studies of laterality where at present comparisons across two opposite types of basic affect (such as anger against happiness) as direct measures of laterality in basic emotional processing are few. Interestingly, a comprehensive review of the interaction between emotional face perception and attention by Palermo & Rhodes, (2007), debunks the suggestion of fearful faces as being registered earlier than other types of basic emotional facial expression. The authors suggest that other primary emotions, such as anger, happiness or sadness, also show a propensity for being registered and recognised with very similar response latencies to those found for fear - albeit from activation pathways derived from different connection networks between subcortical structures – with the main difference being wide variation in the resulting range of response latencies to emotional faces (Palermo & Rhodes, 2007). The authors also highlight that there have been very few studies that have looked at direct comparisons between fearful and other emotional facial expressions that have found any response advantage that was specific to fear.

In contrast to fearful faces, sad facial expressions, although fitting within the general negative emotional description, are not thought of being connected to a situation in which the observer needs to respond quickly and efficiently. Although a negative emotion by social definition norms, the physiological state of sadness does not necessitate an organism to respond quickly and efficiently as it would when in a state of fear. Nonetheless, sadness is an equally commonly used negative stimulus as fear, predominantly in studies exploring the valence hypothesis through visual search paradigms (e.g. Killgore & Yurgelun-Todd, 2007). Sad facial expressions are however rarely used in investigations on the preattentive processing of negative affect, possibly due to the lack of a direct link between stimulus and response specifically similar to that relating to threat. Furthermore, sad stimuli are rarely compared directly to negative emotions other than fear. Usually, sad faces have been used in studies

looking at interactions between personality traits and/or mood disorders (e.g. anxiety, depression) and the propensity to successfully recognise and distinguish sadness as a state (e.g. Bradley, Mogg, & Millar, 2000; Mogg & Bradley, 1999; Moretti et al., 1996). Albeit linked to group differences based on personality traits (i.e. high, medium and low anxiety groups), studies from this scope of the literature consistently report differential attentional biases specific to negative (in this case sad) facial expressions. Considering the usage of angry stimuli in studies on the preattentive processing of threat (e.g. Horstmann et al 2006; 2007), it is puzzling that the emotions constituting negative affect in other emotional perception research domains remain fear and sadness. Particularly in investigations of laterality, where the side of the body more equipped to instigate efficient behavioural responses to a potential aggressor would be recruited, anger would make a valid candidate. In an attempt to explore further the potential benefits of anger as a key type of negative affect in behavioural research, the following section will address response pattern differences in relation to different types of affect, based on the type of experimental task employed.

2.1.2.2 MIGHT RESPONSES TO AFFECT BE TASK-DEPENDENT?

The type of paradigm used in studies of laterality could be seen as guiding both type and pattern of responses collected. For example, behavioural studies looking into the way we recognise and respond to emotional stimuli commonly use free visual search paradigms, with some studies using upright stimuli (natural or chimeric), some inverted, and some a combination of both (e.g. Calvo & Nummenmaa, 2008; Jansari et al., 2000; Reuter-Lorenz, and Davidson, 1981). Such studies do not apply any form of timing restrictions on participant responses, nor do they provide any feedback on individual trial or testing block performance, therefore rendering the disentanglement of cognitive-perceptual timeline for emotional stimuli problematic. For example, as basic affect (negative affect in particular) has been found as being efficiently processed either under or very near to the threshold of awareness (e.g. Horstmann & Bauland, 2006; Horstmann, 2007), the lack of participant response time restrictions might allow for slower, higher-order processing of emotional stimuli and therefore not reflect near-automatic, reflex-like responses. Perhaps that is why studies using angry expressions report findings of overall preferential cognitive engagement following exposure to threatening stimuli (e.g. Horstmann & Bauland, 2006; Marinetti et al.,

2012). Responses other than reflex-like reactions might not give an accurate representation of activation of a subcortically driven alarm system and its manifestation in behaviour.

Regardless of a lack of methodological control and consistency, studies from this portion of the literature do generally agree on a laterality effect translated from a visual field preference depending on the nature of the emotion the stimulus displayed carries. For example, evidence so far points to a lateralised cerebral preference for one type of emotion over another at both a subcortical/perceptual level, as well as at an observable behaviour level (Moretti et al., 1996; Reuter-Lorenz et al., 1990; Reuter-Lorenz, and Davidson, 1981). In order to fully establish whether the directionality of lateralisation is dependent on the nature of the emotion observed (e.g. in accordance with the valence hypothesis whereby positive emotions lateralise to the left hemisphere, and negative emotions lateralise to the right hemisphere), there needs to be a methodologically-controlled behavioural paradigm that utilises a clear definitional distinction between positive and negative affect, and implements response latency allowance restrictions. Through this methodology, the near-threshold behavioural effects specific to positive and negative affect might be better examined.

It is a possibility that different types of primary emotion are not necessarily perceived, recognised and responded to at the same speed. For example, it seems that certain types of negative affect in particular – i.e. sadness – are processed quicker when observed by individuals who have a propensity to melancholic/depressive affect (B. Bradley et al., 2000). Furthermore, in behavioural studies in particular, it is positive stimuli that most commonly yield quicker and more accurate responses, although consistent exploration of why a happy advantage might exist has not insofar been undertaken (Jansari et al., 2000). In addition to this, stimuli of choice in emotional perception research vary from realistic photographs (Blagrove & Watson, 2014) to schematic/chimeric/inverted faces (Calvo & Nummenmaa, 2008; Cooper, Rowe, & Penton-Voak, 2008; Eger, Jedynek, Iwaki, & Skrandies, 2003; Tomalski, Johnson, & Csibra, 2009), and also to masked/phobic stimuli (i.e. IAAPS) (Liddell et al., 2005; Morris et al., 1999; Reker et al., 2010; Paul J Whalen & Kleck, 2008), all of which point to different emotional perception sensitivities. The impact of methodology on interpretations of laterality is therefore evident. A possible suggestion which might address methodological limitations would be to impose strict time limitations for participant responses so as to isolate reflexive reactions, while utilising

two definitionally opposite emotions (i.e. angry vs. happy) in a task which requires participants to indirectly respond to emotional stimuli instead of requiring them to direct their full attention towards them which might involve longer processing times and higher cognitive processes.

2.1.3 HOW MIGHT EMOTIONAL LATERALISATION TRANSLATE INTO APPROACH/AVOIDANCE BEHAVIOURS?

Chapter 1 outlined evidence for the neuroanatomical basis of both experience and perception of basic affect by addressing the question of whether there is a functional need for differential hemispheric engagement relative to the nature of the emotion both being perceived and responded to. The present chapter will now consider the observable behaviour resulting from the respective differential contribution of each hemisphere, in an attempt to translate function into measurable response.

The neuroimaging literature has highlighted a number of areas of interest activated from the processing of basic affect. Identification of these areas has in turn allowed for the outlining of distinctly lateralised subcortical networks which are fine-tuned in responding to positive or negative emotional stimuli (e.g. Wager, Tor, Phan, Luan, Liberzon & Taylor, 2003). Lateralisation at a subcortical level based on the nature of the emotion observed is a widely reported phenomenon, albeit with methodologies remaining limited to using specific basic emotions from the negative spectrum – for example, fear and sadness. On the behavioural findings spectrum however, there is little consensus on how these distinct, lateralised neuronal activation networks might manifest into equally lateralised observable behaviours. A widely accepted hypothesis links the nature of the emotion observed to approach and avoidance behaviours; this assumption posits that emotions which fall on the negative spectrum resemble avoidance behaviours when being responded to, with positive emotions resembling approach behaviours (Casasanto & Chrysikou, 2011; Eder et al., 2007; Farb, Chapman, & Anderson, 2013; Grèzes, Adenis, Pouga, & Armony, 2012). With this linkage in mind, the connection between emotional stimulus and observable, measurable response would therefore be relatively straightforward to decipher. For example, rapid activation of the oculomotor system following exposure to a highly biologically relevant stimulus (such as a spider), would translate in speeded and

highly accurate reactions to avoid danger (Palermo & Rhodes, 2007). It may therefore be the case, that our need to approach or avoid distinctly positive or distinctly negative affective stimuli requires the recruitment of left or right lateralised hemispheric contribution, so as to initiate an appropriate musculoskeletal response.

2.1.4. SUMMARY

Investigations on the suggested lateralised pattern of responses to positive and negative affect point towards lateralised subcortical activation routes that are known to increase vigilance and aid detection and response to basic emotional stimuli. On the behavioural studies front however, there is uncertainty concerning whether lateralised subcortical activation translates into an equally lateralised observable response based on the nature of an emotional stimulus.

Experiment 2.1 described in the following sections of the present chapter addresses the need for a behavioural paradigm that tests the valence hypothesis by utilising manual response latency and accuracy responses between angry and happy facial expressions, with expression salience varying from highly ambiguous to highly unambiguous. The experiment uses a bilateral stimulus presentation forced-choice task, and was designed to combine elements of previous key behavioural investigations from the lateralisation literature (e.g. Moretti, Charlton, & Taylor, 1996; Reuter-Lorenz, and Davidson, 1981) which have been adapted to account for core methodological caveats (i.e. ecological validity of stimuli used, as well as stimulus onset-offset and allowance of overly long participant response latencies). The experimental design also utilises anger (instead of fear/sadness) as a representative negative affect based on suggestions from the literature of anger's triggering of quick and efficient responses by being preattentively processed through a subcortical activation network specific to detecting and responding to threat (Horstmann & Bauland, 2006). In the following section of this chapter, Experiment 2.1 is preceded by a pilot procedure (Stimulus Selection Pilot), whereby the original stimulus set identified for use throughout the studies outlined in the present thesis (Ekman & Friesen, 1976; Calder, Young, Rowland & Perrett, 1997) was examined for its suitability. This pilot procedure is focused in ensuring that the facial expression stimuli to be used in the experiments proper did not present with any extraneous, attention-grabbing features, thus rendering them prone to participant response bias.

Furthermore, the present chapter sees the development of a paradigm (Exp. 2.1) that focuses purely on the observable, near-reflexive behavioural response to basic emotion rather than considering the higher-order, more complex cognitive processes involved in its perception. Based on the valence hypothesis whereby the right hemisphere is expected to show preferential engagement during processing of

negative affect, with the left hemisphere more engaged during processing of positive affect (Schwartz et al., 1979), angry facial expressions are expected to elicit quicker and more accurate responses when displayed on the left visual field, with happy faces eliciting quicker and more accurate responses when shown on the right visual field.

2 PILOT PROTOCOL FOR STIMULUS SELECTION

2.2.1 STIMULUS SELECTION METHODOLOGY

2.2.1.1 OVERVIEW

A pilot experimental protocol was designed as a means of identifying the set of facial expression stimuli to be subsequently used in the experiment proper (Exp. 2.2). The pilot protocol consisted of two parts; (a) a stimulus selection computerised procedure mirroring the experimental procedure to be followed by experiments in this thesis, and (b) an image manipulation procedure, whereby the stimulus set identified suitable for use in the experiments presented in this thesis was further modified to control for further potential stimulus confounds such as face dimensions, luminance, and salience. In the following sections of the present chapter both parts of the pilot protocol are reported by beginning with the computer-based, stimulus selection procedure, and moving on to the additional image manipulation conducted on the filtered stimulus set. The rationale behind designing this protocol was based on ensuring that the stimulus set did not include facial expression images that were particularly distinctive, unique, or attention grabbing, which might potentially generate stimulus confounds and lead to participant response bias which may obscure any effects of emotion-dependent lateralisation.

The preliminary stimulus set was identified as that of Calder et al's (1997) adapted version of Ekman and Friesen's (1976) set of facial expressions greyscale photographs. This set included facial expression photographs for each of the primary emotions (happy, sad, fearful, angry), posed by ten posers. Some of the posers included in the original Ekman and Friesen set (1976) have distinctive physiognomies in terms of facial shape, size and facial features (i.e. teeth, eyebrow shape, head shape), which may render them more memorable than the facial

expressions of other posers also included in the set, especially when presented in a behavioural task where participants need to provide a response within strict time limits. The potential risk of response bias that may result from the inclusion of easily distinguishable photographs in the stimulus set is that it may lead to an obscuring of any emotionality effects, as the more immediately recognised poser-specific facial features may take attentional precedence in recognition and perception. Therefore, in an attempt to select the photographs that are least likely to lead to a potential recognisability response bias, pilot experiment 2.1 utilised response times and accuracy judgments (proportion correct), which were subsequently linearised so as to maximise between-conditions differences across participants. Emotion-dependent laterality hypotheses would not be examined at this pilot stage, as any emotionality influences may be either obscured, or skewed due to potential confounds of including all ten posers in the stimulus set. Additionally, although it could be argued that potential trends of emotional lateralisation resulting from the pilot data may emerge from response rate and accuracy scores elicited during the pilot procedure, it was decided that these would most likely not be valid indicators of emotion-specific lateralisation as they would ultimately be susceptible to stimulus confounds. The following sections will outline each step of the pilot process, beginning with participants and apparatus utilised in the computer-based stimulus selection procedure, and followed by a detailed exposition of the image processing, stimulus presentation, protocol procedure and findings.

2.2.1.2 STIMULUS SELECTION PROTOCOL PARTICIPANTS

Sixty-four neurologically healthy right-handed (9 males) 2nd Year Undergraduate Psychology student volunteers took part in the pilot experiment. Participation was voluntary, and participants were recruited during a Research Methods in Psychology practical lab session.

2.2.1.3 STIMULUS SELECTION PROTOCOL APPARATUS

As the original stimulus set consisting of all ten posers would be utilised at this stage, no hypotheses on emotion-dependent laterality would be examined. To this end, there was no need to test participants individually. For the stimulus selection

process therefore, the testing setup consisted of a University computer laboratory classroom, with identical desktop computer equipment per seat. The computer equipment consisted of DELL Optiplex 780 PCs, connected to 17-inch LCD monitors with 58Hz refresh rate. Responses were provided by pressing the left and right arrow keys on a standard QWERTY computer keyboard, and stimuli were displayed at a 24.4° visual angle.

2.2.1.4 STIMULUS IMAGE PROCESSING & PRESENTATION

Angry and happy emotional expression stimuli were borrowed from Calder, Young, Rowland, and Perrett (1997), who had designed a modification on the original Ekman & Friesen set of facial expression images (Ekman & Friesen, 1976). In this modification, Calder et al (1997) applied a computer-based morphing procedure on the original ten posers from the Ekman and Friesen set, by positioning anatomical landmarks on each poser's neutral photograph with corresponding points to its emotional counterpart.

Faces were then morphed into one of six emotional salience intensities (with '0' being neutral, '4' being the original emotional image, and '5' being exaggerated) by scaling them with respect to the vectors defined by these landmarks (Fig. 2.1). The present thesis applies the usage of these salience morphs across all experiments, as a means of identifying the point at which an emotional expression becomes recognisable accurately, depending on the experimental parameters under investigation in each experiment. Participant accuracy judgements will subsequently be used in calculating thresholds for accurately recognising each type of affect (angry/happy). In the present study, in order to eliminate each poser's easily identifiable peripheral features which were not necessary in identifying the emotion displayed, a further modification on the Calder et al set was applied, whereby photograph dimensions were equated across the set by the application of an oval-shaped window (Fig. 2.2). This windowing method allowed for poser-specific peripheral features such as the hairline and face-width to be equated so that each stimulus photograph was of the same dimensions and shape. To this end, each face was scaled along horizontal and vertical dimensions to the point where facial features

fit within the oval window, with eyes aligned with the middle-horizontal guideline and mouth aligned with the bottom-horizontal guideline.

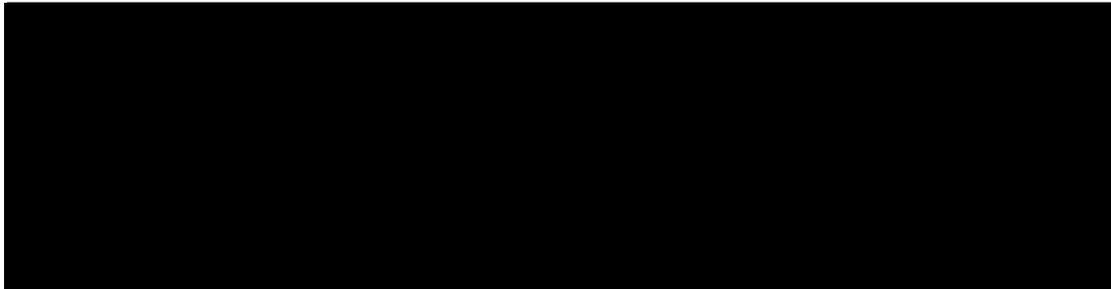


Figure 2.1. Angry stimuli from one Ekman & Friesen poser, displayed on grey background as used in the task. From left to right, expression salience starts from completely neutral (intensity 0) and morphs gradually from highly ambiguous (intensity 1) up to a highly exaggerated expression (intensity 5).

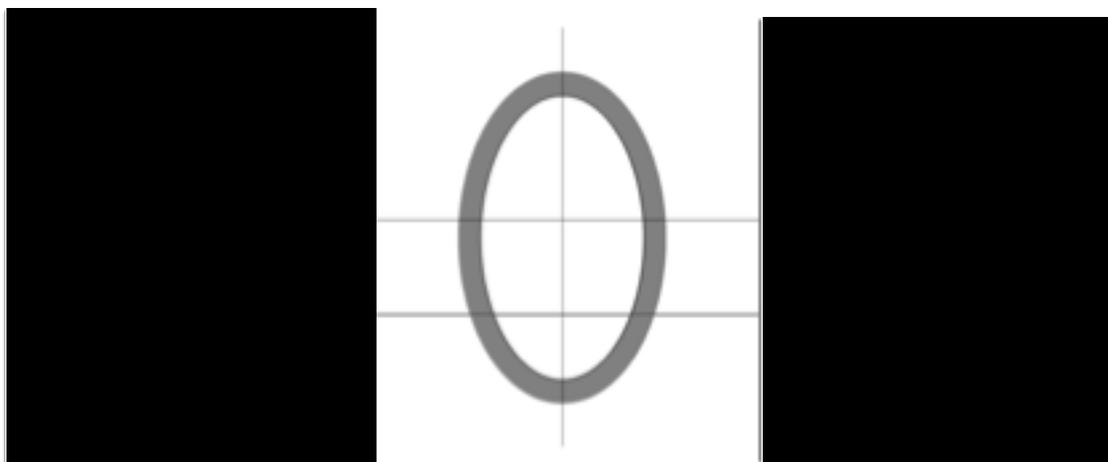


Figure 2.2. Example of stimulus before and after windowing; the far-left picture shows the original photograph whereby poser-specific elements (such as the poser's hairline) could render the photograph easily identifiable. The middle graphic displays the oval-shaped window used to superimpose on the original photograph so as to eliminate poser-specific identifiable features. Aside from the window, the graphic also displays two horizontal and one vertical guides used to align features from each face so as to equate positioning of eyes and mouth across stimuli. The far-right graphic shows the final version of the photograph, post-windowing.

In order to ensure that there were no significant brightness and luminance differences between photographs overall (Fig.2.7a) as well as between the different emotional expressions (angry and happy) (Fig. 2.7b), faces were examined in terms of average image greyscale intensity as a function of emotion intensity (1-5 intensity levels) for all ten angry and all ten happy faces. For this purpose, average image pixel intensity was used as a measure of luminance. On the whole, there were no consistent differences between emotions; additionally, for faces of maximum emotional intensity there was no significant difference between happy and angry emotions [$t(9)=.05$, $p<0.96$].

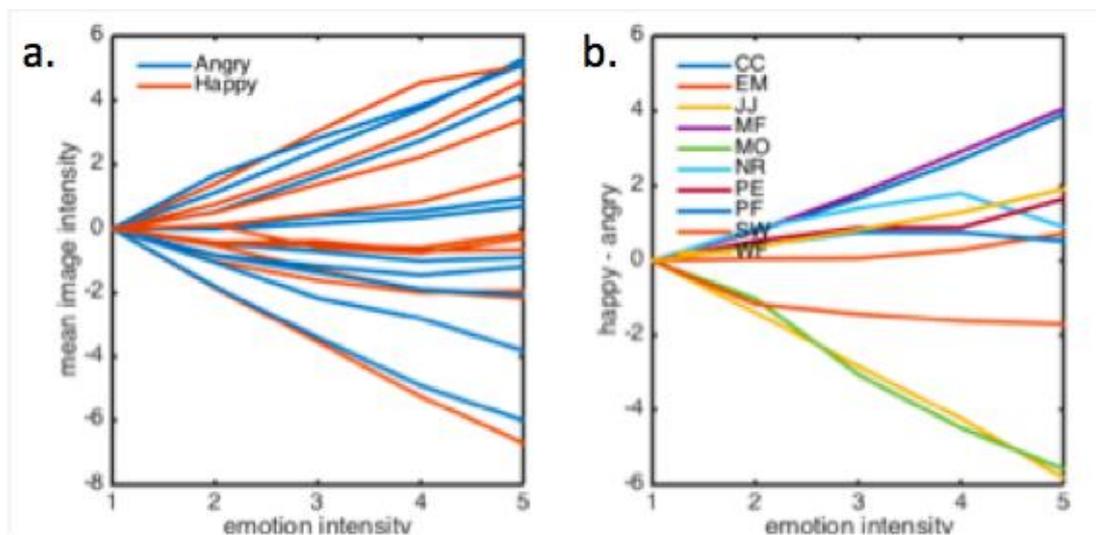


Figure 2.7. Graph 'a.' shows the average image intensity (y-axis) as a function of emotion intensity (x-axis) for all ten angry vs. happy faces. Here, image intensities across the photograph set varied within each image from 0 to 255, and mean image intensity of each poser's neutral photograph was subtracted from each poser. Overall, even though there are small differences between posers and emotions, no consistent differences between angry and happy emotional faces are observed. Graph 'b.' shows the result of subtracting angry image intensity from happy for each poser respectively, as a function of expression salience intensity; here, there are no consistent positive or negative deviations. On the whole, although there are small differences in image intensity (average luminance) between emotions, these differences are non-significant and inconsistent.

Each trial displayed a bilateral presentation of a neutral (intensity 0) and emotional (intensity 1 through to 5) facial expression pair (see Figure 2.3 for examples). Each individual pairing of neutral/emotional photograph always contained photographs from the same poser.

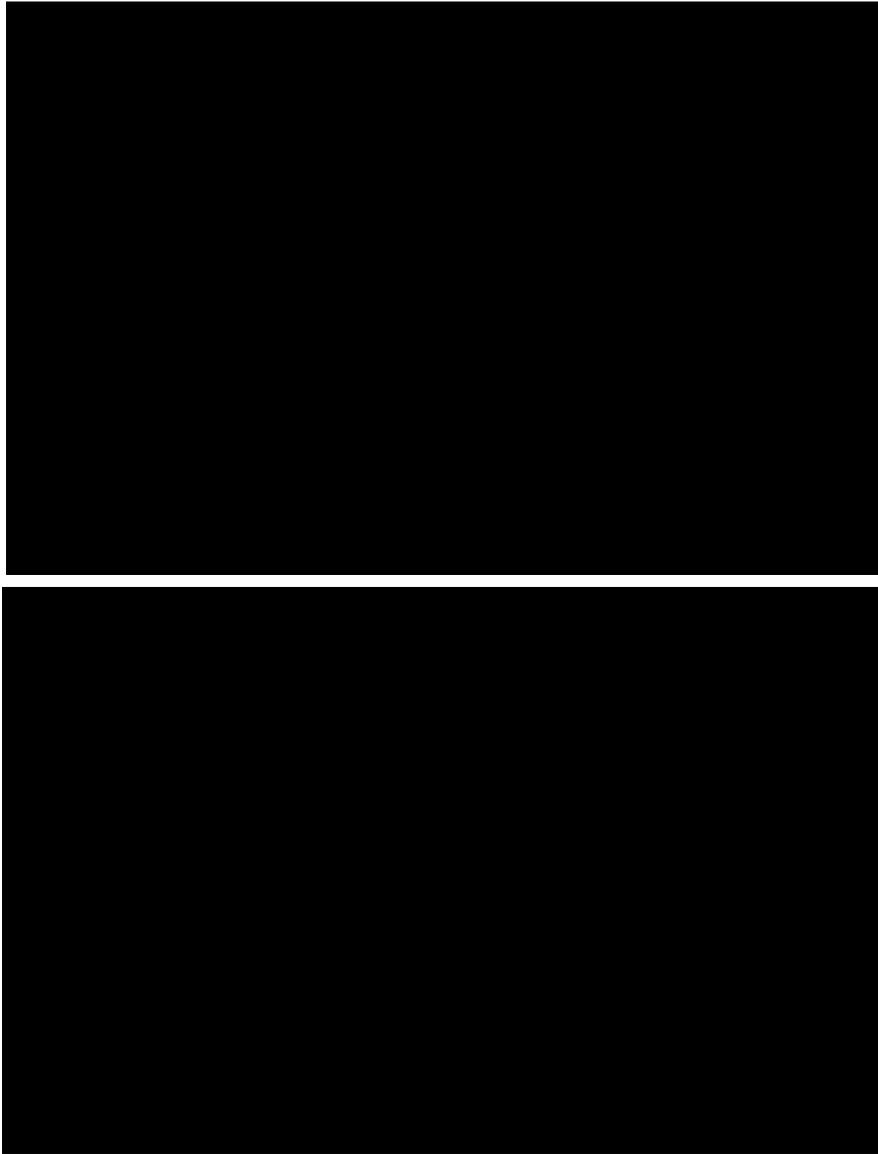


Figure 2.3. Two example stimulus pairs where the target photograph is shown on the right visual field on the top image, and on the left visual field on the bottom image. This example shows an emotional photograph of happy valence shown in salience intensity 2, and one of angry valence shown in salience intensity 4. The 'neutral', 'int 2' and 'int 4' tags are displayed here for information purposes only and were not shown in the actual experiment.

Dimensions (3cm x 10cm) and lateral positioning of stimulus pairs remained constant across trials, whereby the target photograph's location was unpredictable from trial to trial. Each individual photograph was positioned at a distance of 10cm from nasion to central fixation point (see Figure 2.4 for an example). Both left visual field and right visual field stimuli regardless of emotionality were always equidistant from the central fixation point. The pairing of neutral to emotional photograph on

each trial was randomly assigned through E-Prime (E-Prime v2.0, Psychology Software Tools, Pittsburgh MA).

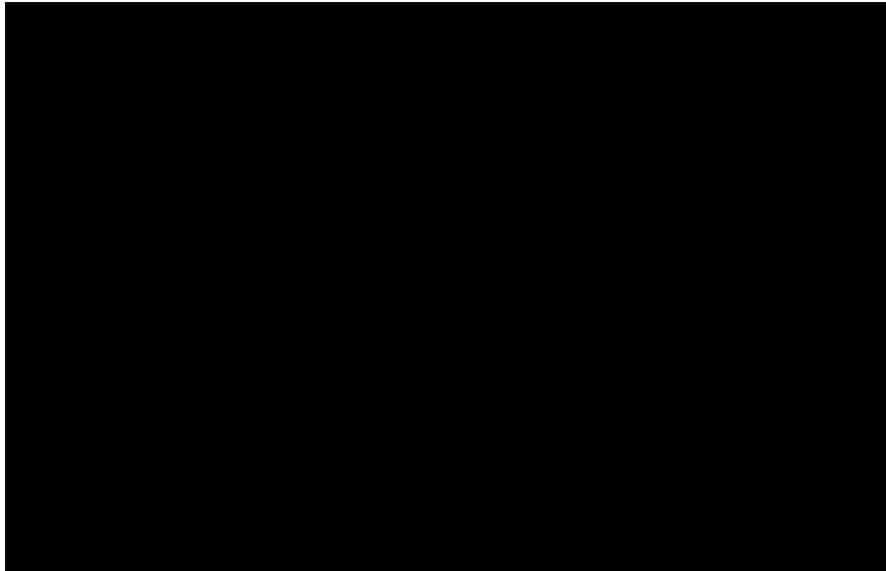


Figure 2.4. Stimulus positioning in a typical trial. Graphic displays one neutral (left photograph) and one emotional (right photograph) expression from the same poser. Dimensions noted on the graphic refer to those used in the actual experiment, which were displayed on a 19-inch monitor.

2.2.1.4 STIMULUS SELECTION PROTOCOL

The computer-based experimental procedure designed to select the posers from the original Ekman & Friesen (1976) set to be utilised in the experiment proper utilised a 2x2 repeated-measures factorial design with emotion, visual field location, and intensity of facial expression as factors. The factors of emotion (angry/happy) and visual field location (left/right) had two levels each. It was decided that for the computer-based stimulus selection process, only photographs of the highest, more exaggerated emotion salience (intensity 5) would be utilised from each of the ten posers, as the emotionally exaggerated images would render participants more susceptible to possible response bias. As a result, there were 20 possible combinations of expression salience (intensity), emotion, and location, the order of which was randomised across participants. Two sets of dependent measures were collected; reaction times (ms), and accuracy scores (% correct scores).

2.2.1.5 STIMULUS SELECTION PROTOCOL PROCEDURE

All participants were tested concurrently in a large computer laboratory classroom. Volunteers were briefed as to the purpose of the task and gave verbal consent prior to

commencing the experiment. Each computer was pre-loaded with the experimental paradigm, and computer monitors were set to the experiment information display so that all paradigm runs were able to commence simultaneously. The paradigm utilised a speeded, forced-choice facial expression discrimination task (see Figure 2.5) and measures of response time (RT) and accuracy (percent correct) were collected. The object of the task was for participants to identify the location of the screen on which the emotional face was presented in each trial (left or right), and participants were briefed to make this judgment regardless of the nature of the emotion observed (angry or happy), or how salient the emotion was. Participants were also informed that after each stimulus offset they would have a time limit within which they could provide their response.

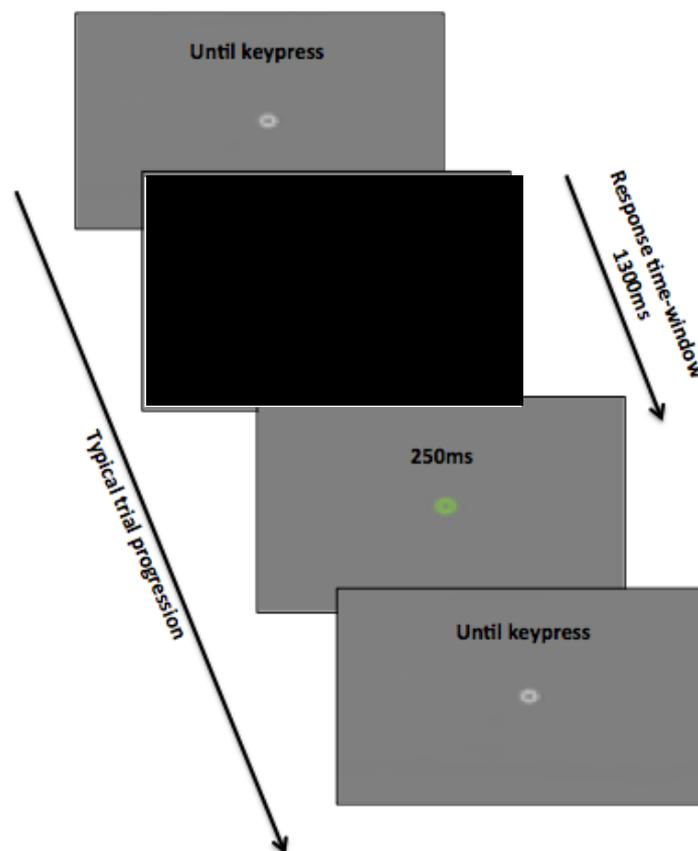


Figure 2.5. The graphic displays the sequence of events in a typical trial, and in order of appearance. Each trial starts with the fixation display that prompts participants to hit SPACE to receive the stimuli. Upon key press, a randomly selected pair of neutral and emotional stimuli appears, with target location unpredictable from trial to trial. Stimuli remain visible for 50ms, after which participants can give responses up until 1300ms post stimulus offset. Once a response is given, a feedback display is presented for 250ms. After this time lapses, the fixation display appears once again, prompting participants to start the next trial.

Photos from all ten original Ekman & Friesen posers (1976), with ten neutral, ten angry (intensity 5) and ten happy faces (intensity 5) were included, yielding a total of 30 unique photographs. In each trial, the neutral photograph from each of the ten posers was paired to one happy or one angry photograph from the same poser. The procedure included six blocks of 40 trials each (total number of trials was 240), and incorporated four conditions accounting for all combinations of emotion (angry/happy) and visual field location (left/right). Each of the ten poser's emotional photograph appeared twice within each block, with their corresponding neutral photograph appearing a total of 4 times. The randomising of visual field location, emotion, and salience intensity across trials rendered target location unpredictable; poser identity within each trial was always the same.

Each trial commenced with the presentation of a fixation point; participants were briefed to press the keyboard SPACE bar when ready. Upon key-press, two stimuli (one neutral and one of high emotional expression salience – intensity 5) were displayed bilaterally on the screen for 50ms. As participants were asked to solely identify the visual field location of the emotional face (left or right) – regardless of whether stimuli displayed a positive or negative emotion, the stimulus onset-offset latency of 50ms was decided based on the a priori assumption of it being close to the awareness threshold (cf. Petersen & Posner, 2012; Posner et al., 1985). The expectation was that responses collected would be spontaneous, reflexive reactions to the presence of emotionally valenced stimuli that originate from individuals' inherent attentional bias towards valenced information.

On each trial, the pairing between emotion and target visual field location was randomly selected. On stimulus offset, participants were required to respond as quickly as possible within a time-window of maximum 1300ms. Post-response, a feedback screen was displayed whereby a green circle indicates a correct response and a red 'x' indicates a false one, with a third feedback option of a question mark ('?') if the participant responded outside the time window, or did not provide with a response at all. The feedback display remained on the screen for 250ms, after which the fixation point display reappeared, prompting the participant to begin the next trial. The total timing of a typical trial, from stimulus onset to feedback display offset lasted 1600ms.

The stimulus presentation software (E-Prime v2.0) recorded reaction times (ms) and accuracy scores (% correct scores) per trial. Mean reaction time and mean accuracy scores were calculated from the raw data for each unique poser and per condition. For reaction times, only data from correctly responded-to trials were used in the analysis, and reaction times less or more than 2 standard deviations from the mean were excluded. The accuracy data were then linearized using the Logit Transform equation:

$$\text{logit}(p) = \log_{10}\left(\frac{p}{1-p}\right)$$

(Fig 2.5). Linearization of the data was only conducted for use in the stimulus selection experimental procedure, in order to maximise differences between conditions and across posers, so as to facilitate selection of stimuli. The mean logit accuracy data showed significant differences between conditions and across posers [t(9)=-2.4, p=.03], suggesting that accuracy of performance was affected by the poser displayed. Following this, RT data were log-transformed, and mean reaction time averages per condition and poser were calculated (Fig 2.6). The RT data showed significant differences between conditions and across posers [t(9)=3.7, p=.005], suggesting that speed of response resulted varied depending on the poser selected.

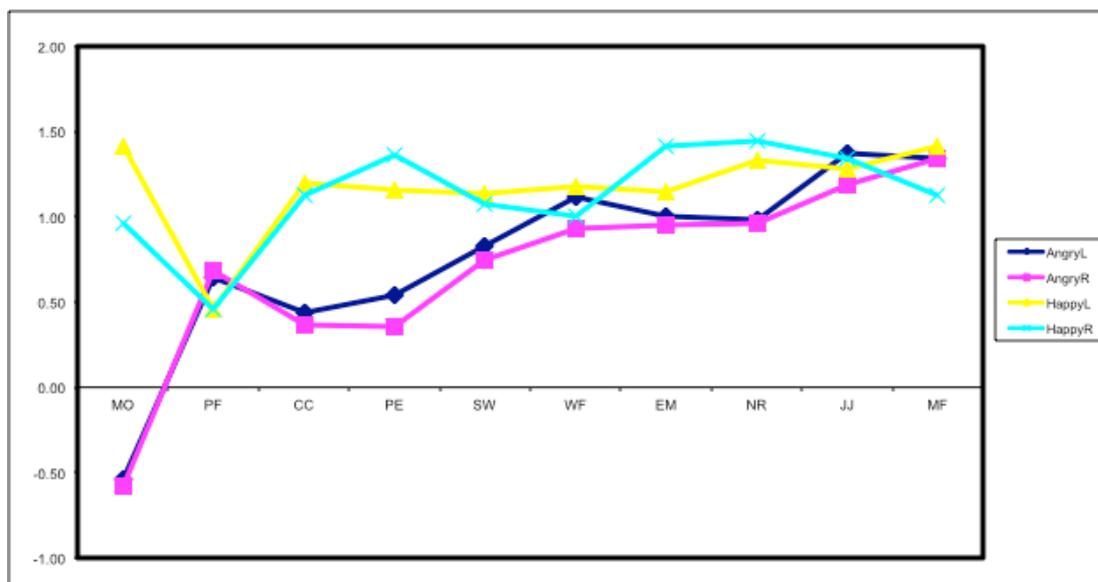


Fig 2.5. The line graph plots log accuracy score distributions for each condition across all 10 posers (x-axis denotes poser ID initials for each poser). From left to right, the first four posers (MO, PF, CC, PE) display either inconsistent (MO, CC, PE), or chance accuracy judgements $\leq 50\%$.

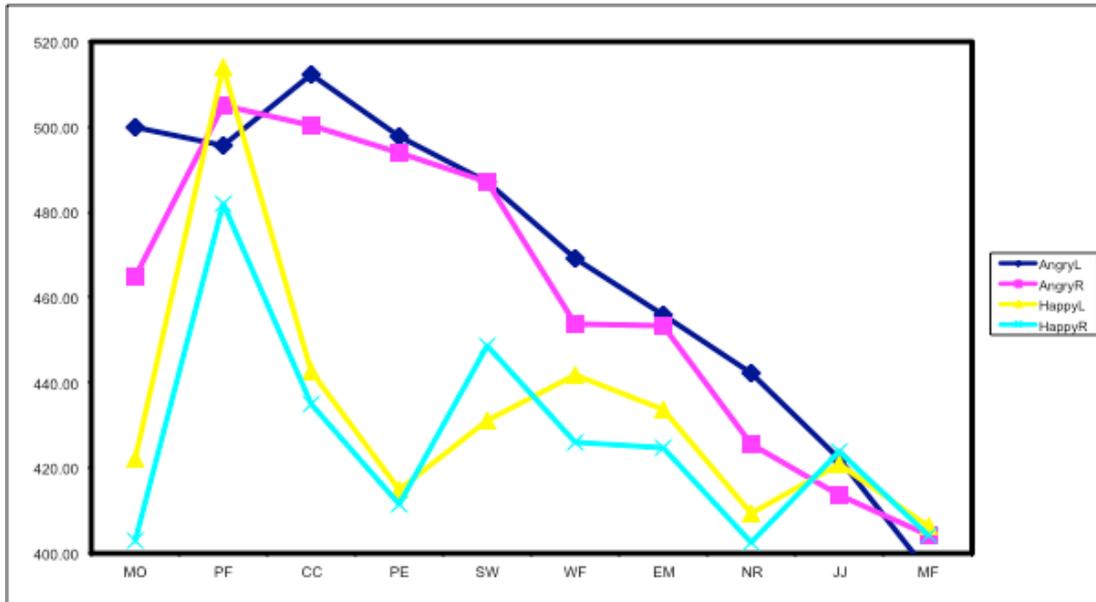


Fig 2.6. The line graph plots log reaction time distributions plotted for each condition across all 10 posers (x-axis denotes poser ID initials from each poser). From left to right, the first four posers (MO, PF, CC, PE) display greatest within-subjects response inconsistency in terms of reaction time distribution.

Upon inspection of responses between conditions and across posers, four posers (poser IDs: MO, PF, CC, PE) consistently displayed large standard error RT distribution variations in comparison to the remaining six posers from the set (poser IDs: SW, WF, EM, NR, JJ, MF), and were subsequently excluded from the experimental stimulus set.

Finally, to examine whether participants showed any overall habituation effects to the emotional faces, a comparison of early and late experimental blocks was run. To this end, response times per condition were averaged across test blocks 1 to 3 to represent mean response for the early part of the pilot, and mean response times across test blocks 4 to 6 was averaged to correspond to the late part of the pilot. Comparison between early and late blocks showed a marginally-significant difference between test block and mean response time performance [$t(63)=-2.4$, $p=.04$]. Given that the significance value of this comparison is marginal, a further measure of habituation was applied. Specifically, the difference in response latency between averaged early and averaged late blocks denoted by ‘ Δ ’ was calculated by subtracting the two averages [(mean early = 460.05) – (mean late = 460.57)]. A positive Δ would signify sensitisation to the procedure, whereas a negative Δ would signify habituation, as performance decreases across the duration of the experiment (cf. Stoeckel, Esser, Gamer, Baschel, & von Leupoldt, 2015). The pilot data yielded a Δ of -0.49, indicating a weak habituation trend across blocks. Given that the stimulus set was not filtered at

this stage, and weak possibility of habituation to the stimuli over time, the decision to maintain 5 testing blocks preceded by one practice block of equal duration was made for application to the experiment proper.

2 EXPERIMENT 2.2

2.2.2 METHODS

2.2.2.1 SUBJECTS

Twenty neurologically healthy adults (all Undergraduate students, Department of Psychology, City University London) participated in this experiment (5 males; mean age: 22.6; SD: 2.7). Participants were recruited through an online advertisement on the University's Psychology Department online participation tool (SONA). Poor quality data from five other participants were excluded due to improbable reaction times (<300ms) and a high percentage of chance accuracy judgments ($\leq 50\%$ correct) on more than half of experimental trials. The response latency cut-off point was set to 300ms, based on the averaged participant response time data from the stimulus selection pilot (see section 2.2.1.5, p.52). All participants were right-handed with normal or corrected-to-normal vision, and had given written consent prior to testing.

2.2.2.2 APPARATUS

Laboratory setup consisted of a darkened and soundproofed room, with a fixed-height table and adjustable-height chair. The paradigm was run on a DELL Optiplex 780 PC connected to a 19-inch LCD monitor (85Hz refresh rate). Subjects provided responses by pressing the left and right arrow keys on a standard QWERTY computer keyboard. To maintain viewing distance across subjects, a height-adjustable chin-rest was fixed on the table and set at a 60cm distance from the monitor, with participants viewing stimuli at a 24.4° visual angle.

2.2.2.3 STIMULI

Photographs from the pilot-excluded 4 posers (poser IDs: MO, PF, CC, PE) were utilised in the paradigm's practice block, during which E-Prime was set to not log participant responses. Photographs from the remaining 6 posers (poser IDs: SW, WF, EM, NR, JJ, MF) were used in the experimental blocks. In the experimental trials 60 five-intensity greyscale emotional faces (30 happy and 30 angry) ranging in expression intensity from 1 to 5 were used, as well as each poser's corresponding

neutral photograph (6 neutral photographs in total). The practice block included a total of 40 (20 happy and 20 angry) greyscale emotional faces ranging in expression intensity from 1 to 5 from the four excluded posers, alongside their corresponding neutral photographs (4 neutral photographs). All stimuli were greyscale photographs, and were displayed against the same mid-grey background throughout the experiment.

2.2.2.4 DESIGN

The experiment utilised a 2x2x5 repeated-measures factorial design with emotion, visual field location, and intensity of facial expression as factors. The factors of emotion (angry/happy) and visual field location (left/right) had two levels each. Intensity of expression was manipulated using a six-level expression salience scale, whereby *Intensity 0* corresponded to neutral expressions and intensities 1-5 corresponded to the range between highly ambiguous (intensity 1) and highly exaggerated (intensity 5) expression. There were 20 possible combinations of expression salience (intensity), emotion, and location, the distribution of which was randomised across participants. Two sets of dependent measures were collected; reaction times (ms), and accuracy scores (% correct scores).

2.2.2.5 PROCEDURE

The paradigm utilised was the same as described in the 2.0 Pilot (see Figure 2.5). Participants were tested individually with each testing session lasting approximately 45 minutes depending on length of breaks taken between each block. Each participant was asked to first complete a practice block of 160 trials, where stimuli shown consisted of photographs from the 4 excluded posers. In the practice block, each emotional photograph appeared twice, with the total number of trials accounting for the two visual field locations (left/right), two emotions (angry/happy), and five expression intensities (1-5). Once the practice block was completed, participants proceeded to complete five testing blocks. The total number of trials per testing block was 240, accounting for each emotional photograph appearing twice within the block, as well as the two visual field locations, two emotions and five expression intensities. The randomising of visual field location, emotion, and salience intensity across trials rendered target location unpredictable; poser identity within each trial was always the same. Data from a total of 1200 trials from the five testing blocks were collected.

Each trial commenced with the presentation of a fixation point; participants were briefed to press the keyboard SPACE bar when ready. Upon key-press, two stimuli (one neutral and one emotional) were displayed bilaterally on the screen for 50ms. On each trial, the pairing between expression intensity, emotion and target visual field location was randomly selected. On stimulus offset, participants were required to respond as quickly as possible within a time-window of maximum 1300ms. Post-response, a feedback screen was displayed whereby a green circle indicates a correct response and a red 'x' indicates a false one, with a third feedback option of a question mark ('?') if the participant responded outside the time window, or did not provide with a response at all. The feedback display remained on the screen for 250ms, after which the fixation point display reappeared, prompting the participant to begin the next trial. The total timing of a typical trial, from stimulus onset to feedback display offset lasted 1600ms.

2.2.2.6 DATA PREPARATION AND ANALYSIS

Each participant's mean reaction time (ms) and accuracy score (% correct) were calculated per condition. Data preparation was conducted using the E-Prime v.2.0 analysis software E-Data Aid and E-Merge (Psychology Software Tools, Pittsburgh MA). For reaction time measures, only data from correctly responded-to trials were included in calculating means per condition, and reaction times less or more than 2 standard deviations from the mean were excluded.

For accuracy scores, logistic functions were fitted as a function of stimulus intensity to calculate the identification threshold per facial expression salience across emotions. Threshold estimates were calculated by identifying the point at which performance is halfway up the psychometric function, set at approximately 75% correct. This 'standard' accuracy performance was then read off from the function. Psychometric function fitting was conducted using the PSIGNIFIT Toolbox for Matlab (v.R2013).

In the following results section, all analyses including factors with more than 2 levels that violated the assumption of sphericity have been Greenhouse-Geisser – corrected. All error bars in the results section represent within-subjects error, calculated using the Cousineau correction (Cousineau, 2005). The Cousineau correction represents y_{ij} as participant i 's score in the j th condition

$(i = 1, \dots, N; j = 1, \dots, M)$. Subsequently, the normalised observations can be defined in terms of the following:

$$z_{ij} = y_{ij} - \sum_{j=1}^M y_{ij} + \sum_{i=1}^N \sum_{j=1}^M y_{ij}.$$

Based on this correction, the resulting variances and size of confidence intervals do not include between-subjects variance (Cousineau, 2005; Morey, 2008).

2.2.2 RESULTS

2.2.2.1 REACTION TIME

A repeated-measures ANOVA was conducted with emotion (angry/happy), visual field location (left/right) and intensity (1-5 expression salience) as within-subjects factors, for the dependent measure of mean reaction times. The analysis produced a significant main effect of emotion [$F(1,19)= 21.1, p < .001, \text{partial } \eta^2 .53$], with happy faces yielding an overall quicker mean reaction time (mean = 516.87, SE = 11.34) than angry (mean = 530.49, SE = 10.46). A main effect of expression salience was also found [$F(4,76)=56.2, p<.001, \text{partial } \eta^2= .74$], with Bonferonni-corrected multiple comparisons revealing significant differences in reaction times in paired intensities 1 through to 4, but with non-significant reaction time differences intensity pair 4 and 5.

A significant 3-way interaction between emotion, visual field location, and expression salience was also found [$F(4,76)=2.59, p=.043, \text{partial } \eta^2=.12$] (Fig 2.8 on following page). Post-hoc comparison analyses revealed a significant interaction between emotion and visual field location for intensity 3 [$F(1,19) = 6.48, p=.02$], where happy faces shown on the right visual field produced quicker reaction times (mean= 496.03) than when shown on the left visual field (mean=507.5), and angry faces shown on the left visual field produced quicker reaction times (mean=510.38) than when shown on the right visual field (mean=524.6) (Fig 2.9 on following page). There were no further significant interactions for the remaining intensities.

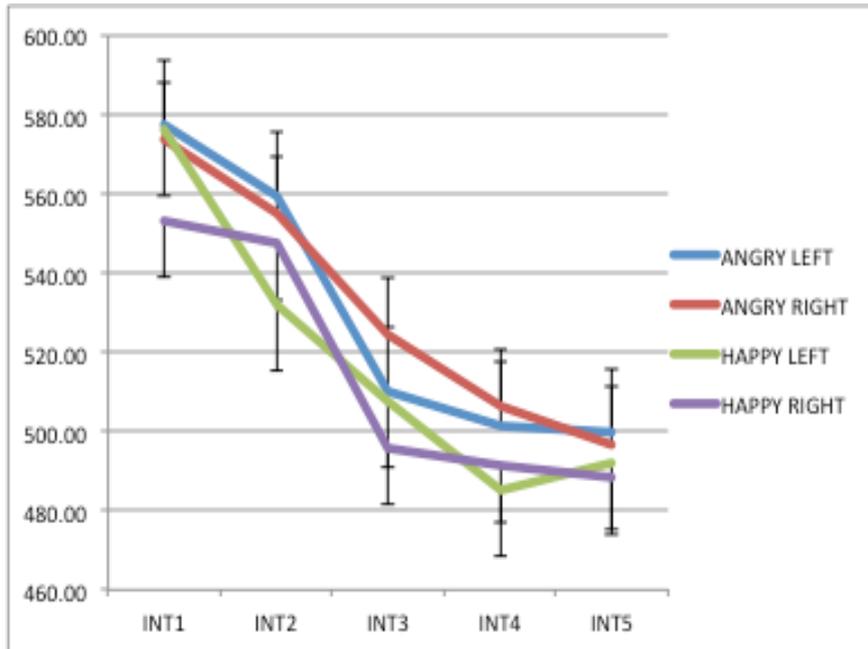


Fig 2.8. The line graph shows response times per condition as a function of emotional expression intensity. Error bars per condition represent Cousineau-corrected (Cousineau, 2005), +/-1 within-subjects error. Across conditions, responses become quicker as the expression intensity is gradually disambiguated from 1 (highly ambiguous) to 5 (exaggerated). Responses to happy faces regardless of visual field location are quicker overall; reaction times however differ within each emotion separately, depending on the visual field location of the target face as a function of expression salience.

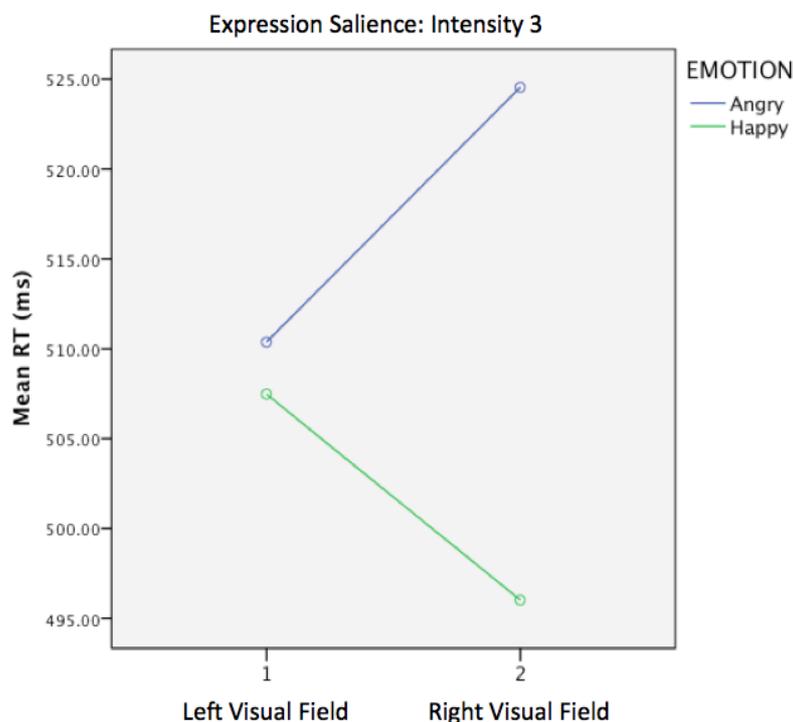


Figure 2-9. Line graph displaying mean reaction times (ms) for Angry (blue) and Happy (green) stimuli across the Left and Right visual fields, for expression salience intensity 3, which was the resulting interaction from post-hoc analyses on the 3-way interaction between emotion, VF location and intensity. For expression intensity 3, happy faces are responded to quicker when presented on the right visual field, and angry faces are responded to quicker when presented on the left visual field.

2.2.2.2 ACCURACY

A repeated-measures ANOVA was conducted with the within-subjects factors of emotion, visual field location and expression intensity for the dependent measure of mean % correct scores. Accuracy analysis resulted in a significant main effect of Emotion [$F(1,19)=19.8$, $p<.001$, partial $\eta^2 =.5$], with higher accuracy achieved for happy stimuli (mean = .82, Std Error = .014), than for angry stimuli (mean = .78, Std Error = .014). A further significant main effect for expression salience (Intensity) was revealed [$F(4,76)=331.9$ $p<.001$, partial $\eta^2 =.95$], with Bonferonni-corrected multiple pairwise comparisons showing significant differences in accuracy scores across all expression intensities.

A significant 2-way interaction between emotion and expression salience [$F(4,76)=2.51$, $p=.04$, partial $\eta^2=.2$] was found; post-hoc paired samples t-tests showed that there were significant accuracy score differences between emotions for intensity 2 [$t=-4.03$, $df=39$, $p<.001$], intensity 3 [$t=-.4.14$, $df=39$, $p<.001$], intensity 4 [$t=-.29$, $df=39$, $p=.006$], and intensity 5 [$t=-2.73$, $df=39$, $p=.009$] (Fig. 2.10 on following page). Paired samples t-test for intensity 1 showed non-significant accuracy score differences depending on emotion ($p=.31$).

A further significant 2-way interaction between visual field location and expression salience was also observed showing an overall left visual field advantage across conditions [$F(4,76)=3.9$, $p=.006$, partial $\eta^2=.2$]; post-hoc paired samples t-tests revealed significant accuracy scores differences for the two visual field locations only for intensity 1 [$t=-.23$, $df=19$, $p=.032$] (Fig. 2.10). Paired samples t-tests for accuracy score differences depending on visual field location were non-significant for intensity 2 ($p=.5$), intensity 3 ($p=.8$), intensity 4 ($p=.6$), and intensity 5 ($p=.6$) (Fig. 2.11).

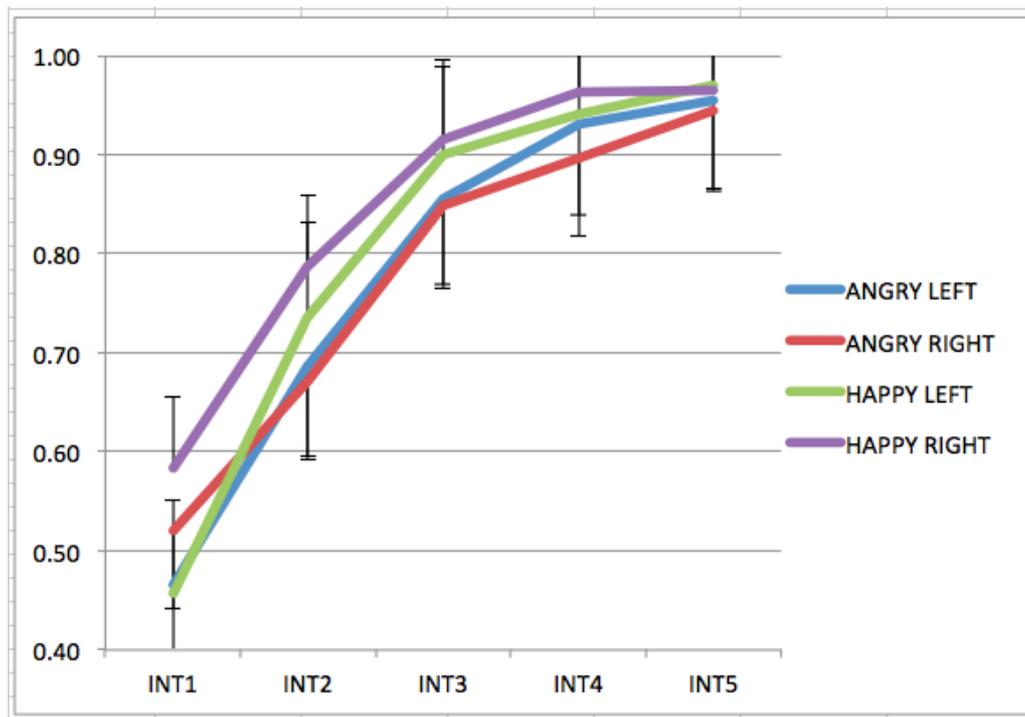


Figure 2.10. The line graph shows accuracy scores per condition as a function of emotional expression intensity. Each of the colour-coded lines represents one of four conditions of type of emotion and visual field location. Error bars per condition represent Cousineau-corrected, +/-1 within-subjects error. Across conditions, responses become more accurate as the expression intensity is gradually disambiguated from 1 (highly ambiguous) to 5 (exaggerated). Accuracy score significant differences in terms of type of emotion (angry/happy) regardless of visual field location are observed in intensities 2 through to 5; significant differences in terms of visual field location regardless of emotion are only observed for intensity 1.

The accuracy analysis revealed a further, significant 2-way interaction between emotion and visual field location [$F(1,19) = 8.06, p=.01, \eta^2=.298$]. This interaction revealed a visual field location accuracy difference only for happy stimuli, which elicited higher accuracy when displayed on the right visual field (mean = .84, Std Error = .016) as opposed to the left visual field (mean = .80, Std Error = .014) (see Figure 2.11 on following page). There was no accuracy difference for the angry stimuli when displayed on the left visual field (mean=.78, Std Error= .017) and when displayed on the right visual field (mean=.77, Std Error= .016). There were no significant 3-way interactions for the accuracy data.

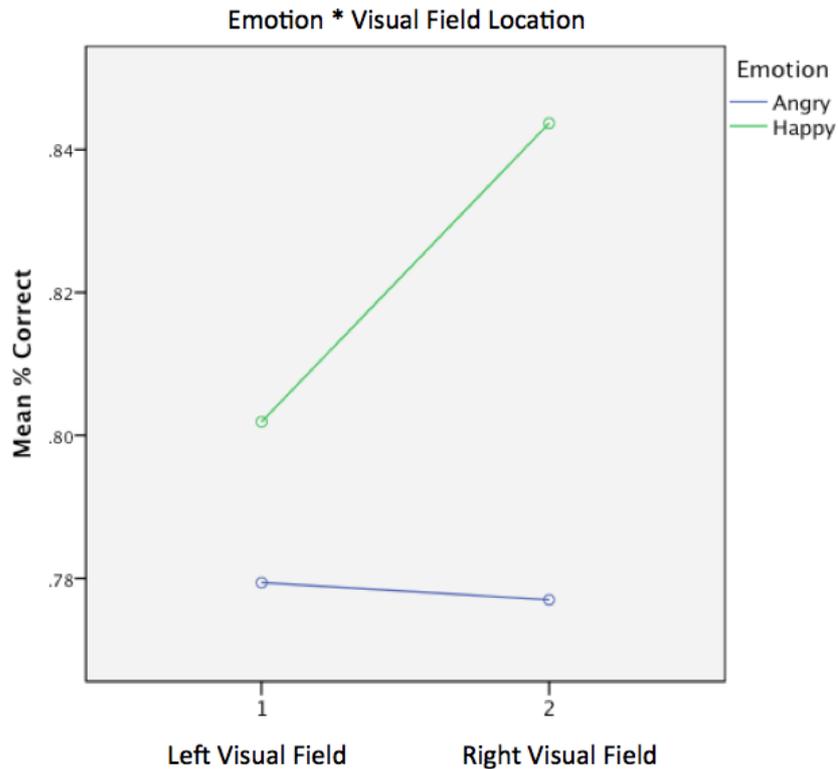


Figure 2.11. Interaction plot displaying mean % correct scores for angry (blue line) and happy (green line) stimuli, plotted across the left and right visual fields respectively. It is evident that the overall interaction is driven by happy stimuli only, which displayed higher accuracy when shown on the right visual field as opposed to the left. Angry faces showed a negligible difference in accuracy based on visual field location.

2.2.2.3 THRESHOLD ANALYSIS

A repeated measures ANOVA with emotion (angry/happy) and visual field location (left/right) was calculated for the threshold data. A significant interaction between emotion and visual field was observed [$F(1, 19) = 5.17, p = .03$], whereby calculated threshold estimates per emotion showed that happy faces were recognised more accurately when shown in the right visual field, and happy faces were recognised more accurately when shown in the left visual field. On the whole however, happy faces required a lower intensity threshold than that needed for angry faces so as to be recognised accurately (Fig. 2.12).

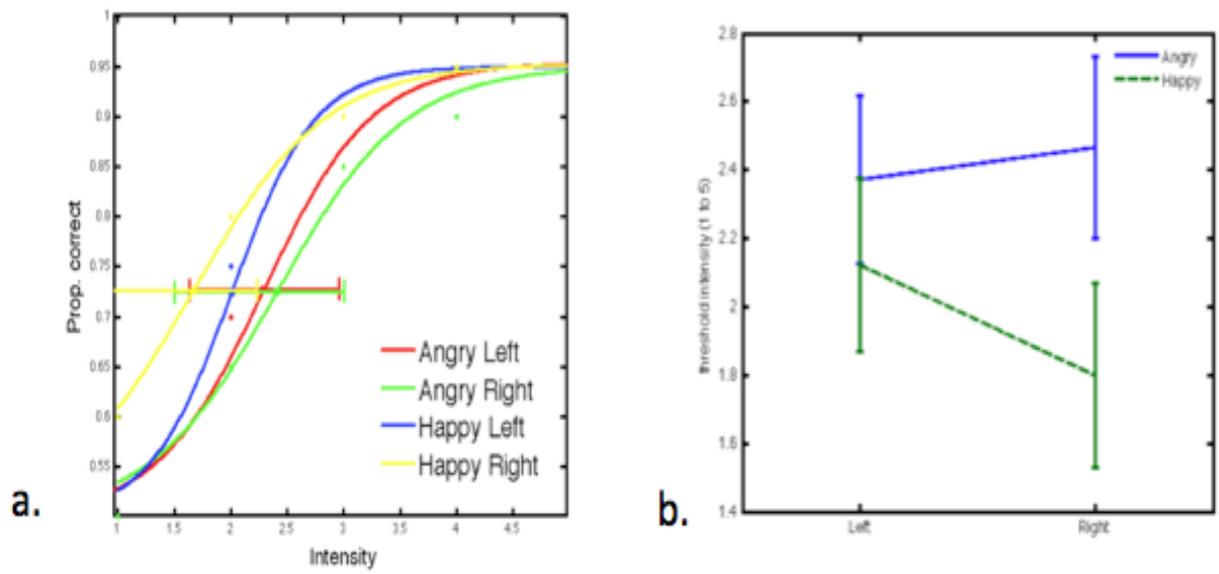


Figure 2.12. Graph a. displays the mapping of 95% CI against the required intensity (saliency) per condition, which is then re-plotted as Intensity by Visual Field with separate error bars representing angry and happy faces on Graph b.

2.2.3 SUMMARY

Experiment 2.1 shows evidence for a lateralised pattern in observable behaviour towards angry and happy facial expressions, which regarding response latency only appears when stimuli are halfway between ambiguous and exaggerated. For accuracy, it is only happy stimuli that elicit a lateralised response, subsequently creating an interaction between the nature of the emotion observed (angry vs. happy) and visual field location (left vs. right). The data also show that happy faces are in general more easily identifiable as emotional than angry, by requiring a lower expression salience intensity to produce high-accuracy responses. This happy face advantage is further intensified by the visual field location of the stimuli; happy faces displayed on the right visual field tolerate a more ambiguous salience intensity than when on the left visual field for accurate recognisability. Additionally, results from the threshold calculations are particularly convincing (happy faces were recognised more accurately when shown at the right visual field, and happy faces were recognised more accurately when shown at the left visual field), as they are not dependent on specific intensities or non-linearities of the measurement scales compressing data at floor and ceiling. This psychophysical measure of perceptual sensitivity further complements the RT and accuracy results.

2.3 DISCUSSION

This chapter addressed the need for a core behavioural paradigm that can effectively investigate whether there is differential hemispheric contribution to two distinct facial expressions of basic affect (anger and happiness), by measuring the behaviours that these emotions relate to. Response time and accuracy measures were collected through a forced-choice, location-identification behavioural task with target location unpredictable in each trial. Contrary to the types of behavioural task commonly used in emotional lateralisation research, the present paradigm did not require participants' subjective emotion-categorisation (e.g. Eder et al., 2007; Fox et al., 2002), or direct type of emotion identification judgments (e.g. Reuter-Lorenz et al., 1990), and also did not use competing, cognitively loaded tasks (e.g. Carver, 2004). The design of the present paradigm was instead motivated by the lack of consistently replicable findings for either the valence or the right-hemisphere hypotheses in an attempt to address the conflicting conclusions found in emotional perception research. As participants were asked to solely identify the visual field location of the emotional face (left or right) – regardless of whether stimuli displayed a positive or negative emotion, and given the use of a stimulus duration timing close to the awareness threshold, responses collected can be viewed as spontaneous, reflexive reactions to the presence of emotionally-loaded stimuli that originate from individuals' inherent attentional bias towards valenced information.

In summary of the findings, two main outcomes resulted from data analysis; *first*, a lateralised response pattern was observed for measures collected, showing an angry face advantage for response latency and a markedly less pronounced accuracy effect of responses when displayed on the left visual field (i.e. right hemisphere), and a happy face advantage for speed and accuracy when displayed on the right visual field (i.e. left hemisphere). In terms of response latency, this lateralised pattern was only significant for salience intensity 3 and diminished when stimuli became explicitly angry or happy (intensities 4 & 5). In terms of accuracy, happy faces showed specific advantageous processing for accurate recognition when displayed on the right visual field while angry stimuli produced negligible differences. *Second*, there was an overall

happy-face advantage for both reaction time and accuracy data, and across salience intensities and visual field locations.

The laterality pattern shown only for expression salience intensity 3 for response latency in the present chapter could also be interpreted in terms of potential differences in perceiving threat from a socially relevant stimulus as opposed to a biologically relevant one. Specifically, the expression intensity where an interaction between visual field location and type of emotion was found is neither fully ambiguous nor highly explicit. Stimuli at this intensity are suprathreshold for correct recognisability and for both types of affect (see Figure 2-4). The stimulus duration time used (50ms) in experiment 2.1 could therefore accentuate effects of earlier instead of later cognitive processes, which could potentially eradicate initial, reflexive response effects.

The first outcome of a distinctly lateralised response pattern with an angry face advantage for response efficiency (albeit for accuracy the effect was less pronounced than for response latency) when displayed on the right visual field, and higher response efficiency for happy faces when displayed on the left visual field, lends support to the hypothesis of lateralised responses to primary affect at a behavioural level based on their nature (positive or negative) (Adolphs, 2002; Jansari et al., 2000; Killgore & Yurgelun-Todd, 2007; Reuter-Lorenz, and Davidson, 1981; Wedding & Stalans, 1985). Furthermore, the data show that this lateralised behaviour occurs under very specific, contextual, stimulus-related circumstances; this could suggest that behavioural lateralisation is not a constant phenomenon, but instead its presence might fluctuate and depend the presence of additional emotion-enhancing factors (i.e. salience of expression, stimulus duration, nature of the emotion observed). For example, in order for participants to display a clearly lateralised behavioural response, stimuli of positive valence need to be at a specific level of intensity, combined with presentation on the right visual field. As soon as such conditions are violated, positive stimuli tend to dominate the behavioural response. Nonetheless, this might still be an artefact of floor/ceiling compression; the complementary threshold results are however not subject to this potential artefact. The second finding of an overall happy face advantage could be interpreted from the impact of perceived social intent on attentional engagement; aside from the possibility of a stimulus confound (e.g. attention-grabbing effects of teeth), one possible explanation could be that when viewed for extremely short durations (i.e. 50ms), happy facial expressions potentially

carry an underlying ambiguity regarding their relevance or significance to the organism.

2.3.1 EMOTIONAL MODULATION OF BEHAVIOURAL LATERALISATION

The response latency data provide some support for early, behavioural accounts of differential hemispheric contribution towards positive and negative affect (e.g. Moretti et al., 1996; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz, and Davidson, 1981; Root, Wong, & Kinsbourne, 2006). However, behavioural lateralisation research has not as of yet provided a clear, replicable conclusion as to whether or not the distinct, emotion-specific lateralisation existing at a subcortical level (e.g. Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Campbell, 1982; Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Schepman et al., 2012; Wager et al., 2003) might translate into observable behaviour. According to the chapter's predictions based on the valence hypothesis (Ahern & Schwartz, 1979), happy faces should result in best response efficiency (quicker and higher in accuracy responses) when on the right visual field (left hemisphere lateralised), with angry faces eliciting best response efficiency when on the left visual field (right hemisphere lateralised). The results of Exp. 2.2 showed that this lateralisation pattern occurs when stimuli for both emotions are past the detection threshold.

In the present results, the lateralised pattern specific to response latency appears to be dependent on an interaction between visual field location of the stimuli and the expression intensity of the emotion displayed. One interpretation might be that subtle changes in salience intensity appear to modulate the lateralised pattern observed – the more disambiguated the emotion becomes, the less likely it is that differential hemispheric contribution will be engaged due to observing a happy or an angry facial expression. It could be that it is a number of perceptual and contextual elements that are responsible for the high level of disparity across findings from the behavioural literature. Based on findings from Experiment 2.1, it is evident that the main element guiding participants' responses by acting as a type of attentional cue is the nature of the emotion displayed in combination with the clarity of the emotional expression. The following sections offer an interpretation of the level of influence of emotion and salience, by suggesting that the response pattern per emotion is a product of a distinct and specifically modulated process.

2.3.1.1. EMOTION-SPECIFIC MODULATION

The overall happy-face advantage reported here is not necessarily an altogether surprising result; the quicker and more accurate response to positive affect has often been mentioned in behavioural lateralisation research, yet its implications on how emotion might be cognitively lateralised have historically been left uninterpreted (Jansari et al., 2000). For example, happy faces produced quicker and more accurate responses in visual search tasks compared to angry and fearful faces (Juth et al., 2005). A similar happy face advantage has also been observed when using schematic faces as opposed to realistic photographs in an attempt to control for subtle differences in the physiology of the face across angry, happy and fearful emotions that could potentially skew responses (Leppänen & Hietanen, 2004).

The happy face advantage found in the present experiment might be interpreted based on hypotheses of the ambiguity of the social intent that happy facial expressions could be interpreted as threatening; it may be that our inability to instantly recognise and interpret the intentions of an unfamiliar happy face triggers similar approach/avoidance reactions elicited following exposure to openly threatening stimuli (Bindemann, Burton, & Langton, 2008; Bindemann, Burton, Hooge, Jenkins, & de Haan, 2005). For example, there have been some reports of happy facial expressions as being perceived in a similar way to that if they carried a threatening contextual association; reports of this effect however have so far been limited to happy facial expression stimuli where eye gaze has been manipulated to appear averted (e.g. Bindemann et al., 2005; 2008). For the present findings, it could be that a similar perceptual bias occurs; the near-detection threshold stimulus display time of 50ms, paired with the simultaneous bilateral presentation of both neutral and happy stimuli could be falsely perceived as carrying a similar propensity for ambiguity of social intent to that of a happy face with averted gaze as seen in Bindemann et al's work (2005; 2008). It could be the case that very brief displays of happy faces of varying salience are perceived as equally ambiguous (or potentially threatening) as those of happy faces with averted gaze (Bindemann et al., 2008). However, it could also be argued that if happy faces were perceived as equally threatening, they would evoke a similar pattern of results to those for angry faces.

The combination of short presentation times with inter-stimulus competition (neutral vs happy), could have acted as a potent attention-grabbing cue within participants' short time-window for providing a response, as stimulus competition might create a

fine balance between hemifields that amplifies early effects of differential salience between them. It is therefore possible that this ambiguity of social intent of a happy facial expression has manifested here as a result of overall short stimulus display time. The added manipulation of facial expression salience in the present study further accentuated the overall preferential processing of happy faces.

One possibility could be that each separate type of emotion – be that positive or negative – draws from different, emotion-specific identification and recognition attentional systems, which in turn yield differing patterns of response that may occur at distinct, separate latencies; this is an assumption which has been extensively researched in both the human and animal neuroimaging literature but only for negative emotions such as fear, anger, and sadness (e.g. Adams, Gordon, Baird, Ambady, & Kleck, 2003; Adolphs, Russell, & Tranel, 1999; Bishop, Duncan, & Lawrence, 2004; Hoffman, Gothard, Schmid, & Logothetis, 2007; Kuraoka & Nakamura, 2007; Liddell et al., 2005; Straube, Langohr, Schmidt, Mentzel, & Miltner, 2010). For example, in an fMRI study by Adams et al (2003) the authors investigated assumptions of increased amygdala sensitivity following presentation of fearful and angry facial expressions that were either gazing directly, or away from the participant. The authors reported heightened left amygdala sensitivity following displays of angry faces gazing directly to the observer, and fearful faces gazing away from the observer. Behaviourally, what might appear as happy face advantage, might instead be a product of a different activation network with distinct timing and processing cognitive demands, that results in a timescale of recognition and response events other than the one observed for another basic emotion – in this case anger.

The valence hypothesis (Ahern & Schwartz, 1979) suggests angry stimuli are processed more efficiently when present on the left visual field (i.e. right hemisphere). Data from the present experiment do show this pattern, but under specific contextual circumstances, i.e. when stimuli are past the detection threshold (even more so for response latency, whereby the lateralised pattern is observed only at intensity 3), and when data from intensity 1 conditions are filtered out. Furthermore, current findings for angry facial expressions go against the consistently reported preferential processing of threat (e.g. Horstmann & Bauland, 2006). Specifically, data from the present experiment point towards a bias for happy facial expressions, with happy faces taking over participants' attention and engagement in addition to them requiring a less salient expression intensity for successful recognisability. When looked at in

comparison to data for the happy stimuli, Experiment 2.1 data for angry faces did not suggest the presence of an anger superiority effect (Horstmann, 2007; Horstmann & Bauland, 2006), whereby angry stimuli tend grab attention instead of other facial expression stimuli, resulting in quicker responses. In isolating responses to angry affect, their resulting pattern of responses appears to be modulated based on what additional stimulus-specific contextual information is present at a given trial. For example, expression salience appears to determine the pattern of response for anger, as angry faces need to be more salient than happy in order to be correctly perceived as emotional.

According to the threat advantage hypothesis (Horstmann & Bauland, 2006) – i.e. more efficient responses for angry faces over any other form of basic affect – one would expect that in the present experiment, participants would show an overall bias towards angry stimuli, which would in turn be even more accentuated if the angry faces were presented on the left visual field (i.e. right hemisphere). In the present experiment, this pattern has only been found for intensity 3 and only for the reaction time data; the accuracy data show a marginal difference between angry faces when on the left or right visual field. Therefore, the picture for angry facial expressions seems to be focused primarily on the speed of response. This might mean that the effectiveness of anger as an attentional cue only manifests as a speeded response by maintaining accuracy constant, if the angry facial expression is correctly identified. In contrast to happy faces, anger appears lacking in eliciting efficient responses; this is perhaps best interpreted in terms of response patterns for different types of emotion occurring at different times and magnitudes (e.g. Adams et al., 2003).

Relating back to the approach/avoidance perspective, such speeded responses could be the resulting behaviour of engagement of a somatosensory response system of vigilance, closely linked to action readiness; in consequence, individuals are more likely to respond quickly to stimuli possibly pertaining to threat, without necessarily cognitively processing whether the threat is of direct relevance to them or not. The fact that a lateralised pattern was observed for anger only in terms of response latency could therefore be rationalised in terms of avoidance behaviours.

A final, possible explanation for the lack of a robust, overall threat/anger superiority effect (i.e. quicker and more accurate responses) in the present data could be that the processing advantage for anger seems to emerge in specific experimental paradigms (i.e. face-in-the-crowd) when competing against many neutral distractors compared to

when a single happy face appears within a number of neutrals (i.e. Juth et al., 2005; Maratos, 2011; Yiend, 2010). Additionally, this behavioural manifestation of this threat advantage tends to emerge when specific types of stimuli are used (i.e. schematic vs. photographic). For example, in a study by Juth and colleagues, the authors examined response latency towards angry, happy, and fearful photographs of facial expressions over three experiments, all of which employed a visual search paradigm (face-in-the-crowd). In the first of these experiments participants were tasked with correctly identifying the target emotional stimulus amongst a crowd of neutral distractors; the authors observed that happy faces elicited quicker and more accurate responses compared to the angry or fearful targets. This effect was also replicated when using inverted as opposed to upright emotional faces in the same visual search/face in the crowd paradigm (2nd experiment). However, in their 3rd study which utilised schematic emotional face targets instead of photographic stimuli, the authors noted that the angry stimuli elicited quicker and more accurate responses (Juth et al., 2005). In face in the crowd type paradigms, participants are tasked with choosing the odd one out target; conversely in experiment 2.1 the target is always present while participants are tasked to make a decision on its location (left vs. right). Threat superiority might therefore result from the engagement of earlier, cruder attentional mechanisms, fine-tuned in detecting the overall presence of danger; these mechanisms may potentially be engaged prior to the emotional stimulus having to undergo any further, higher-order attentional processing. In the present experiment, participants were forced to make a location-based decision, which may have meant that further attentional processing and interpretation of the visual scene was necessary. Given that in Expt. 2.2 each trial presented two faces with one always being the target (regardless of type of affect), and without any attentional cue pre-empting target location, it could be the case that the more robust behavioural effect of a happy advantage was prevalent across participant responses.

2.3.2 CONCLUSION

Experiment 2.1 was developed to elicit the direct measurement of lateralised responses to basic affect. In order to control for methodological limitations met in the behavioural literature (discussed in chapter 1), the present experiment tightened

methodological control by imposing short participant response time cut-offs, equating across stimuli for luminance and feature distinctiveness, and by utilising a forced-choice, bilateral presentation target location identification paradigm. In agreement with predictions, experiment 2.1 showed evidence for hemispheric lateralisation, with the laterality pattern more pronounced for happy stimuli. This chapter has considered possible interpretations that might account for the overall positive affect advantage, which goes against recent hypotheses of negative affect superiority. In doing so, the importance of the relationship between attention and emotional perception was identified, which led to the rationalisation and development of the following chapter.

3 CHAPTER 3: NASAL-TEMPORAL ASYMMETRIES IN SUPRATHRESHOLD FACIAL EXPRESSIONS OF PRIMARY AFFECT

3.1 INTRODUCTION

In chapter 2, a behavioural paradigm was introduced to investigate the differential hemispheric contribution to the perception of facial expressions of primary affect. This was achieved by examining two main types of behaviour that lateralised hemispheric contribution may be associated with; participant response times and accuracy scores. Firstly, findings from chapter 2 confirmed predictions of an asymmetric hemispheric contribution in emotional responses, and highlighted that aside from the nature of the emotion observed (positive vs negative), lateralisation appears to be modulated by the salience of facial expression. Secondly, chapter 2 results showed that the directionality of lateralised behaviour varies depending on the type of response measure being investigated. For example, when looking at response latency, emotional stimuli need to be half-way between ambiguous and salient for differential hemispheric contribution to be effectively observed. For accuracy however, hemispheric preferential engagement for positive or negative emotions appears to be modulated by the interaction between the emotional valence of a stimulus (angry/happy), and its visual field location (left/right).

Having established that the paradigm introduced in chapter 2 provides a behavioural methodology which is sensitive to modulating factors for highlighting emotion-dependent preferential hemispheric engagement, the present chapter aims to investigate whether emotion-specific, subcortically driven hemispheric asymmetries might be indirectly examined via solely behavioural means. We used eye patching, which has been established as effective in investigating effects of monocular viewing on perceptual tasks (Roth, Lora, & Heilman, 2002). Following Zackon et al's recommendation for behaviourally distinguishing between subcortical and cortical contributions in visual attention tasks (Zackon, Casson, Stelmach, Faubert, & Racette, 1997), the present chapter adapts the behavioural methodology developed in chapter 2 so as to indirectly detect asymmetrical subcortical contributions to emotion detection through monocular viewing. Specifically, Zackon

et al explored the properties of monocular viewing as a determinant of asymmetrical distribution of attention; they reported on a subcortical attentional advantage observed during oculomotor tasks under monocular viewing conditions, but not in perceptual tasks (Zackon et al., 1997) – they implemented the monocular viewing condition by patching either the left or right eye; eye-patching allowed for stimulation of subcortical as opposed to cortical retinotectal pathway (Fig. 3.1).

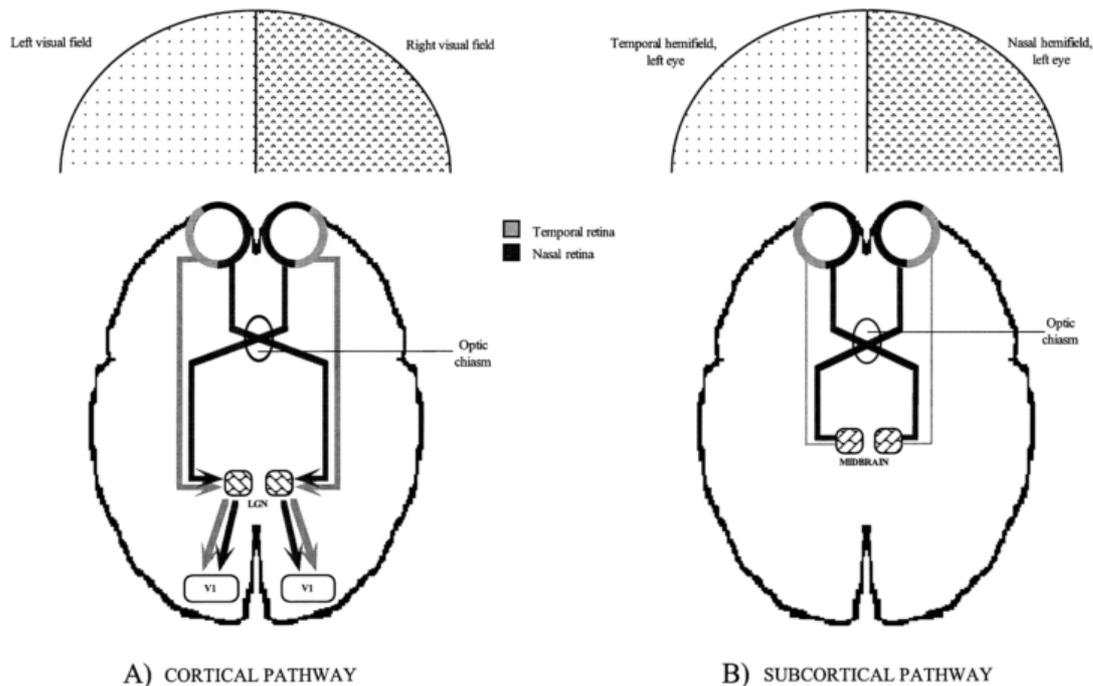


Figure 3.1. Graphic illustrates the cortical (A) and subcortical (B) retinotectal pathways through projections from nasal and temporal hemiretinae (figure borrowed from Zackon et al., 1997).

Based on their findings, the authors suggested that since retinotectal projections primarily arise from the nasal retina, and therefore appear in the temporal hemifield to the unobstructed eye, the asymmetric distribution of subcortical attention is to be expected, along with an overall bias towards the temporal hemifield (as a temporal hemifield advantage is a well-replicated effect in oculomotor dominance tasks i.e. Zackon et al, 1997; Katz & Crowley, 2002) (Fig. 3.2).

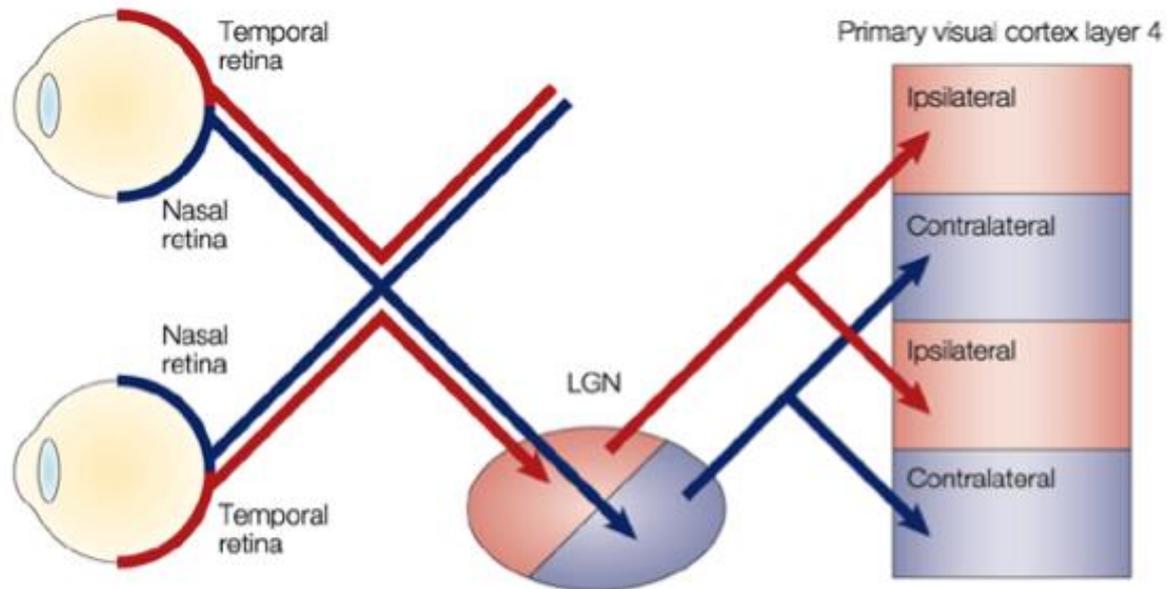


Figure 3.2. Graphic illustrates the pathway from the nasal and temporal hemiretinae through to lateral geniculate nucleus and into the primary visual cortex in binocular vision. Red shaded blocks represent ipsilateral and purple shaded blocks represent contralateral areas (figure borrowed from Katz & Crowley, 2002).

To introduce the rationale of the present chapter's methodology, the following sections will consider the evidence for lateralised behaviour resulting from attending to emotional facial expressions by addressing subcortical attentional asymmetries in relation to primary affect. As a conclusion, the potential for utilising nasotemporal asymmetries as an index of subcortical, asymmetrically distributed attention during emotional face perception will be explored.

3.1.1. ASYMMETRIC DISTRIBUTION OF SUBCORTICAL LOCI OF ACTIVITY IN EMOTIONAL ATTENTION

Emotion-relevant research on subcortically originating hemispheric asymmetries of attention has historically been almost exclusively linked to the non-conscious perception of emotional stimuli. For example, Liddell and colleagues reported on a left-lateralised bottom-up alarm attentional activation system which follows the brainstem- amygdala-somatosensory/temporal cortical route that showed increased BOLD activity during perception of subliminally-displayed fearful stimuli (Liddell et al., 2005). Specifically, the authors' regions of interest analysis showed significant left-lateralised activation in the amygdala, pulvinar, superior colliculus, locus coeruleus and anterior cingulate, while whole brain analysis showed further left-lateralised activation in the insula and postcentral gyrus of the somatosensory cortex, as well as

in the superior and middle temporal gyri and inferior and middle temporal gyri (Liddell et al., 2005).

In Tamietto and de Gelder's paper on the neural bases of non-conscious perception of affect, the authors summarise both well-established as well as newly identified subcortical structures that have been linked with the perception and processing of unconsciously perceived affect (Tamietto & de Gelder, 2010). The authors identify two coexisting networks of subcortical structures that are involved in nonconscious affect perception; while one network is responsible for the visual encoding of affective stimuli, the other is concerned with any other function necessary to process the stimuli outside of vision. Structures linked to the visual encoding network are perhaps more prominently reported in the neuroimaging literature on emotion perception, and their role in emotional stimulus disambiguation and organisation of response has been robustly identified. Structures such as the superior colliculus (e.g. Cesarei & Codispoti, 2015; Ellenbogen & Schwartzman, 2009; Vuilleumier, Armony, Driver, & Dolan, 2003), amygdala (e.g. Adolphs, Russell, & Tranel, 1999; Pessoa & Adolphs, 2010; Pessoa, 2010; van der Zwaag, Da Costa, Zürcher, Adams, & Hadjikhani, 2012), substantia innominata (e.g. Mesulam, 1998; Viinikainen et al., 2010; Whalen et al., 1998), and nucleus accumbens (e.g. Carretié et al., 2009; Duncan & Barrett, 2007; Haegelen, Rouaud, Darnault, & Morandi, 2009; Richter-Levin & Akirav, 2003) have all been studied in extensive detail as to their role in emotional perception. On the other hand, the role and involvement of structures more recently identified as being involved in processing nonconscious affective stimuli has not been fully established. This lesser known network includes the locus coeruleus, periaqueductal grey, nucleus basalis of Meynert, the hypothalamus and the hippocampus (Tamietto & de Gelder, 2010).

As the important role of these subcortical structures in the perception and processing of primary affect has become clearer through the use of neuroimaging methodologies, studies have also tried to address the question of overall laterality at a subcortical level based on the nature of the emotion observed (positive/negative). As a result, a large body of work into the lateralised activation of subcortical attention networks has been published (for an overview see chapter 1). However, the isolated consideration of specific brain structures does not readily allow for generalisation in terms of overall brain region functionality; whether or not specific structure activation can be observed across a range of emotional perception tasks instead of a specific

type of task has not yet been fully clarified (Phan, Wager, Taylor, & Liberzon, 2002; Wager et al., 2003). Additionally, whether or not a number of behavioural indices (i.e. button-press, saccades etc.) are all equally successful in reflecting lateralisation is also under some debate (Wager et al., 2003). Therefore, the identification of right or left lateralised, subcortically originating emotional networks is rather difficult through usage of behavioural indices. Although an overall mapping of left and right cerebral preferential engagement to particular types of affect (right hemisphere/negative affect and left hemisphere/positive affect) has been attempted since the late 70s (e.g. Natale, Gur, & Gur, 1983; Reuter-Lorenz, & Davidson, 1981; Sackeim & Gur, 1978; Strauss & Moscovitch, 1981), more recently a proportion of neuroimaging studies have attempted the identification of overall subcortically-originating networks that are specific to each type of primary affect. One example from the literature that attempted to provide an overall account of primary affect-dependent laterality based on neuroimaging data is that by Wager and colleagues in the early 2000s, who conducted a meta-analysis of 65 studies on subcortical emotion lateralisation (Wager et al., 2003). The authors utilised two dichotomisations of affect: positive/negative and approach/avoidance (for a discussion of these conceptualisations see Chapter 1), and divided the brain into 11 regions of interest to include subcortical structures from the lateral, medial, temporal and posterior cortices, including structures such as the brainstem, amygdala, and hippocampus alongside other commonly reported subcortical structures involved in the processing of basic affect. To investigate laterality, the authors conducted binomial tests on peak activation counts between the two hemispheres that compared the right and left peaks against equivocal activation across the two hemispheres, and observed lateralised activations for specialised brain regions often described in behavioural studies of laterality (Lane et al., 1997; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz, & Davidson, 1981), as opposed to whole cerebral hemisphere lateralisation (Wager et al., 2003).

What remains to be clarified, is how emotion-specific lateralised subcortical regions manifest into observable behaviour. As of yet, there has been no clear way of behaviourally investigating emotional subcortical laterality, perhaps for the obvious reason that subcortical activation cannot be directly inferred through behavioural means. However, there is a possibility of using behavioural measures as an indirect index, not only of subcortical activation resulting from different types of affect, but

also of whether or not this activation is lateralised depending on the nature of an emotional stimulus. The following sections will first introduce nasotemporal visual field asymmetries as a possible index of asymmetrical subcortical distribution, and will discuss the novel suggestion of using these visual hemifield asymmetries as an indirect measure of investigating lateralised subcortical emotional activation based on the type of primary affect.

3.1.2 NASAL-TEMPORAL ASYMMETRIES AS AN INDEX OF SUBCORTICAL DISTRIBUTION OF ATTENTION

Studies on nasotemporal hemifield asymmetries and their usage as indirect behavioural measures of subcortical attentional activity gained in popularity roughly 30 years ago. In the vision literature, the investigation of subcortical attentional distribution through observing the competing influences of nasal and temporal asymmetries has so far successfully been accomplished in perceptual and spatial attention tasks. A core example from early work in this field is by Fahle (1987), who proposed that the nasal and temporal parts of visual field periphery are processed by the eye asymmetrically, with both resolution and visual hyperacuity being superior in the temporal hemifield (Fahle, 1987). The inference of nasotemporal asymmetries through behavioural means may be best understood when first considering the pathway from the nasal and temporal hemiretinae to the visual cortex under binocular viewing conditions (Fig. 3.3). When describing this pathway, Katz and Crowley report that upon crossing the optic chiasm, both temporal and nasal hemiretinae inputs pass through the LGN where they separate into nasal and temporal retina-specific layers before being sent onto layer 4 of the primary visual cortex (Katz & Crowley, 2002). When in the primary visual cortex, the eye-specific separation is maintained, as nasal and temporal inputs terminate in different areas; the continuation of this separation into the primary visual cortex can be seen as signalling both ocular and nasotemporal dominance (Katz & Crowley, 2002).

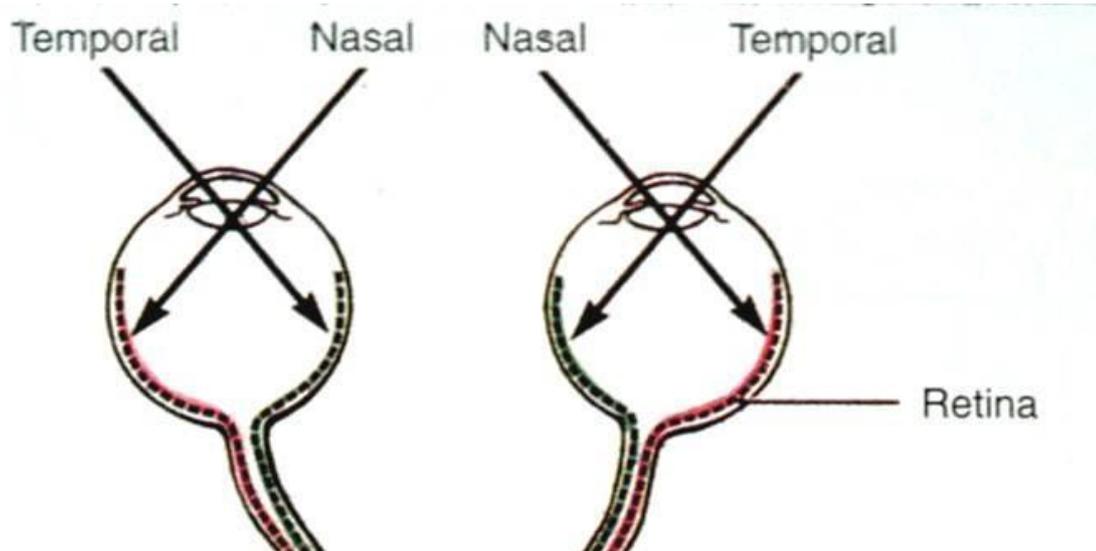


Figure 3.3. Graphic displays the inverted inputs from the lens to the nasal and temporal hemiretinae; the nasal retina receives input from the temporal hemifield, and conversely the temporal retina receives input from the nasal hemifield (Katz & Crowley, 2002).

The expectation of an overall temporal hemifield dominance is based on earlier evidence reported by Rafal and colleagues, whereby participants tested under monocular viewing conditions implemented through eye-patching were asked to respond to peripherally-displayed stimuli by either directing their saccades towards them, or by providing response times by manually pressing a response button (Rafal et al., 1991). Rafal et al (1991) found that for both saccade and reaction time responses, an overall temporal hemifield advantage surfaced. The evidence further supported their observation when compared to earlier data from patients with occipital and midbrain lesions, who also displayed an overall temporal hemifield dominance, thus strengthening the pivotal role the retinotectal pathway plays in controlling and distributing visual behaviour (Rafal et al., 1991).

In another example Zackon and colleagues (1999) hypothesised that the asymmetrical distribution of visual attention might be determined through monocular viewing conditions in a temporal order judgment task that utilised stimuli of variable onset asynchrony (Zackon, Casson, Zafar, Stelmach, & Racette, 1999). Over three experiments (no cue, exogenous cue, and endogenous cue) conducted under both binocular and monocular viewing conditions, the authors observed an effect for subcortical processing only in the monocularly viewed exogenous cue condition, while the no cue and endogenous cue conditions showed no differences. Zackon and colleagues therefore concluded that when attention is directed voluntarily,

attentional asymmetries are diminished and cortical processing takes over, with temporal order perception being modulated by presenting an exogenous cue to the temporal hemifield during monocular viewing (Zackon et al., 1999). Similarly, Roth and colleagues, by investigating the effects of monocular viewing conditions during perceptual tasks in individuals with spatial neglect, suggested that through the patching of one eye, the subcortical loci interacting with cortical attentional systems may be activated (Roth et al., 2002). Roth and colleagues reported that in patients with unilateral spatial neglect, they observed an overall attentional improvement to the neglected space once the eye ipsilateral to their injury was patched; the authors conclude that through eye patching, one can increase the activation of attentional systems which are contralateral to the viewing eye, by biasing the competition in favour of the left hemifield (Roth et al., 2002).

This section highlighted that in the anatomy of the nasal and temporal pathways from the hemiretinae, there exist a number of known asymmetries that have subsequently been linked to resulting asymmetries in behaviour (Jóhannesson, Asgeirsson, & Kristjánsson, 2012). Although the use of observable asymmetries between the temporal and nasal hemifields has been effective in general attentional tasks as mentioned above, their effectiveness has not as of yet been investigated in relation to emotional attention. The present chapter has considered evidence that suggest the successful inference of subcortical activation through solely behavioural means (i.e. saccades, manual button presses etc.), and aims to investigate the linkage between nasal-temporal asymmetries and emotional attention (as opposed to visual attention and perception) which has so far been left largely unexplored.

3.1.2.1. MIGHT NASAL-TEMPORAL ASYMMETRIES ACT AS AN INDEX OF SUBCORTICAL ASYMMETRICAL DISTRIBUTION OF EMOTIONAL ATTENTION?

A relatively small proportion of the literature has investigated the existence of nasal-temporal asymmetries in responding to face stimuli. For example, Simion and colleagues examined whether newborns show preferential orienting towards face stimuli by comparing saccade orientation towards face-like and non face-like schematic representations (Simion, Valenza, Umiltà, & Dalla Barba, 1998). Infant visual behaviour is thought to be rooted primarily in subcortical structures – as from a developmental perspective the visual cortex has not yet reached full functioning

maturity – and subsequently any visual behaviour asymmetries could be assumed to result from subcortical activation (Simion et al., 1998). Indeed, Simion et al's findings confirm hypotheses of infant orienting preference towards face-like stimuli; furthermore, infants showed more efficient performance if face-like stimuli were presented in the temporal hemifield rather than the nasal, therefore adding support to the suggestion of an overall temporal hemifield superiority (1998). More recent work by Tomalski and colleagues also examined the suggested nasotemporally-lateralised processing for face stimuli (Tomalski et al., 2009). The authors tested the assumption of the subcortical visual route acting as a mediator for the rapid orientation towards faces in the visual periphery. Using schematic face stimuli, the authors observed nasal-temporal asymmetries in participants' responses, whereby saccades to the temporal hemifield of each eye were quicker than to the nasal; although response times were also collected, they did not show any response latency effects (Tomalski et al., 2009).

The literature on emotional perception suggests the speeded processing of non-consciously perceived negative affect, which is fast-tracked through attentional filters. Based on the enhanced biological significance emotionally-loaded stimuli have for the individual (e.g. Tamietto & de Gelder, 2010), emotional faces should display a similar distribution of nasal-temporal asymmetries found when using face or face-like stimuli. Work using non-consciously perceived negatively valenced stimuli has been found to trigger the bottom-up network from the brainstem through to the amygdala and cortex (Liddell et al., 2005; Tamietto & de Gelder, 2008; 2010). Surprisingly however, and despite the high biological relevance of emotional faces as stimuli that could be assumed to instigate advantageous perceptual processing, the existence of nasal-temporal asymmetries in our responses to these stimuli has not insofar been examined.

3.1.2.2. HOW MIGHT THE LINK BETWEEN NASAL-TEMPORAL ASYMMETRIES AND THE RETINOTECTAL PATHWAY INFLUENCE ASYMMETRY?

Aside from questions on the appropriateness of manual response efficiency measures in establishing whether nasal-temporal asymmetries would be produced following displays of emotional face stimuli, the literature has also been concerned

with investigations on whether the network between nasal-temporal asymmetries through the retinotectal pathway and the superior colliculus influences asymmetry. For example, Bompas et al (2008) observed that using s-cone stimuli could effectively induce nasal-temporal asymmetries for saccadic responses; in addition, the authors' manipulation of stimulus luminance appeared to further enhance this effect. It is possible that direct projection to the superior colliculus is not a necessity for the presence of nasal-temporal asymmetries, which in turn implies the involvement of other nasal-temporal asymmetry sources (Bompas, Sterling, Rafal, & Sumner, 2008). Specifically, in the Bompas et al study, the behavioural nasal-temporal asymmetries observed similar to those found in attentional (e.g. Posner, Rafal, Choate, & Vaughan, 1985), and face perception studies (e.g. De Gelder & Stekelenburg, 2005), should not be viewed as being the exclusive product of the retinotectal pathway, as in the Bompas et al study the s-cone stimuli used did not produce a larger effect than luminance (Bompas et al., 2008).

The vision literature has documented the presence of anatomical asymmetries between nasal and temporal hemiretinae and function. Anatomical asymmetries have been identified and linked to cognitive function in connection to saccade selection and attention (Jóhannesson et al., 2012), Vernier acuity (Fahle, 1987), and in projections from the hemiretinae to the superior colliculus (Sylvester et al., 2007). Although predictions on the existence of nasal-temporal asymmetries could be logically based on the existence of structural asymmetries in retinal projections to the midbrain, as well as on the existence of attentional asymmetries across the hemifields, findings from this field of research have not proven conclusive. For example, when attempting to identify the presence of asymmetries across a number of saccadic tasks by looking at landing point accuracy and saccadic latency, Jóhannesson and colleagues reported that while the saccadic latency measure identified no asymmetries, the landing point accuracy showed very moderate asymmetric activation (Jóhannesson et al., 2012). Jóhannesson et al highlight that superior colliculus mediated responses (in this case in the form of choice saccades) might be less pronounced than originally hypothesised, as they are influenced by areas that receive direct input from the lateral geniculate nucleus (Jóhannesson et al., 2012). In terms of visual anatomy, the limited number of primary retinal projections direct to the superior colliculus has been established for some time now. For example, Perry and Cowey suggested that only 10% or less of retinal ganglion

cells have primary projections to the superior colliculus (Perry & Cowey, 1984). More recently, Sato and Schall suggested that the connection between saccades and attention might not be as straightforward as originally thought, as in their study one third of FEF neurons displayed non-correlated responses between saccades and selective attention (T. R. Sato & Schall, 2003). This might offer an explanation as to why nasal-temporal asymmetries either come across as subtle effects, or not at all. Similar to the majority of studies in this field, the entirety of the discussion on the exclusivity of the link between the retinotectal pathway and nasotemporal asymmetries relies on studies utilising saccadic responses. In terms of manual motor responses the same question is as of yet completely unexplored.

3.1.2 SUMMARY

To summarise, the literature so far suggests interplay between emotion and attention. However, this is a complex and highly dynamic process that is as yet to be fully disambiguated. Given the prioritising nature of attentional mechanisms that are fine-tuned for filtering environmental information so that stimuli that are biologically significant (such as emotional faces) to the organism can be prioritised and responded to efficiently, an equally efficient and developmentally mature subcortical network might be expected to be at play. The neuroimaging and neurophysiological literatures have so far investigated in great detail the role of different subcortical structures in recognising, perceiving, and attending to emotions. The behavioural literature has in turn successfully used asymmetries in visual attention and behaviour through the means of nasal-temporal hemifield asymmetries as an index of subcortical activation. However, there is an evident gap in the literature in terms of using nasal-temporal asymmetries as an indicator of subcortically led attention to emotional stimuli, and specifically to facial expressions of affect.

The following experiment addresses this gap by adapting the behavioural paradigm introduced in chapter 2 so as to utilise nasal-temporal asymmetries as a mediator of lateralised behaviour towards positive and negative facial expressions of affect. The following experiment also addresses another gap in the literature; insofar, only non-consciously perceived, negative affect has been utilised in relation to subcortical attentional activation. The present chapter addresses this gap by utilising visible, and of varying expression salience emotional facial expressions in an attempt

to highlight the modulating properties of visible and therefore consciously perceived emotion on nasal-temporal asymmetries. Based on the conclusions from the present chapter's introduction, the following experiment therefore tested the assumption of a nasal-temporal differential hemifield contribution in responding to emotional faces instead of neutral, which is expected to be further enhanced if the valence of the emotional face is negative, and furthermore if the emotional face is present in the temporal hemifield. This prediction also follows on from experiment 2.1, chapter 2 hypotheses of overall visual field asymmetry as being dependent on the nature of the emotional stimulus observed.

3 EXPERIMENT 3.1

3.2.1. METHODS

3.2.1.1. SUBJECTS

Twenty-four neurologically healthy adults (Undergraduate students, Department of Psychology, City University London) took part in this study (7 males; mean age: 24.8; SD: 2.1). Participants were recruited through an online advertisement on the University's Psychology Department online participation tool (SONA). Poor quality data from three other participants were excluded due to improbable reaction times (<300ms). All participants were right-handed with normal or corrected-to-normal vision. Handedness was used as an index of eye dominance, based on an established strong statistical association between handedness and eye dominance (McManus, Porac, Bryden, & Boucher, 1999). All participants had given written consent prior to testing.

3.2.1.2 APPARATUS

Laboratory setup and apparatus was the same as described in Experiment 2.1, Chapter 2. In addition, a concave-shaped black canvas eye-patch with adjustable elastic strap was also used.

3.2.1.3. STIMULI

Stimuli and stimulus display dimensions, layout, and lateral positioning in the display were the same as those used in Experiment 2.1, chapter 2. In terms of poser selection, the same 4 posers used in the practice trials in Experiment 2.1 were also used in the practice trials for the present study. Similarly, photographs from the 6 posers used in experiment 2.1 were also used in the testing blocks for the present study (see Figure 2.8, chapter 2).

3.2.1.4. DESIGN

The experiment utilised a 2x2x2x5 repeated-measures factorial design, with temporal vs nasal hemifield, emotion, visual field location, and intensity of facial

expression as within-subjects factors (Table 3.1). The within-subjects factors of hemifield (nasal/temporal), emotion (angry/happy), and visual field location (left/right) all had two levels, while expression salience (intensities 1-5) had five. There were 40 conditions of possible combinations between hemifield, emotion, visual field location, and expression salience per testing session, with conditions randomised across participants. Manual (button press) reaction times (ms) and accuracy scores (% correct scores) were the two dependent measures collected.

| Target Location/Visual field | Patched Eye | Activated Hemifield |
|-------------------------------------|--------------------|----------------------------|
| LVF | Left | Nasal hemifield |
| RVF | Left | Temporal hemifield |
| LVF | Right | Temporal hemifield |
| RVF | Right | Nasal hemifield |

Table 3.1. Table maps each possible combination between right and left visual field location of the target stimuli (emotional expressions) and patched eye, with its equivalent stimulated hemifield.

3.2.1.5. PROCEDURE

Testing took place in a darkened, soundproofed laboratory room. The speeded, forced-choice facial expression discrimination task introduced in Experiment 2.1, chapter 2 was used in the present study with the collected measures being response time and accuracy (see chapter 2, figure 2.10). To briefly recap, participants viewed bilateral presentations for 50ms each of one emotional and one neutral facial expression of angry or happy affect, and were required to press the right or left keyboard arrow keys depending on which side they saw the emotional face on. The task rendered target location unpredictable across trials, and the target emotional faces varied in expression intensity from 1(ambiguous) to 5(exaggerated).

The additional factor of nasal/temporal hemifield was manipulated by alternating between patching the left or right eye to manipulate the nasal/temporal hemifield presentation of stimuli. When the right eye was patched, target stimuli presented on the right visual field were nasal, and when presented on the left visual field were temporal. The opposite pattern occurred when the left eye was patched (e.g. target on the LVF was nasal and target on the RVF was temporal). This resulted in 5 testing blocks viewed monocularly with one eye patched, and 5 testing blocks

viewed monocularly with the other eye patched (total of 10 testing blocks completed per participant). Participants were tested individually, and a typical testing session lasted approximately 90 minutes depending on length of break time taken between testing blocks. When starting the testing session, participants were asked to first complete a practice block of 160 trials, in which stimuli were viewed binocularly. On successful completion of the practice block, participants wore the eye patch on either the left or right eye, and proceeded to complete 5 testing blocks viewed monocularly. After completing the first 5 testing blocks, the alternate eye was patched and participants completed a further 5 testing blocks, again viewed monocularly. The order of eye patching was counterbalanced across participants with 12 participants starting the experimental trials with the right eye patched first, and 12 participants starting with the left eye patched first. Each testing block consisted of 240 trials. Overall, data were collected from a total of 2400 trials with 10 testing blocks completed per participant. There were no changes to fixation and feedback display timings, stimulus onset-offset or response time window implemented (see Figure 2.10, chapter 2).

3.2.1.6. DATA PREPARATION AND ANALYSIS

Each participant's mean RT (ms) and accuracy score (% correct score) were calculated per experimental condition. Calculations were conducted using E-Data Aid and E-Merge, part of the E-Prime v2.0 software package (Psychology Software Tools, Pittsburgh, MA). Raw reaction time data were filtered to exclude values from incorrectly-responded to trials, and were further filtered as to exclude reaction times less or more than 2 standard deviations from the mean. For accuracy scores, mean accuracy performance was calculated for each participant per condition. In the following results section, all analyses involving factors with more than 2 levels violating the sphericity assumption have been Greenhouse-Geisser – corrected, and all error bars represent within-subjects error, calculated using the Cousineau correction (Cousineau, 2005; Morey, 2008).

3.2.2 RESULTS

3.2.2.1 REACTION TIME

A repeated-measures ANOVA was conducted with hemifield (nasal/temporal), emotion (angry/happy), visual field location (left/right) and intensity (1-5) as within-subjects factors on the reaction time data. The analysis resulted in a significant main effect of emotion [$F(1,20)=8.7$, $p=.008$, partial $\eta^2=.3$], with quicker responses for happy faces (mean=510.2, SE=12.14) than angry faces (mean=518.7, SE=12.6). A main effect of expression intensity was also found [$F(4,80)=48.6$, $p<.001$, partial $\eta^2=.7$]. No further significant main effects were found.

A marginally significant interaction between nasal/temporal hemifield and emotion (angry/happy) was found in the reaction time data [$F(1,20)=3.7$, $p=.07$, partial $\eta^2=.3$]. Unpacking the interaction showed no differences for angry faces viewed in the nasal (mean =518, SE=14.5) or temporal (mean = 514, SE=14.8) hemifields. However, for happy stimuli viewed on the temporal hemifield reaction times were quicker (mean = 506, SE=11), than when viewed on the nasal hemifield (mean=519, SE=12) (Figure 3.4 on following page).

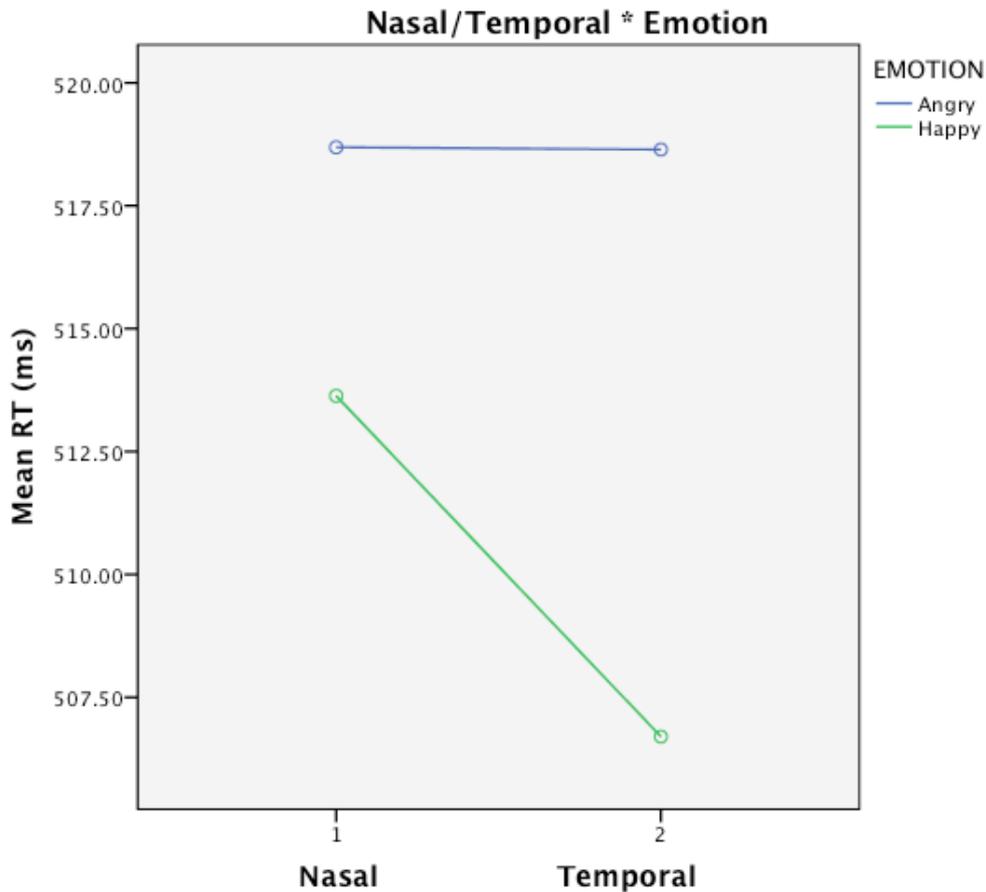


Figure 3.4. Interaction plot displaying mean reaction time (ms) scores for angry (blue line) and happy (green line) emotional face stimuli when plotted across the nasal and temporal hemifields respectively. Happy stimuli when viewed on the temporal hemifield were responded to quicker than when on the nasal hemifield. No such difference was observed for the angry faces.

3.2.2.2. ACCURACY

A repeated-measures ANOVA with the within-subjects factors of hemifield (nasal/temporal), emotion (angry/happy), visual field location (left/right) and expression intensity (1-5) was conducted for the dependent measure of mean % correct scores. The analysis resulted in a significant main effect of emotion [$F(1,20)=7.61$, $p=.012$, partial $\eta^2=.3$] with happy faces scoring higher accuracy (mean=.80, SE=.023) than angry faces (mean=.76, SE=.024). Accuracy analysis also showed a significant main effect of expression intensity [$F(4/80)=217.73$, $p<.001$, partial $\eta^2=.91$]. The factors of hemifield [$F(1,20)=6.4$, $p=.43$, partial $\eta^2=.3$], and visual field [$F(1,20)=1.2$, $p=.21$, partial $\eta^2=.05$] were found to be non-significant.

The analysis also produced a significant interaction between emotion (angry/happy) and intensity [$F(4,80)=6.09$, $p<.001$, partial $\eta^2=.23$]. Post-hoc paired-samples t-tests revealed that the interaction resulted from significant differences between the angry and happy stimuli for intensity 2 [$t=-2.5$, $df=20$, $p=.02$], intensity 3 [$t=-3.52$, $df=20$, $p=.002$], intensity 4 [$t=-3.73$, $df=20$, $p=.001$], and intensity 5 [$t=-2.36$, $df=20$, $p=.03$] (Fig 3.5 on following page). There was no significant difference between angry and happy stimuli for intensity 1 ($p=.3$) were responses were at chance level (approx. 50-55%) (Figure 3.6).

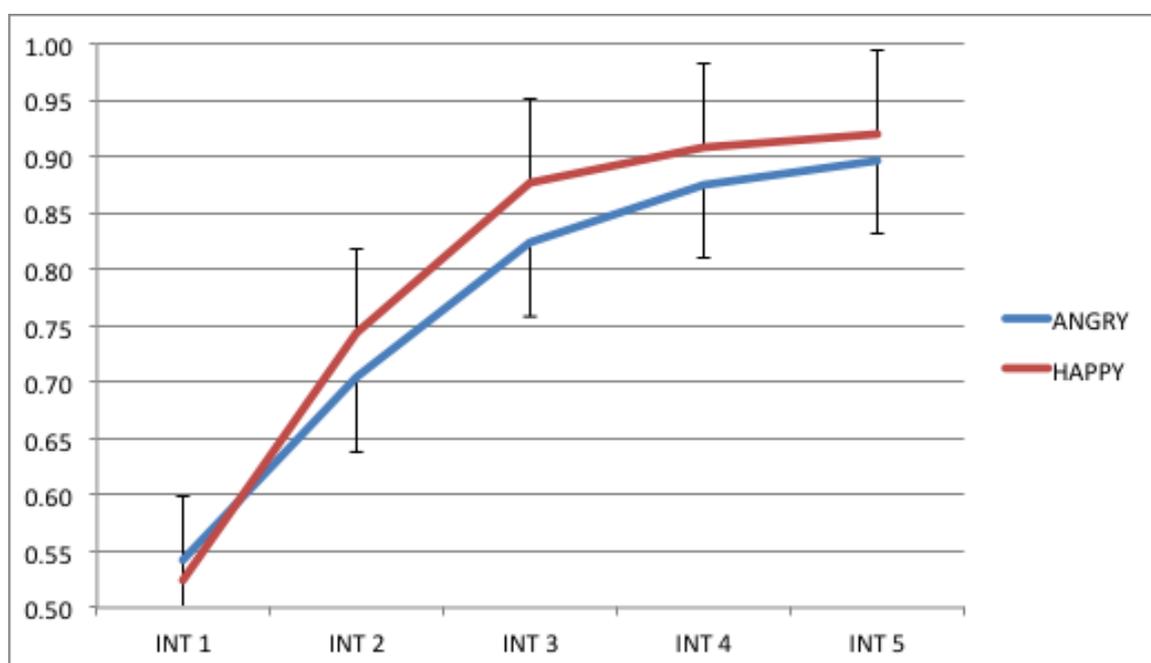


Figure 3.5. Line graph representing accuracy scores for each emotion (angry/happy) as a function of expression intensity. Error bars represent Cousineau-corrected, ± 1 within-subjects error. No difference is shown between emotions for intensity 1, and for this expression intensity accuracy scores for both emotions is just above chance. From intensity 2 through to intensity 5, happy faces show consistently higher, significantly different accuracy scores than angry faces, with intensity 3 producing the largest difference in accuracy scores between the two emotions.

No significant interactions were found between the factors of emotion and hemifield [$F(1,20)=.4$, $p=.53$, partial $\eta^2=.01$], visual field and hemifield [$F(1,20)=.02$, $p=.9$, partial $\eta^2=.001$], or between emotion and visual field [$F(1,20)=.07$, $p=.7$, partial $\eta^2=.004$]. Similarly, the three-way interaction between hemifield, emotion, and visual field location was non-significant [$F(1,20)=1.5$, $p=.23$, partial $\eta^2=.07$].

3.2.2.3. THRESHOLD ANALYSIS

A repeated measures ANOVA with emotion (angry/happy) and visual field location (left/right) was calculated for the threshold accuracy data. A significant interaction between emotion and visual field was observed [$F(1, 20) = 7.23, p = .02$]. Similarly to the detection thresholds per emotion found in Exp.2.2, chapter 2, happy faces were recognised more accurately overall as opposed to angry. This difference was even more prominent when the happy faces were displayed on the RVF (Fig. 3.6).

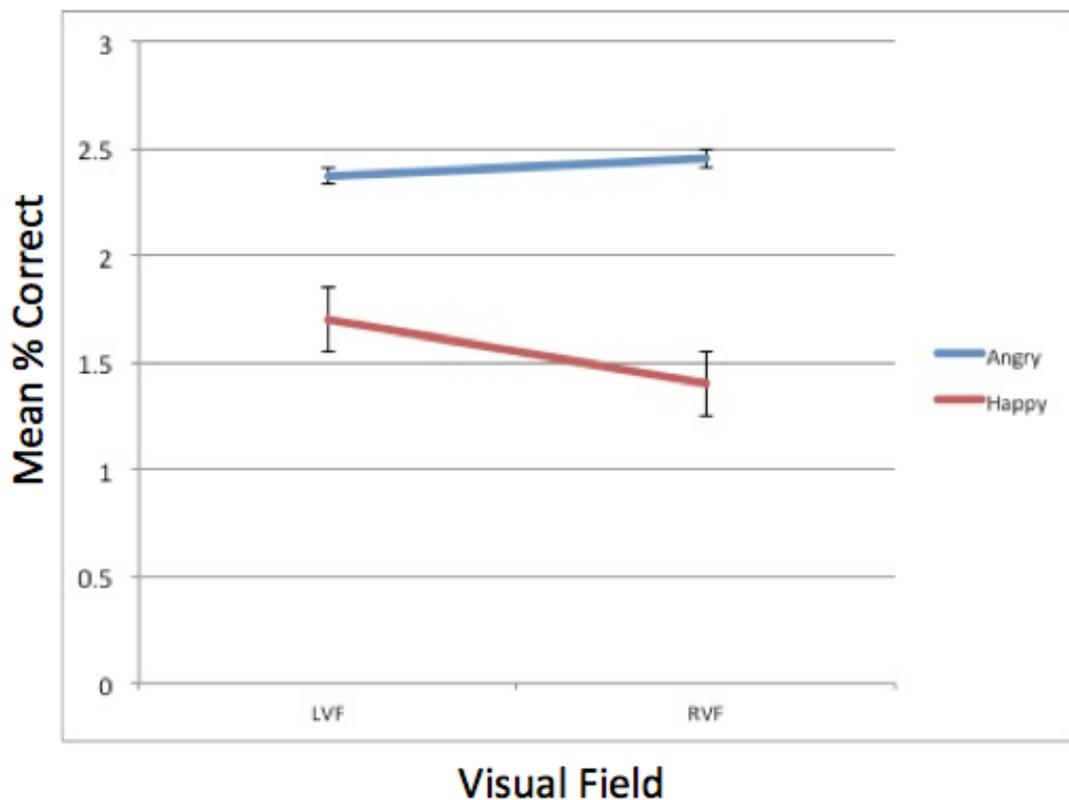


Figure 3.6. Graph displays detection thresholds for the happy and angry faces utilised in the present study, when displayed on the LVF and RVF. Error bars represent ± 1 SE of the mean.

3.2.3 SUMMARY

The results point towards a trend for a temporal hemifield advantage but only for happy stimuli. However, this trend was only marginal and solely observed in the manual response time data. Contrary to predictions, both reaction time and accuracy data did not result in lateralised patterns of behaviour as dependent on type of emotion (angry vs happy), hemifield (nasal vs temporal), or visual field location (left vs right). Findings from experiment 3.1 add support to the overall preferential response towards happy stimuli, initially observed in experiment 2.1. Happy stimuli - regardless of nasal or temporal hemifield, or left or right visual field presentation, were consistently responded to quicker and more accurately than angry stimuli.

The reaction time data - aside from a marginally significant interaction between nasal-temporal hemifield and emotion - showed no significant interactions of visual field location and intensity for the two emotional facial expressions. Unpacking of the marginal interaction confirmed predictions of quicker responses to temporal hemifield only for happy facial expressions. Angry faces produced a negligible difference across nasal and temporal hemifields. Potentially, a larger sample would strengthen interaction significance, as the current effect size observed is somewhat modest (partial $\eta^2=.3$). The reaction data also produced an effect of emotion, where happy facial expression stimuli resulted in decreased response latency than angry, regardless of visual field location or nasal/temporal hemifield. The data also showed a significant effect of expression salience (intensity), with significant differences resulting from paired comparisons of the majority of intensity pairs (intensities 1 through to 4), but not for the comparison between the two high-salience intensities (4 and 5).

The same significant effects of type of emotion and intensity were also observed in the accuracy data, with happy facial expression stimuli resulting in higher accuracy responses than angry, while paired comparisons between all intensity pairs resulting in significant differences. In addition, the accuracy data revealed a significant interaction between type of emotion (angry vs. happy) and expression salience (intensities 1 through to 5). Unpacking of the interaction confirmed an anticipated ceiling effect: just above chance level accuracy resulted from the most ambiguous expression intensity (intensity 1), showing no difference between the two emotions,

and a gradual increase of performance as the expression salience disambiguates with high accuracy performance reaching a plateau for the highly salient intensities (4 and 5). Across comparisons of intensities 2 to 5, a significant difference between the two emotions is maintained, with happy faces scoring higher accuracy than angry.

3.3 DISCUSSION

Experiment 3.1 predicted that subcortically driven attentional asymmetries, previously reported in the literature as resulting from using subliminal or masked emotional stimuli would manifest as nasal-temporal hemifield preferences when using suprathreshold facial expressions of positive and negative affect. A further prediction considered that such asymmetries would be modulated by the nature of the emotion observed (positive-happy vs negative-angry). The present experiment utilised participant manual reaction times and accuracy scores as a response mode that might represent an accurate reflection of oculomotor behaviour. Contrary to predictions, data from experiment 3.1 did not establish the presence of robust nasal-temporal asymmetries, apart from in the form of a marginally non-significant interaction between emotion and nasal/temporal hemifield for reaction times. In this interaction trend for manual reaction times, temporally viewed happy faces were responded to quicker than nasal. The assumption of such asymmetries being a product of the nature of the emotion observed (positive vs. negative) was partially confirmed, with temporally viewed happy faces producing marginally quicker response times.

Data from both manual response times and accuracy scores added support to a happy-face advantage also observed in experiment 2.1, chapter 2. Additionally, in the present experiment, and while factors of expression salience and visual field location did not significantly influence response latency, accuracy was influenced by an interaction between emotion observed and expression salience, with the largest differences between emotions occurring at intensity 3. The following discussion will consider possible reasons for the lack of robust nasal-temporal asymmetries in this case.

3.3.1 MIGHT THE PRESENCE OF NASAL-TEMPORAL ASYMMETRIES BE METHODOLOGY-DEPENDENT?

3.3.1.1 RESPONSE TYPE

Manual, button-press responses do not feature heavily in the vision literature for nasal-temporal asymmetries. Although these responses form sometimes part of a number of response types collected, nasal-temporal asymmetries are mostly reported in relation to participant choice saccades or covert orientation to stimuli. Interestingly, the bulk of this research uses data from infant participants instead of adults. For example, Simion et al identified newborns' tendency to preferentially orient to face-like over non face-like stimuli through nasal-temporal asymmetry manipulation (Simion et al., 1998), while Mulckhuyse and Theeuwes showed evidence of preferential saccadic responses towards temporal hemifield presented and validly cued targets (Mulckhuyse & Theeuwes, 2010).

A possible reason why this might be the case could be that different response types might play a modulating role in the presence or absence of identifiable, subcortically originating asymmetries in behaviour (Sylvester, Shulman, Jack, & Corbetta, 2007; Sylvester, Josephs, Driver, & Rees, 2007). Saccades and covert orientation to stimuli could be responses that might be better suited in establishing the presence of nasal-temporal asymmetries as they might represent the immediate and reflex-like activation of oculomotor behaviour. This might explain why although there is mounting evidence for temporal hemifield superiority in infants, this effect is not as commonly reported in adults, as infants are more subject to reflex-like oculomotor responses compared to adults (Sylvester et al., 2007).

A more direct example of the differences between manual responses and saccades in their sensitivity towards nasal-temporal asymmetries can be seen in Tomalski et al's work, who by using face-like schematic stimuli, found increased saccadic response latency for temporal hemifield presentations but did not observe the same effect when looking at manual response times (Tomalski et al., 2009). The possibility exists that manual response latency is not a sensitive enough measure to successfully establish subcortically originating hemifield asymmetries, while saccades might be a more direct reflection of oculomotor activity and response. Conversely, manual response times perhaps might be a more accurate reflection of sensitivity to more crude hemispheric asymmetries in response to stimulus

contextual elements such as type of an emotion or the ambiguity of a facial expression, which might explain why under monocular viewing conditions any effect of nasotemporally lateralised behaviour is diminished. A possible reason may be that whereas some types (i.e. manual responses) of behavioural response might be well-established for indicating overall, asymmetrical distribution of cortical attention by observing hemispheric preferential engagement as dependent on valence (i.e. Reuter-Lorenz & Davidson, 1981; Moretti et al, 1996), other forms of behavioural responses (i.e. saccades) are more effective in engaging subcortically originating asymmetries depending on the nature of the emotion observed (Tomalski et al, 1999). Specifically, subcortical attentional engagement as a response to primary emotional stimuli has been shown to occur very early on (i.e. Palermo & Rhodes, 2007). Tasking participants to shift their gaze towards the emotional target therefore, would more closely resemble an automatic, reflex-like movement that is very quickly elicited. However, when the extra requirement of movement is added by asking participants to press a button, response latency would be expected to decrease due to the additional cognitive processing involved in planning for and executing the movement to respond. The fact that the bulk of research in nasal-temporal asymmetries utilises saccadic responses or covert orientation and does not take into account manual responses makes the comparison across different types of responses within the same context problematic. However, although saccades are often the response of choice, the directness of their relationship to subcortical attention has not been fully established. For example, in early work by Posner and Cohen, a distinct dissociation between asymmetries in saccadic responses and the lack of asymmetries in temporal order judgement tasks was observed, suggesting that choice saccades might be influenced by a pathway separate to that supporting attention (Posner & Cohen, 1980; 1984). It is possible therefore, that the appropriateness of saccades as measures of subcortically-originating attentional networks – regardless of what type of stimulus they are activated as a response to - is not fully straightforward. Although manual and saccadic responses have shown some overall differences in reference to different types of stimuli in the vision and attention literatures (i.e. Bompas & Sumner, 2008), these differences have not been investigated in relation to successful identification of nasal-temporal asymmetries. Bompas and Sumner compared the efficiency of saccades and manual responses towards S-cone and luminance stimuli (Bompas & Sumner, 2008). In an experiment

tasking participants with identifying a target's visual field location, Bompas and Sumner found response latency differences only for S-cone stimuli for both measures, with saccadic responses showing a more pronounced bias than manual responses (Bompas & Sumner, 2008). Importantly, in this example both response types displayed the predicted differences towards the two competing stimuli, with the differences being however, of differing magnitudes. If manual response times are sensitive enough to distinguish extremely subtle differentiations between stimuli in temporal order judgement tasks (Bompas & Sumner, 2008), then they should be able to establish differences between nasally and temporally presented, biologically relevant stimuli. Evidently, in the present chapter's results, manual responses are not sensitive to this, perhaps because they are based on a separate symmetrical system, unlike saccades.

3.3.1.2 PARADIGM TYPE

The influence of type of paradigm used on resulting behavioural patterns – especially concerning effects of laterality – has been discussed in chapter 1. Manipulations of type of stimuli used, stimulus onset-offset timing, type of emotion used (positive vs negative or fear vs sadness vs anger), and type of stimulus used (schematic vs photographic, colour vs greyscale) are some of the factors which have contributed to inconclusive findings concerning lateralised, preferential processing of emotional stimuli. Similar inconclusive findings concerning nasotemporal asymmetries might perhaps be attributed to the same suite of methodological influences. There are some examples from the literature suggesting that deviation from attentional cueing paradigms or distractor effect tasks might significantly impact the resulting presence or absence of behavioural nasal-temporal asymmetries. For example, Bompas and colleagues, comment on the lack of replicable nasal-temporal asymmetry findings when different paradigms to the ones commonly reported have been used (Bompas et al., 2008). Bompas et al report that nasal-temporal asymmetries might originate from differences in processing times instead of levels of activity in a study investigating both manual and saccadic response times to S-cone stimuli and luminance signals (Bompas et al., 2008). In their discussion, the authors suggest that as they observed differences in response latencies between the two

types of response times collected, this might be attributed to differences in the time taken from processing stimuli to making a decision to respond.

It might also be the case that the number of conditions in the present chapter's experiment eradicated any lateralised effects. Specifically, as in the present experiment the number of conditions was double to those in the original paradigm (Exp. 2.2) to account for nasal/temporal hemifields, overall lateralised behavioural patterns that are present short-term post the detection threshold, they diminish once participants habituate to the stimuli. It seems that although in experiment 3.1 the valence of the faces had an observable effect on participant responses displayed as an overall happy face advantage, this effect was modulated by nasal-temporal hemifield presentation.

3.3.2 MIGHT NASAL-TEMPORAL ASYMMETRIES BE SENSITIVE TO FACES OVERALL, BUT NOT TO DIFFERENT TYPES OF FACIAL AFFECT?

The present chapter aimed to address an additional notable gap in the literature on nasal-temporal asymmetries which relates to visible, consciously perceived facial expressions of affect. Although work has been done on establishing the subcortical – and often lateralised (depending on type of stimulus used) – networks responsible for recognising and responding to emotional cues (e.g. Tamietto & de Gelder, 2010), attempts at translating subcortical asymmetrical activation into visual behaviour through manipulation of nasal-temporal hemifield asymmetries in conjunction with valence are not reported in the literature (Reuter-Lorenz et al., 1995). The present chapter discussed that emotion-aside, there is evidence to suggest that face-like stimuli are included in the stimulus category which should theoretically elicit such asymmetries. For example, in a comparative study between prosopagnosics and control participants, de Gelder and colleagues identified nasal-temporal asymmetries specific to the processing of faces in the control group, but not in participants with prosopagnosia (De Gelder & Stekelenburg, 2005).

In earlier work, Farroni et al investigated whether newborns show particular orienting preference towards positive, neutral, or negative affect; despite the mounting evidence for an overall threat attentional advantage which is suggested as being mitigated by a subcortical alarm system through the amygdala, the authors observed that newborns showed preferential orientation to happy faces (Farroni, Menon, Rigato, & Johnson, 2007). It would be logical therefore to assume that nasal-

temporal asymmetries could occur from emotional faces, which could stretch to these asymmetries being modulated by the nature of the emotion observed. A happy face advantage was found for both response time and accuracy data in the present experiment, yet this was not concretely attached to overall, clear nasal or temporal hemifield preferences. If taking into account the marginal interaction between nasal/temporal hemifield and emotion observed for the response time data in the present experiment, a modest conclusion for the modulating power of positive facial expression stimuli could be reached. Nonetheless, emotion as an additional contextual factor to face stimuli did not appear to elicit distinctly asymmetrical responses. Interestingly, although robust nasal-temporal asymmetries have been observed in response to face-like stimuli (e.g. Tomalski et al., 2009), these were not confidently reproduced in the present study which included the additional factor of valence. It could be that when emotional faces are concerned, the attentional processing required – although bearing many similarities to that of subcortically-originating processing that produces nasal-temporal asymmetries – is distinct and independent.

The introduction of a monocular viewing condition in experiment 3.1 eradicated previously established lateralised response patterns from experiment 2.1; although in experiment 2.1 happy faces were also responded to quicker overall across conditions, specific facial expression intensities produced distinctly lateralised responses for both types of affect. A possible reason for this could be that although when viewed binocularly emotional faces elicit distinctly lateralised responses at a point where stimuli are half way between salient and ambiguous, when viewed monocularly participant responses fully switch to an overall happy-face advantage which is not influenced by the visual field location of the stimuli, or by their nasal-temporal hemifield presentation. It might be the case that differences in ocular dominance have caused variance when patching different eyes, therefore hiding subtle effects.

3.3.3 CONCLUSION

The present chapter sought to establish the novel prediction of eliciting nasal-temporal asymmetries when viewing bilateral presentations of facial expressions of visible emotion (happy and angry). In order to behaviourally establish such

asymmetries that have previously been suggested to arise from asymmetrical subcortical distribution of attention, participants viewed bilateral presentations of face stimuli (emotional paired with neutral) under monocular viewing conditions. To the author's knowledge, no attempt of eliciting such asymmetries in relation to visible emotional faces has previously been made. Both manual response times and accuracy scores were collected, and while a modest trend of nasotemporal asymmetries was observed only for happy stimuli in manual responses, accuracy scores supported a happy-face advantage which was not modulated by visual field location or intensity of facial expression salience. This chapter has considered a number of possibilities, both methodological and theoretical that might account for the lack of robust nasotemporal asymmetries when attending and responding to emotional faces. It appears that such asymmetries might only be elicited under specific methodological circumstances and predominantly for saccadic responses instead of manual reactions.

4 CHAPTER 4: AUDITORY THREAT AND GAZE DIRECTION MODULATE LATERALISED RESPONSES TO AFFECT

4.1 GENERAL INTRODUCTION

So far, the present thesis has presented results for an emotion detection paradigm that can effectively investigate lateralised processing of primary affect through behavioural measures of response efficiency. Chapter 2 set the scene for the behavioural methodology, and chapter 3 explored the possibility of nasal temporal asymmetries in visual emotion perception as being indicative of subcortically originating, emotion specific lateralisation. The present chapter will now seek to examine how the valence-enhancing properties of sounds and gaze direction might further modulate differential hemispheric contribution in the processing of facial expressions of primary affect.

Auditory stimuli have been frequently used in studies of emotional perception and its resulting behaviour. Our ability to detect and localise sounds – especially if these sounds carry or elicit emotional meaning– is crucial for our survival, as it allows us to identify the presence or the impending arrival of potential danger. The biological relevance and increased attentional urgency that sounds represent in the individual has been explored in studies of sensory processing (Lang & Bradley, 2010; LeDoux, 2012), with some research focusing on the specific effects sounds might have on emotional attention, perception, and processing. For example, negative emotions have been found to directly influence early, low-level auditory processing in responding to speech (Wang, Nicol, Skoe, Sams, & Kraus, 2009), and emotional sounds have been found to significantly bias attention (Bröckelmann et al., 2011). More recently, the influence of biologically-relevant sounds in overall visual perception has been broadly established (Sutherland, Thut, & Romei, 2014), without however specifically examining the link between biased early auditory processing and the visual attentional processing of emotion. Instead, research on the interplay between emotion and attention has remained in its majority within the vision literature. The present chapter will therefore seek to investigate how and to what extent the increased biological significance of an audiovisual emotional stimulus will

manifest into lateralised biases towards visual stimuli, as indicated by measures of response efficiency.

Gaze direction of a facial expression is another ecologically significant stimulus feature shown to modulate emotional attention. For example, facial expressions with direct gaze to the observer have been found to grab and hold attention to the face, whereas averted gaze of the poser to either the left or right visual hemifield can direct and shift the observer's attention, acting as a strong attentional cue and biasing responses when visual targets appear on the hemifield congruent to the direction of gaze (i.e. faster target detection when on the left visual field following stimulus with left gaze direction) (Bindemann et al., 2008, 2005; Spence & Driver, 1997).

In addition, similarly to emotional sound localisation, effects of gaze direction on behaviour when paired with negative facial expressions have also been interpreted as signifying the location of potential threat. The threat localisation abilities of gaze have been reported in both the human (e.g. Adams, Gordon, Baird, Ambady, & Kleck, 2003; George, Driver, & Dolan, 2001; Hadjikhani, Hoge, Snyder, & de Gelder, 2008) and animal literature (e.g. Hoffman, Gothard, Schmid, & Logothetis, 2007), confirming the biological importance of gaze as a signal of threat location. For example, Adams and colleagues (2003) suggested that in fearful and angry stimuli, gaze direction alerts an observer as to the location of potential threat, on the assumption that angry faces signal threat that is directly facing the observer, and fearful faces imply threat existing in the surrounding environment of the observer. The authors therefore hypothesised that angry faces paired with direct gaze and fearful faces paired with averted gaze would be recognised more efficiently than angry faces looking away, and fearful faces looking toward the observer (Adams, Gordon, Baird, Ambady, & Kleck, 2003). Indeed, the authors found that fearful stimuli where the direction of gaze was averted, produced a near-automatic processing of fearful faces with averted gaze, (Adams, Gordon, Baird, Ambady, & Kleck, 2003) as exposure to such stimuli has been suggested to preferentially stimulate the short-route attentional network to the amygdala, activated in the presence of potential danger (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Adams & Kleck, 2003; Haxby, Hoffman, & Gobbini, 2000). Adams and colleagues however did not find a similar activation pattern for angry faces with direct gaze (Adams et al., 2003).

Seeing facial expressions signifying fear (or anger) that are completely isolated from any additional contextual information outside of direction of gaze is however exceedingly rare, and is not representative of natural occurrences in our environment. Resulting interpretations from research utilising gaze manipulation on facial expressions therefore ultimately lack in their consideration of the biological value that localisation of threat has on observable behaviour; a biological value that might perhaps be better understood by examining threatening stimuli that effect both visual and auditory modalities. So far, the differential effects of gaze direction when combined with other, equally biologically salient threat localising factors on how we process and respond to facial affect have not yet been examined. The present chapter will therefore attempt to increase the ecological validity of gaze-manipulated facial expression stimuli, by attaching additional valence-enhancing properties (e.g. auditory threat) and examining their effects on behaviour.

The present chapter reports on two studies designed to investigate the valence-enhancing effects of sounds on lateralised processing of affect on the first instance, and secondly on the cumulative valence-enhancing effect sound and gaze direction might have on lateralisation. Specifically, Section 1 reviews the literature on valenced sounds and their resulting effect on behaviour and Experiment 4.1 addresses the modulating properties on behaviour of positive and negative facial expressions of affect of varying salience, when paired with a looming or receding sound. Section 2 reviews the evidence on the influence gaze direction has been found to have on the perception of negative emotions, with Experiment 4.2 designed to investigate the implications of the cumulative effect gaze direction and sound may have on lateralisation, by manipulating gaze direction of fearful and angry facial expressions in addition to presence/absence of auditory threat (looming vs receding sounds).

SECTION 1

4.1.1 MODULATING EFFECTS OF SOUND ON EMOTIONAL ATTENTION AND BEHAVIOUR

Identification and localisation of sound sources is a skill crucial to our survival. Biologically salient sounds in particular convey a direct and immediate need for

accurate identification, attentional prioritisation, and selection of an appropriate response, as they might signify the presence of threat within our environment. Auditory emotion-inducing signals such as the sound of a predator approaching, have special relevance to the self; the threat imminence they signal necessitates their speeded decoding, encoding, and accurate interpretation (Sutherland et al., 2014). The particular effects of valenced sounds on behaviour have been thoroughly investigated, particularly through psychopharmacological animal models looking at the effects of inhibiting subcortical networks through the inferior colliculus that are relevant to the production of defensive behaviour (e.g. Nobre, Sandner, & Brandão, 2003). In one such example from the animal literature, the startle reflex of rats responding to a sudden noise was examined in terms of changes in auditory evoked potentials (ARPs) and subsequent changes in behavioural responses ('freeze' vs. startle response) (Nobre et al., 2003). In this study, behavioural effects and ARPs were compared between times when the rats received microinjections of a pharmacological inhibitor to the inferior colliculus that surprisingly caused reduction of GABA levels (given the inhibitory role of GABA), and times when the rats were administered apomorphine which causes overall arousal (Nobre et al., 2003). The authors noted that during pharmacological inhibition of the inferior colliculus, the rats displayed increased 'freezing' behaviour to sudden sound stimuli; administration of apomorphine on the other hand showed no effect on rats' freeze/startle behaviour (Nobre et al., 2003).

Aside from playing an important role in observable behaviour, emotional sounds are highly salient stimuli that have been suggested to be preferentially processed and prioritised for selective attention. The selective prioritisation of environmental information that pass on to attention is a highly complex and competitive process, which requires low-level rapid identification and categorisation of stimuli in terms of their direct relevance to the organism (Compton, 2003). The rapid onset of emotional modulation of audition reported in the literature, suggests a prioritisation of valenced sounds through the fast-route to the amygdala (i.e. Bröckelmann et al., 2011; Wang et al., 2009) that had previously been predominantly linked to visual stimuli. The speeded reaction to sound stimuli that are inherently valenced, or have acquired valence (i.e. through conditioning) has been extensively reported (e.g. Armony & LeDoux, 2010; Bröckelmann et al., 2011; LeDoux, Sakaguchi, & Reis, 1984; Wang et al., 2009). For example, using variations of the classical conditioning paradigm

whereby a neutral stimulus gradually acquires valence after its continued, reinforced pairing with an additional aversive stimulus, an animal fear conditioning study paired neutral sounds (tones) to negative stimuli (mild electric shocks) and found evidence of rapid, startle-like behavioural reactions (LeDoux, Sakaguchi, & Reis, 1984). Apart from resulting in startle-like rapid behaviours, auditory stimuli that have acquired an emotional load by being combined to emotive visual stimuli have been found to be processed earlier than other, non-valenced auditory stimuli. For example, in an EEG investigation of listeners' physiological responses to non-valenced auditory speech stimuli, Wang and colleagues found that the viewing of negative pictures (e.g. IAPS) resulted in particularly early ERPs (20ms), with these effects remaining evident up to 129ms post-stimulus offset (Wang et al., 2009). A more recent MEG study was conducted to investigate the influences of valenced tones on attention during early auditory processing (Bröckelmann et al., 2011). In this example, the authors hypothesised that valenced auditory conditioning would result in the rapid engagement of auditory attention; the authors observed that auditory target stimulus processing occurred as early as 20-50ms post negatively-valenced conditioning, and between 100-130ms following positively-valenced conditioning (Bröckelmann et al., 2011). Taken together, the above examples illustrate the rapid hold on attention that auditory stimuli paired with valenced visual stimuli seem to have. This audiovisual combination seemingly results in more efficient, approach/avoid type behaviours.

Although processing of emotional stimuli is reported as being relatively equally distributed across sensory modalities (Compton, 2003), auditory emotional stimuli in particular may be especially important in the speeded and accurate categorisation of a stimulus as biologically-relevant or not, and in having an enhancing effect on visual acuity (e.g. Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Noulhiane, Mella, Samson, Ragot, & Pouthas, 2007). For example, emotionally valenced negative sounds (i.e. looming/approaching) have been shown to significantly increase excitability of the visual cortex within a very short timescale post-stimulus (i.e. 80ms), thus suggesting potential enhancement of the preattentive properties of the combination of auditory and visual stimuli (Romei et al., 2009). The effect of sound on different aspects of attention has produced some interesting results that highlight the extent of auditory modulation on how we attend to and perceive our environment. For example, emotional sounds have been shown to affect temporal judgements, rendering participants prone to the illusion of valenced sounds lasting longer in

comparison to neutral sounds (Noulhiane et al., 2007). Earlier work had shown how emotional prosody influences the way we respond to speech (Mitchell et al., 2003) and how listening to different types of music while making judgements on the valence of a visual stimulus results in distinctly lateralised cortical activation with positive emotional attributions lateralised to left temporal regions and negative ones lateralised to right temporal regions, reflecting biased attention (Altenmüller, Schürmann, Lim, & Parlitz, 2002). Additionally, sound source location has also been shown to modulate lateralised effects in visual spatial attention. For example, Leo and colleagues compared the effects of looming and receding sounds in an orientation discrimination task (clockwise vs. counter-clockwise) using Gabor patches as visual targets (Leo, Romei, Freeman, Ladavas, & Driver, 2011). The Gabor patches appeared in either the left or right visual hemifield, with the looming/receding sounds being administered either congruently (i.e. left hemifield sound and left visual field target), or incongruently (i.e. left hemifield sound with right visual field target). The authors found that when hemifield-congruent trials were paired with looming sound stimuli, visual orientation sensitivity was increased, without, however, the converse effect shown for hemifield incongruent conditions. The effect of looming sounds was also significantly stronger than that of receding sounds, therefore suggesting that looming sounds increase participants' visual orientation sensitivity (Leo et al., 2011). The attention-grabbing properties that valenced sounds have been shown to have (Leo et al., 2011), even at a preattentive level, is consistent with the involvement of the subcortically-originating pathway through superior colliculus, pulvinar and amygdala that has been found to show increased activation during processing of valenced information in the visual domain. To draw parallels between the visual and auditory sensory modalities in the processing of valenced information, the following section will outline the subcortical pathway involved in the processing of auditory affect.

4.1.1.1 SUBCORTICAL LOCI OF ACTIVITY IN THE PROCESSING OF AUDITORY EMOTION

The establishing of the subcortical pathway involved in processing auditory emotion has been based predominantly on studies from the fear-conditioning literature. For example, studies have shown evidence for either the complete disappearance of fear-specific responses to auditory stimuli in cases of bilateral

amygdala lesions (Armony & LeDoux, 2010), or the significant decrease in fear responses in cases of left-lateralised partial amygdala lesions (Baker & Kim, 2004). When an emotional auditory stimulus is delivered, this information passes through the cochlear receptors and follows through the brainstem, auditory thalamus, and medial geniculate body route. At that point, the emotional information attached to the sound is passed to the amygdala through direct projections from the medial geniculate body ('fast route') (LeDoux, 2000). A second, slower route ('slow route'), which also transmits emotional information through to the amygdala, also exists projecting from the medial geniculate body to the auditory cortex, after which the information is sent to the amygdala (Armony & LeDoux, 2010; LeDoux, 2000) (Figure 4.1).

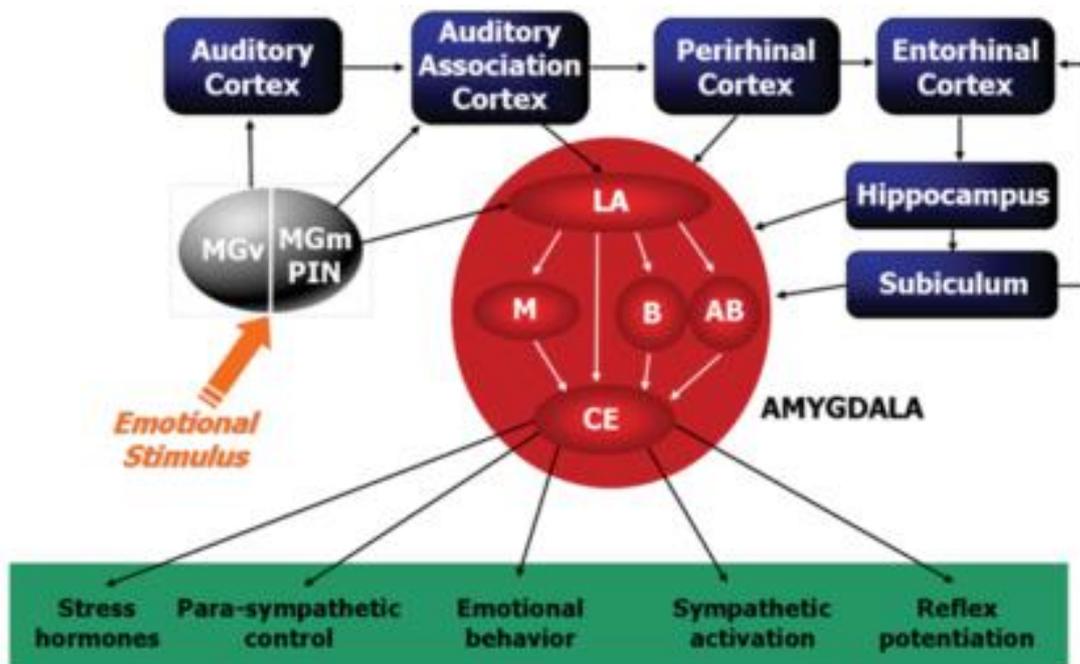


Figure 4.1 Schematic illustrating the two routes auditory emotional stimuli pass through before reaching the amygdala. After being received by the cochlear receptors, the information either travels directly from the medial geniculate body (grey oval) to the amygdala (red oval) ('fast route'), or pass through the slower route via the auditory cortex and additional cortical areas (blue route) before reaching the amygdala ('slow route'). Both routes then result in fear responses from the organism (i.e. elevation of stress hormones, reflex reactions etc.) (Figure from Armony & LeDoux, 2010).

Investigations on whether specific types of valenced sounds are more effective in activating the fast route to the amygdala are ongoing. The question of whether different types of valenced sounds (naturalistic vs. artificial) might show an equally effective activation of the fast-route to the amygdala, thus resulting in increased response efficiency has been the subject of much recent research. The following section will address this question, and suggest that looming vs. receding sounds

may represent an equally ecologically valid stimulus type to naturalistic threatening sounds in investigations of the influences of audiovisual threat on attention and response efficiency.

4.1.1.2 LOOMING SOUNDS AS ECOLOGICALLY-VALID EMOTIONAL STIMULI

Research in emotional attention has focused predominantly in the visual domain (see Ch. 3 for a discussion). Although previous sections in this chapter highlight recent work investigating emotional attention in audition (e.g. Altenmüller et al., 2002; Bröckelmann et al., 2011; Leo et al., 2011; Leonard & Cummins, 2011; Mitchell et al., 2003; Noulhiane et al., 2007; Wang et al., 2009), the range of studies using naturalistic emotionally valenced sounds (or sounds which induce an emotional physiological response in the organism) in attentional tasks is limited in comparison. The neuroimaging literature on auditory affect (e.g. Bradley et al., 2007) offers some explanation for this limitation, by suggesting that the highly dynamic nature of ecologically-valid affective sounds (such as crying) causes wide fluctuations of neurophysiological signals, thus making their processing slower than that of a visual stimulus of equal valence, even though overall the processing of visual stimuli is generally slower than that of auditory stimuli. Therefore, the necessary rapid identification of an auditory stimulus as emotional may be lengthier than that of a visual emotional stimulus, as the disambiguation of the emotional intent of a visual stimulus is near-instantaneous (Bradley et al., 2007). Work by Bröckelmann and colleagues (2011) supports the suggestion of rapid processing of valenced auditory stimuli; by utilising valenced tones instead of naturalistic auditory stimuli through associative learning, the authors reported evidence for the recruitment of selective attention subcortical networks, as well as evidence supporting the early modulation of auditory processing (Bröckelmann et al., 2011).

Similarly, Romei and colleagues had previously identified structured looming sounds as particularly attention-engaging at a very early processing stage, prior to the discrimination threshold for perception (Romei et al., 2009). Specifically, the authors combined occipital lobe TMS measures (human and primate subjects) with psychophysics measures (human subjects) for measuring changes in low-level excitability of the visual cortex and changes in perception, and observed that structured looming sounds elicited higher visual cortex excitability when compared

with controls (white noise) and with other sound stimuli (receding sounds). By examining the temporal progression of this effect, the authors established that the changes in visual cortex excitability observed in comparisons of looming vs. other sound stimuli became evident for sounds of a short duration (80ms), which were significantly lower than the detection threshold (Romei et al., 2009). As an auditory stimulus, a looming sound is defined by rapidly increasing intensity (in dB), which is thought to simulate the approaching of a threatening sound source (Bach, Furl, Barnes, & Dolan, 2015; Neuhoff, 2001). Looming sounds have been shown to significantly influence excitability of low-level visual cortex (Romei et al., 2009). Both humans and primates have been found to display heightened responsiveness to looming sounds (Bach et al., 2015; Leo et al., 2011; Romei et al., 2009), as the dynamic temporal profile of such sounds might be indicative of the sound source fast approaching towards the listener (Neuhoff, 2001). The superiority of looming sound signals over other emotional auditory stimuli has recently been conceptualised into hypotheses of a looming bias, where the auditory perceptual system is inherently biased and fine tuned to detect an implied approaching threat (Gagnon, Geuss, & Stefanucci, 2013). Comparatively to other artificial sounds, such as white noise or static sound signals, looming sounds have displayed a specific attentional advantage, which additionally influences visual attention, acuity, and perception (Leo et al., 2011; Romei et al., 2009). For example, looming sounds have been shown to influence the way subjects perceive the physical properties of a static visual stimulus; looming sounds paired with static visual stimuli resulted in the visual stimuli being perceived as larger and brighter – an effect which diminished when visual stimuli were paired with receding or static sounds (Sutherland et al., 2014). Similarly, looming sounds have been shown to influence in-depth orientation perception of point-light walker stimuli presented in frontal/back projections, whereby looming sounds biased visual stimuli in appearing more looming (i.e. looming sounds caused ambiguous walkers to appear to be walking towards the observer) (Schouten, Troje, Vroomen, & Verfaillie, 2011).

Given the early-onset influence of looming sounds on visual attention and perception (e.g. Bröckelmann et al., 2011; Romei et al., 2009; Sutherland et al., 2014), and the overall visual attentional benefits looming sounds have been shown to elicit (e.g. Leo et al., 2011) there is surprisingly little research on the potential influences of such sounds on an already emotionally valenced visual stimulus. The

present chapter therefore, will utilise looming (versus receding) sounds combined with two types of facial expressions of affect (angry versus happy), to investigate whether the combined effect of the two stimuli's increased attentional demands manifests as a lateralised response. It may be the case, that the underlying threat looming sounds may convey when paired with a negative facial expression will result in best response efficiency, particularly when the face is presented on the left visual field. This combination of threatening sound and image with the visual field location should therefore benefit a quicker and more efficient hold on attention than when auditory or visual stimuli are presented stripped of the attentional benefits audiovisual (and therefore more realistic) stimuli would allow.

Auditory threat in the form of looming sounds is a highly effective, emotionally salient stimulus that has been shown to elicit lateralised approach/avoidance responses. Given the benefits that looming sounds have been reported as having on visual attention and perception, it is somewhat surprising to find a lack of research combining this ecologically-valid stimulus to another equally ecologically significant stimulus; facial expressions of affect. When paired with an emotional facial expression, auditory threat might be expected to modulate behaviour even further, enhancing it in different patterns depending on the type of facial emotion observed (i.e. angry vs happy). Specifically, based on the valence hypothesis of emotional perception (see ch.1 for a definition), negative (angry) facial expressions displayed on the left visual field might produce quicker and more accurate responses when paired with auditory threat (looming sound), than when they appear on the right visual field. Conversely, positive facial expressions paired with looming sounds and displayed on the right visual field would elicit quicker and more accurate responses than when displayed on the left visual field.

4 EXPERIMENT 4.1

OVERVIEW

This experiment was designed to test the suggested threat localisation benefits that looming sounds combined with visual target stimuli are thought to elicit. The present experiment hypothesises that when looming sounds are paired with negative facial

expressions that are displayed on the left visual field, behavioural responses will be quicker and with higher accuracy. Conversely, quicker and more accurate responses will be elicited when looming sounds are paired with happy facial expressions that are presented on the right visual field.

4.2.1. METHODS

4.2.1.1. SUBJECTS

Twenty-three neurologically healthy adults (Undergraduate students, Department of Psychology, City University London) took part in this study (4 males; mean age: 22.3, SD: 2.1). Participants were recruited through online advertisements on the University's online experiment participation tool (SONA). Poor quality data from a further two participants were omitted from analyses due to improbable reaction times (<300ms). All participants were right-handed with normal or corrected to normal vision and had given written consent prior to testing.

4.2.1.2 APPARATUS

Laboratory setup and apparatus was the same as described in Experiment 2.1, Chapter 2. In addition, for the binaural administration of the auditory stimuli used in the present experiment, stereophonic headphones were used (Technics, model RP-F350).

4.2.1.3. STIMULI

4.2.1.3.1 VISUAL TARGET STIMULI

Visual stimuli and stimulus display dimensions, layout and lateral positioning within the display were the same as those used in Experiment 2.1, Chapter 2.

4.2.1.3.2 AUDITORY STIMULI

Two sounds, one looming and one receding, were used as auditory stimuli in the present study. Both auditory stimuli were 400Hz structural waveforms of 100ms duration each, sampled at 44kHz, with the looming stimulus rising in intensity, following an exponential amplitude profile from 55 to 75dB, and with the receding stimulus being of opposite temporal pattern with decreasing intensity from 75 to 55dB (cf. Leo, Romei, Freeman, Ladavas, & Driver, 2011; Romei, Murray, Cappe, &

Thut, 2009). Auditory stimuli were administered with equal amplitude for left and right ear.

4.2.1.4. DESIGN

Experiment 4.1 employed a 2x2x2x5 repeated measures factorial design, with sound (looming/receding), emotion (angry/happy), visual field location (left/right) and facial expression salience (1 to 5) as within-subject factors. The factors of sound, emotion, and visual field location all had two levels, while intensity had five. There were a total of 40 experimental conditions, accounting for all combinations across factors, with conditions presented in a randomised order per participant. Manual button press reaction times (ms) and accuracy scores (% correct) were the two dependent measures collected.

4.2.1.5. PROCEDURE

Testing took place in a darkened, soundproofed laboratory room and each participant was tested individually. Experiment 4.1 utilised a forced-choice visual target location identification task whereby participants viewed bilateral pairings of two photographic stimuli (one neutral and one emotional) simultaneously to receiving one of two auditory stimuli (looming or receding) through headphones. In each trial, participants were tasked with making a visual target location judgement based on which visual field the emotional photograph was presented in; auditory stimuli did not require a response. It is important to note at this stage, that for the looming and receding sound effect to be achieved, the length of the soundwave was set to 100ms with the visual stimulus display time increased from 50ms (in the previous experiments) to 100ms to match. According to Posner et al (1985), the threshold range for rapid attentional engagement – such as that expected to be at play when exposed to self-relevant emotional information – is from 50 to 100ms. Based on this established range, the expectation was that as the extended onset-offset of the visual stimulus remains within the rapid attentional engagement range, no differential effects of stimulus duration would be observed.

The paradigm rendered target location unpredictable from one trial to the next. Participants were required to respond using the left or right arrow keyboard keys

depending on whether the emotional face was presented in the left visual field (left arrow key), or right visual field (right arrow key).

A typical testing session lasted roughly 50 minutes, depending on length of breaks taken between blocks. Each testing session commenced with a practice block of 160 trials with no data collected. Upon completion of the practice block, each participant then continued to complete 5 testing blocks, each consisting of 240 trials. A total of 1200 trials were collected per testing session.

In a typical trial, a fixation point appeared at the centre of the display. Stimulus onset was initiated when participants pressed the SPACE key on the keyboard. Upon keypress, participants viewed a random pair of one emotional (of varying expression salience intensity from 1 to 5) and one neutral (intensity 0) greyscale photograph, while simultaneously hearing a looming or receding auditory stimulus. The pairing between auditory and visual stimuli was randomised in the paradigm. Stimuli were visible and audible for 100ms, immediately after which participants were required to provide a response up until 1300ms post stimulus offset. If participant responses were within this 1300ms time-window, participants would receive feedback (green circle if correct, red 'x' if incorrect). If participants failed to provide a response within the 1300ms, a blue question mark symbol appeared. Feedback or question mark symbol remained on the screen for 250ms, after which the fixation point reappeared signalling the start of the next trial (Figure 4.1)

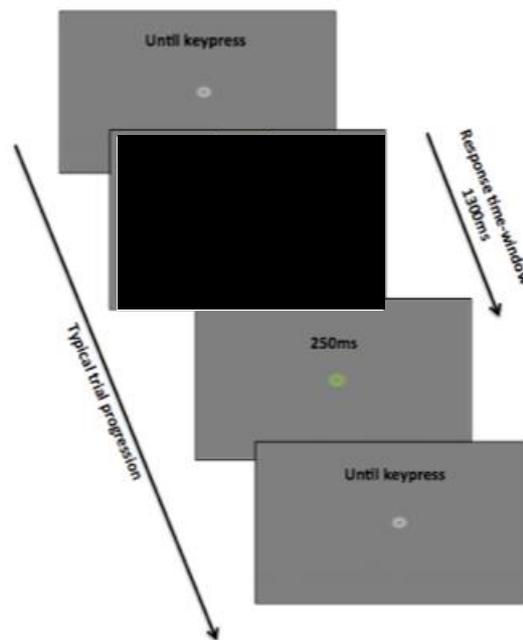


Figure 4.2. Graphic illustrates the progression of a typical trial.

4.2.1.6. DATA PREPARATION AND ANALYSIS

Raw reaction time data were filtered to exclude values from incorrectly responded to trials, as well as reaction times less or more than 2 standard deviations from the mean. Mean reaction times (ms) and mean accuracy scores (% correct) were calculated per experimental condition, per participant. Calculations were run using E-Data Aid software (E-Prime, Psychology Software Tools, Pittsburgh, MA). In the following results section values reported from variables with more than 2 levels that violated the sphericity assumption have been Greenhouse-Geisser corrected. All error bars reported represent within-subjects error, calculated using the Cousineau correction (see Exp.2.1, Chapter 2) (Cousineau, 2005; Morey, 2008).

4.3.1 RESULTS

4.3.1.1 REACTION TIME

A repeated-measures ANOVA was conducted using sound (looming/receding), emotion (angry/happy), visual field location (left/right) and expression salience

intensity (1-5) as within-subjects factors on the reaction time data. The analysis produced a significant main effect of emotion [$F(1,22)=34.5$, $p=.001$, partial $\eta^2=.6$], where happy faces were responded to quicker (mean=495, SE=15) than angry (mean=506, SE=16). A further significant main effect of sound was also found [$F(1,22)=15.2$, $p=.001$, partial $\eta^2=.4$], with the receding sound resulting in quicker responses (mean=488, SE=15.3) than the looming sound (mean=511, SE=16). A final significant main effect for expression salience intensity was observed [$F(4,88)=66$, $p=.001$, partial $\eta^2=.8$].

A significant interaction was found between visual field (left/right) and expression salience intensity (1-5) [$F(4, 88)=5.2$, $p=.001$, partial $\eta^2=.2$] (Figure 4.2), whereby left visual field stimuli produced quicker responses overall, with the largest difference observed between left and right visual field presentations for intensity 1 stimuli. Intensity 1 stimuli on the left visual field produced quicker responses than stimuli on the right visual field. Post-hoc paired samples t-tests confirmed that the interaction resulted from significant differences between left and right visual field presentations only for intensity 1 stimuli [$t=-3.1$, $df=22$, $p=.005$], whereby when shown on the left visual field were responded to quicker (mean=532, SE=19.3) than when on the right visual field (mean=554, SE=19). Comparisons between the remaining intensities in terms of visual field presentation did not reveal any further significant differences.

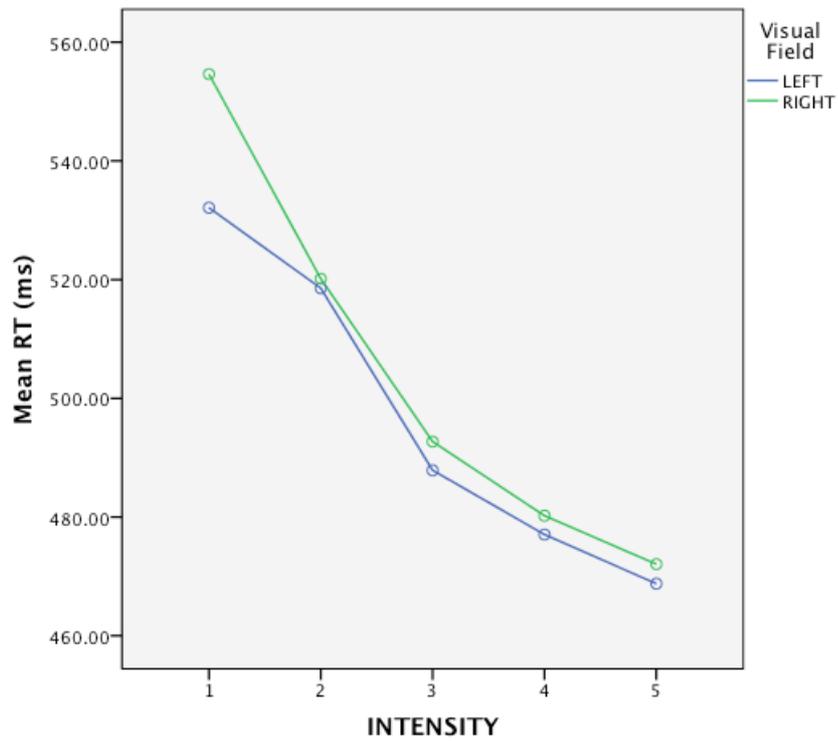


Figure 4.3. Line graph depicts left (blue line) and right (green line) visual field faces plotted as a function of expression salience intensity.

Conversely to Ch.2, no significant interaction between emotion and visual field location was observed in the reaction time data [$F(1,22)=.67, p=.5$] (Fig. 4.4).

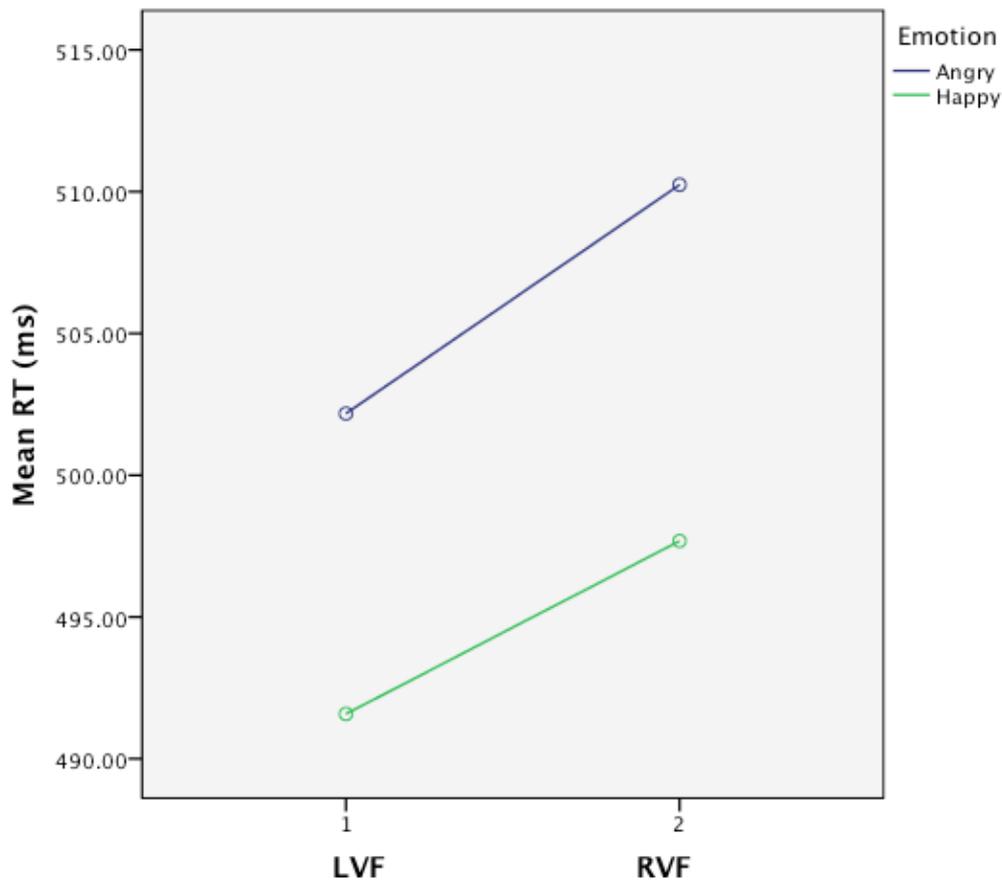


Figure 4.4. Line graph depicts angry (blue line) and happy (green line) faces plotted as a function of visual field presentation (LVF vs RVF).

A significant 3-way interaction between emotion (angry/happy), sound (looming/receding) and expression salience intensity (1-5) was also found [$F(4,88)=3.2$, $p=.02$, partial $\eta^2=.2$] where there seems to be a reversal of the emotion effect at low intensity for looming sounds, though the conditions are not significantly different (Figures 4.3, 4.4a&b). In unpacking the interaction, emotional faces paired with receding sounds were quicker overall across intensities (quicker still for happy faces). For looming sounds, happy faces produced quicker response times across intensities, with angry faces being slower overall (Fig. 4.5). Bonferonni-corrected (new p value = .002) post-hoc paired samples t-tests revealed significant differences between receding and looming sounds for angry faces in intensities 3, 4 and 5, as well as for intensities 4 and 5 for happy faces (Table 4.2). Differences were also observed between emotions (angry vs. happy) for looming sound stimuli only, across

intensities 3, 4, and 5 (Table 4.2). There were no further significant interactions for the reaction time data.

| Intensity | Stimulus | Mean | SE | t | df | Sig. |
|-----------|-------------|------|------|------|----|-------|
| 1 | AngryLoom | 553 | 18.4 | 1.5 | 22 | .2 |
| | AngryRecede | 536 | 21.6 | | | |
| 2 | AngryLoom | 534 | 16.9 | 2.3 | 22 | .02 |
| | AngryRecede | 514 | 16.3 | | | |
| 3 | AngryLoom | 512 | 16.5 | 3.4 | 22 | .002* |
| | AngryRecede | 486 | 17.3 | | | |
| 4 | AngryLoom | 497 | 15.7 | 4.4 | 22 | .000* |
| | AngryRecede | 473 | 13.3 | | | |
| 5 | AngryLoom | 486 | 14.7 | 3.8 | 22 | .001* |
| | AngryRecede | 464 | 12.7 | | | |
| 1 | HappyLoom | 563 | 18.2 | 2.4 | 22 | .02 |
| | HappyRecede | 520 | 22.2 | | | |
| 2 | HappyLoom | 525 | 17 | 2.8 | 22 | .009 |
| | HappyRecede | 502 | 16.1 | | | |
| 3 | HappyLoom | 488 | 16 | 2.6 | 22 | .01 |
| | HappyRecede | 472 | 14.2 | | | |
| 4 | HappyLoom | 480 | 15.3 | 3.6 | 22 | .001* |
| | HappyRecede | 461 | 13.3 | | | |
| 5 | HappyLoom | 476 | 14 | 3.5 | 22 | .002* |
| | HappyRecede | 456 | 13 | | | |
| 1 | AngryLoom | 553 | 18.4 | -1.1 | 22 | .3 |
| | HappyLoom | 563 | 18.2 | | | |
| 2 | AngryLoom | 534 | 17 | 1.2 | 22 | .2 |
| | HappyLoom | 525 | 17 | | | |
| 3 | AngryLoom | 512 | 16.5 | 4.8 | 22 | .000* |
| | HappyLoom | 488 | 15.5 | | | |
| 4 | AngryLoom | 497 | 16 | 4.5 | 22 | .000* |
| | HappyLoom | 480 | 15.3 | | | |
| 5 | AngryLoom | 486 | 15 | 2.4 | 22 | .02* |
| | HappyLoom | 474 | 14 | | | |
| 1 | AngryRecede | 536 | 22 | 2.1 | 22 | .04 |
| | HappyRecede | 520 | 22.2 | | | |
| 2 | AngryRecede | 514 | 16.3 | 2.3 | 22 | .03 |
| | HappyRecede | 502 | 16 | | | |
| 3 | AngryRecede | 486 | 17.3 | 2.6 | 22 | .01 |
| | HappyRecede | 472 | 14.2 | | | |
| 4 | AngryRecede | 473 | 13.3 | 2.7 | 22 | .01 |

| | | | | | | |
|---|-------------|-----|------|-----|----|-----|
| | HappyRecede | 461 | 13.4 | | | |
| 5 | AngryRecede | 464 | 13 | 2.7 | 22 | .01 |
| | HappyRecede | 456 | 13 | | | |

Table 4.3 Table lists Bonferonni-corrected (new p value = .002) multiple pairwise comparisons across the five intensity levels and compared both within the same emotion in terms of looming or receding auditory stimuli, as well as within the same sound across angry and happy visual stimuli. Stimuli highlighted in red depict quickest responses within a comparison while greyed-out rows represent non-significant comparisons. Significant comparisons are denoted by *.

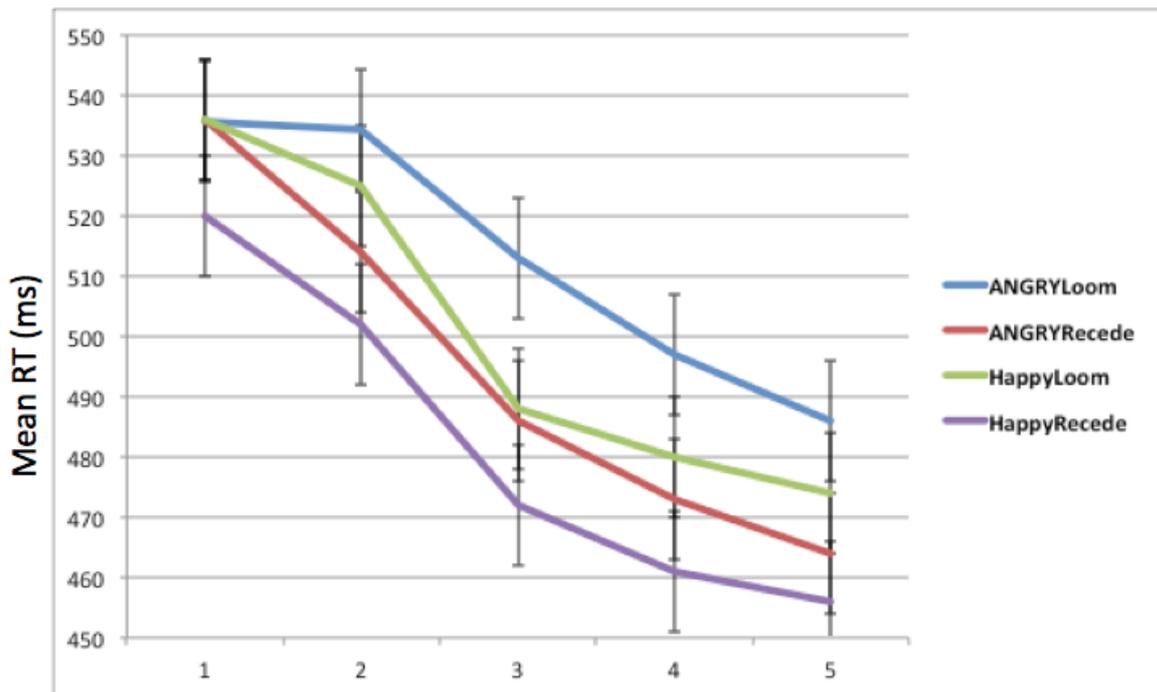


Figure 4.5. Line graph depicts reaction times per emotion/sound condition, plotted as a function of expression salience intensity. Error bars represent Cousineau-corrected +/-1 within-subjects error.

4.3.1.2 ACCURACY

A repeated-measures ANOVA with the within-subjects factors of sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) was conducted for the dependent measure of % correct scores. The analysis produced a significant main effect of emotion [$F(1,22)=35$, $p=.001$, partial $\eta^2=.6$], with happy faces scoring higher accuracy (mean=.80, SE=.01) than angry (mean=.76, SE=.01). A further significant main effect of expression salience was found [$F(4,88)=586$, $p=.001$, partial $\eta^2=.9$]. A final significant main effect was found for visual field location [$F(1,22)=5$, $p=.03$, partial

$\eta^2=.2$], where left visual field-presented stimuli produced higher accuracy (mean=.80, SE=.01) than right visual field-presented stimuli (mean=.75, SE=.01).

The accuracy data analysis also produced a significant interaction between emotion (angry/happy) and visual field location (left/right) [$F(1,22)=5.2$, $p=.03$, partial $\eta^2=.2$] (Figure 4.4). Post-hoc paired samples t-tests revealed significant differences between angry and happy stimuli for the left visual field [$t=-2.75$, $df=22$, $p=.01$] and right visual field [$t=-8.8$, $df=22$, $p=.001$] respectively. Additionally, although for angry stimuli there were significant differences between left and right visual field presentation [$t=2.5$, $df=22$, $p=.02$], where angry faces on the left visual field scored higher accuracy (mean=.80, SE=.02) than when on the right visual field (mean=.73, SE=.07), no such differences were found for happy stimuli ($p=.08$).

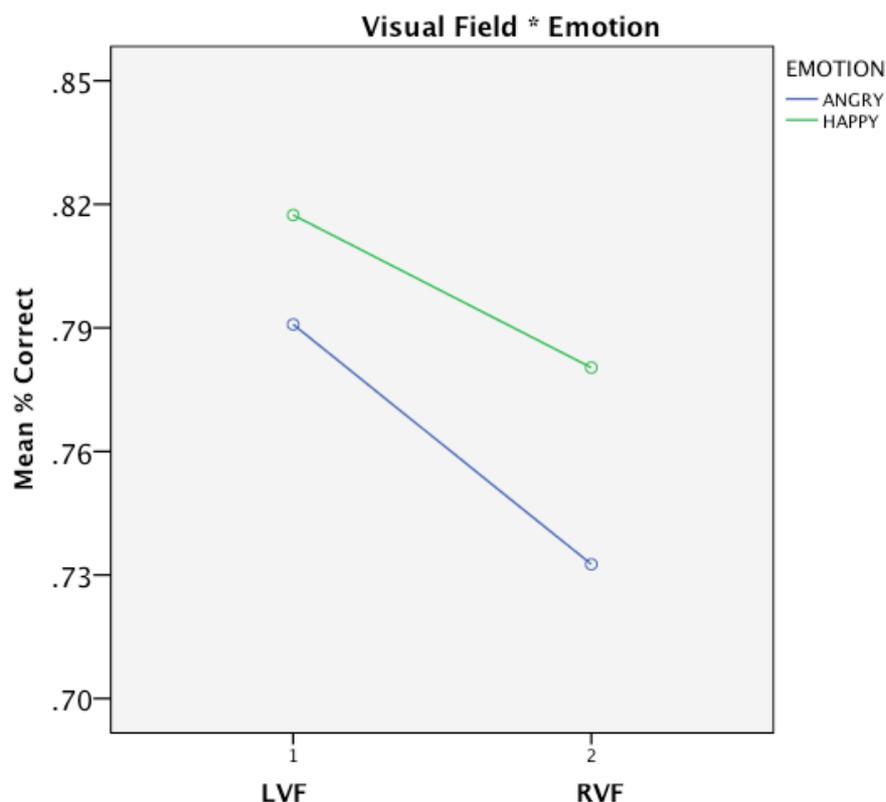


Figure 4.5 Line graph shows mean accuracy scores for angry (blue line) and happy (green line) stimuli respectively in terms of left and right visual field target location.

A further significant interaction between emotion (angry/happy) and expression salience intensity was also found [$F(4, 88)=2.6$, $p=.04$, partial $\eta^2=.2$] (Figure 4.6), with happy faces eliciting overall higher accuracy across intensities 2-5 than angry

faces. Post-hoc paired samples t-tests revealed significant differences between angry and happy stimuli for intensity 2 [$t=-5.6$, $df=22$, $p=.001$], intensity 3 [$t=-4.3$, $df=22$, $p=.001$], intensity 4 [$t=-4.2$, $df=22$, $p=.001$], and intensity 5 [$t=-3.3$, $df=22$, $p=.003$]. There were no significant differences between angry and happy stimuli for intensity 1 ($p=.4$) where performance was at chance level.

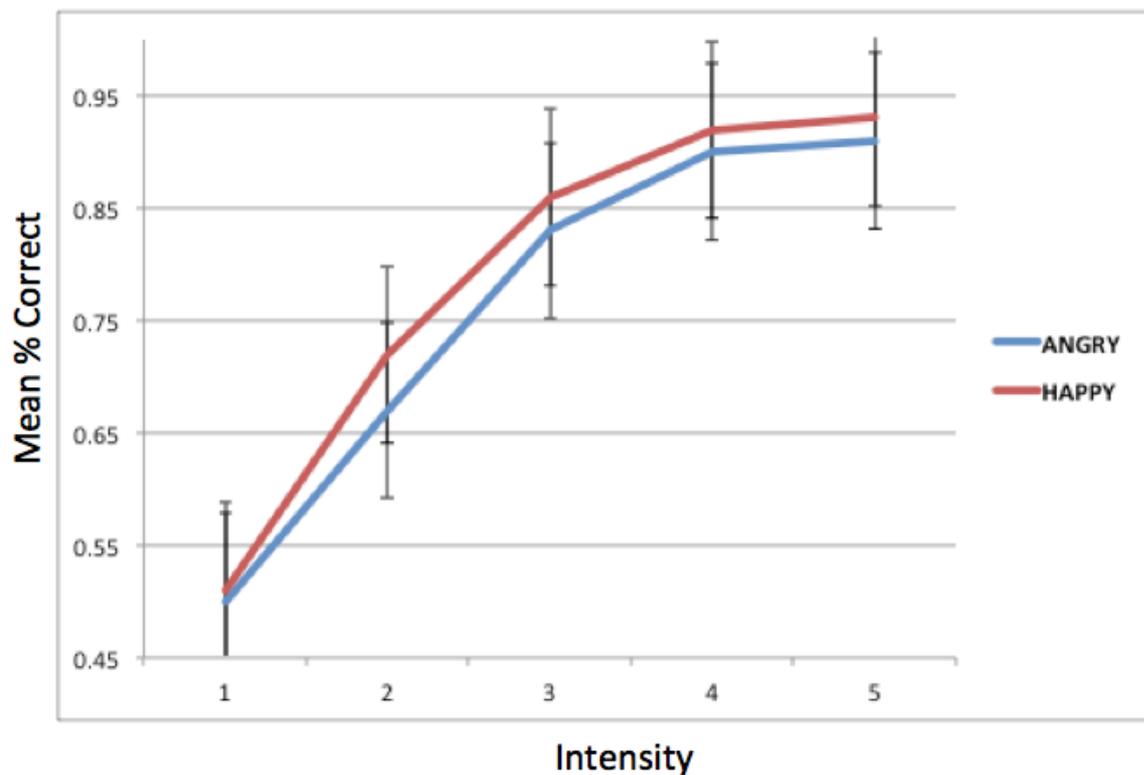


Figure 4.6 Line graph displays differences between accuracy scores for angry (blue line) and happy (red line) stimuli respectively, plotted as a function of expression salience intensity. Error bars represent Cousineau-corrected ± 1 within-subjects error.

4.3.1.3 THRESHOLD ANALYSIS

A repeated-measures ANOVA with emotion (angry/happy) and visual field location (left/right) was calculated for the threshold accuracy data. For these data, there was no significant difference between VF locations for thresholds of angry and happy faces [$F(1,22)=.3$, $p=.6$], with both angry and happy faces being accurately recognised at highly ambiguous intensities (approx. between 1.5 and 2) (Fig. 4.7)

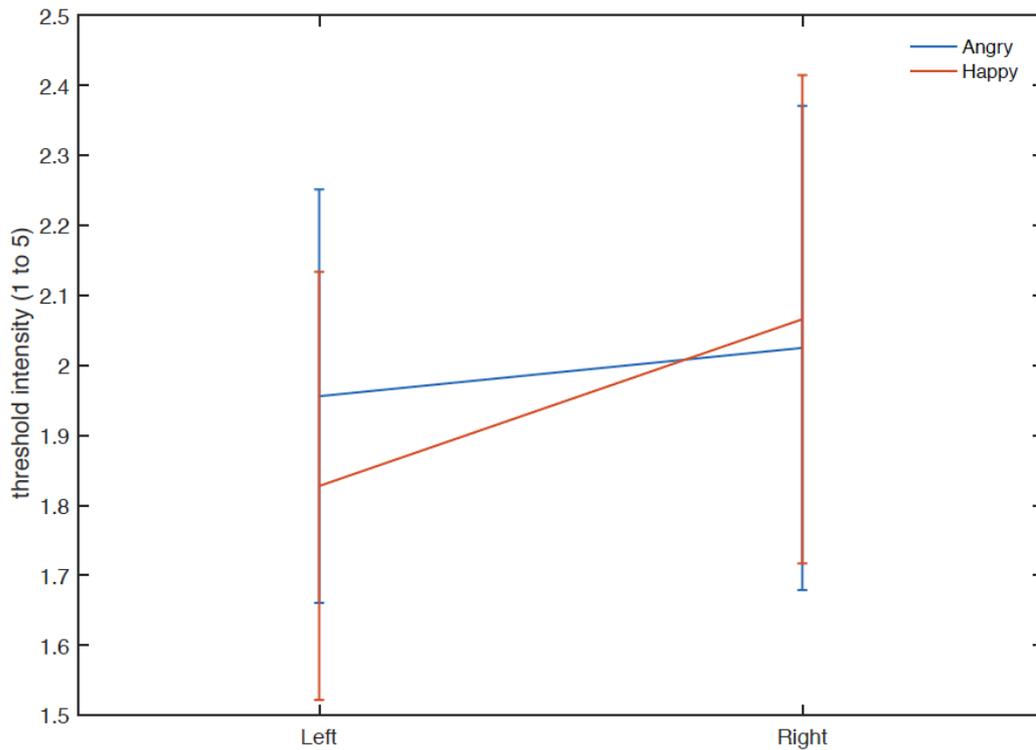


Figure 4.7 Graph displays recognition thresholds for angry (blue) and happy (red) faces respectively, depending on presentation on the Left or Right visual field.

4.3.1 EXPERIMENT 4.1 SUMMARY

Findings from experiment 4.1 confirmed predictions of sound playing a modulating role on responses to primary affect, albeit not in the direction hypothesised, and only for response times. Specifically, for the reaction time data it was the receding sound that caused quickest response times for both happy and angry facial expressions, with happy faces paired with a receding sound being responded to even quicker. This however, could be the result of the two additive main effects; the main feature of this interaction is that looming sounds appear to selectively speed angry face responses in the intensity 1 condition, thus violating simple additivity of the factors. When looking at the effects between looming and receding sounds, both angry and happy faces were responded to quicker when paired with receding sounds. A further interaction between visual field and expression salience revealed a right visual field response time bias for stimuli regardless of type of emotion or sound, but only for the lowest in salience expression (intensity 1).

The accuracy data did not provide evidence for modulation based on the presence of a looming or receding sound. For accuracy, the visual field location was shown to guide participant responses, with an overall, left visual field bias observed for both angry and happy faces. This interaction between emotion and visual field replicates isolated effects from previous experiments in the present thesis, if one discounts the overall leftward bias. Specifically, higher accuracy towards angry faces was found when on the left visual field as opposed to the right; for happy faces, the difference between visual field locations was non-significant. On the whole however, the present data do not replicate the laterality trends reported in chapter 2. One possibility may be that enhanced emotive load that the auditory stimuli add to the facial expressions overtake what may have originally been a happy-face advantage, as that observed in chapter 2. In the case of emotional stimuli tapping into additional modalities to that of vision (i.e. Expt. 4.1), accurate identification of the target may fall back to a visual field bias relative to the handedness of participants; specifically, with right-handed subjects, the contralaterally corresponding left visual field may present a stronger response bias specific to identifying the correct target location.

SECTION 2

4.1.2 MODULATING EFFECTS OF GAZE DIRECTION ON EMOTIONAL ATTENTION

In the visual domain, gaze direction is a highly-salient facial expression feature that is known to influence attentional engagement, and to modulate emotional face perception (George et al., 2001; Hadjikhani et al., 2008). The direction of gaze on a face has been suggested to be the first step in social interactions, as it signifies where the attentional resources of the observer should be directed to (N. George et al., 2001); the preliminary role gaze direction has on our social interactions has been examined in both human (e.g. George et al., 2001) and primate (e.g. Mineka, Davidson, Cook, & Keir, 1984) populations. For example, an fMRI study comparing direct vs. averted gaze in terms of their influencing properties on face perception found that neutral face stimuli with direct gaze elicited higher activity in the ventral occipitotemporal cortices of the fusiform gyrus that correlated highly with amygdala activation, a functional correlation known to be involved in emotional perception and stimulus salience (N. George et al., 2001). Conversely, the authors observed that neutral faces with gaze averted from the observer elicited an activity correlation between the fusiform gyrus and intraparietal sulcus, which has been associated with attentional shifting to the periphery (N. George et al., 2001). In another fMRI study examining the influence of gaze direction on emotional attention, Hadjikhani and colleagues compared the effects of manipulated gaze direction on attention, only for fearful facial expression stimuli (Hadjikhani et al., 2008). The authors hypothesised that the direction of gaze on a negatively valenced facial expression (i.e. fear) would act as a signal of threat in the environment, or as a cue to evoke empathy-related feelings in the observer; fearful faces with averted gaze may be suggestive of peripheral, environmental threat, whereas fearful faces with direct gaze may be evoking the observer's empathy as the fearful face is experiencing something negative. Indeed, the authors found increased BOLD activity for fearful faces with averted gaze (vs. direct) in areas responsible for processing gaze (i.e. superior temporal sulcus and intraparietal sulcus), rapid stimulus detection (i.e. left amygdala), face identification areas (i.e. fusiform gyrus, inferior temporal sulcus),

fear processing areas (i.e. left amygdala, hypothalamus, pallidum), and in motor preparation areas (premotor and motor cortices, superior temporal lobule) (Hadjikhani et al., 2008).

Specifically for negative affect such as fear and anger, gaze direction carries important threat localisation information for the self, which is crucial for deciding on the most appropriate response. Negative facial expressions are generally ambiguous stimuli, as it is not always clear whether they are communicating an experienced threat (therefore provoking empathy-related reactions to the observer), or whether they are signalling threat (therefore provoking the observer to act to avoid the implied threat) (Adams et al., 2012; Hadjikhani et al., 2008). For example, an angry face with gaze facing directly ahead, and toward the observer renders the location of the threat non-ambiguous (i.e. it is the angry facial expression that presents with the threat) (Adams et al., 2012). Conversely, an angry face with eyes gazing away does not present with the same direct threat to the observer. Manipulation of gaze direction on a fearful face however changes the directionality and attribution of the location of threat; a fearful face with eyes gazing directly ahead at the observer might signal that the threat is the observers themselves. Fearful faces with gaze directed away from the observer however, signify that threat is present within the environment, in the location where the fearful face's gaze is directed (Adams et al., 2012). This section addressed the assumption of the modulating role of direction of gaze on stimuli on emotional attention; the following section will now consider whether the modulating effect of gaze manifests differently depending on the nature of the emotion of valenced stimuli.

4.1.2.1 MIGHT THE MODULATING EFFECT OF GAZE DIRECTION DIFFER DEPENDING ON TYPE OF EMOTION?

The linkage between gaze direction-manipulated facial expressions of affect and behavioural response has been broadly interpreted through the approach/avoidance behaviour hypothesis. For example, observers encountering happy facial expressions with gaze directed towards them exhibit motivation to approach behaviours (Adams & Kleck, 2003a; Davidson, Jackson, & Kalin, 2000). However, the pattern of behavioural responses to negative affect (i.e. anger) with eyes directed to the observer is not as clear. For example, evidence suggesting action-readiness of the observer during processing of negative facial expressions with direct gaze could be conceptualised as either preparation to avoid a threat (i.e. flee) (e.g.

Hadjikhani et al., 2008), or could be interpreted as preparing the observer to engage with the threat (i.e. fight), by eliciting similar motivation to approach behaviours to those primarily observed for positive expressions with direct gaze (Adams et al., 2003b). For example, when comparing responses to angry and happy facial expressions with direct gaze, behavioural responses to both angry and happy stimuli tend to be quicker and more accurate relative to those for fearful or sad facial expressions, suggesting an overall action readiness to approach and engage with the stimulus (Adams & Kleck, 2003a); whether or not the resulting engagement will be a positive (familial, social in the case of happy stimuli), or a negative one (aggressive, confrontational in the case of angry stimuli) is irrelevant at this early processing stage.

The majority of studies in gaze direction of facial expressions focus on negative affect (i.e. fear and anger) with considerably less research conducted on the effects of gaze direction on positive affect. The overall lack of research interest in the interaction between positive affect and gaze direction has been interpreted in terms of possible methodological reasons. For example, in the behavioural literature, the majority of tasks investigating valence-specific behavioural differences commonly use emotion categorisation, or subjective interpretation of emotion tasks (e.g. Leppänen & Hietanen, 2004; Wedding & Stalans, 1985). Specifically, when happy faces were compared to negative ones (sad/disgusted) in terms of accuracy and recognition speed, a happy face response latency advantage was observed, which was maintained even when subtle, low-level physical differences between positive and negative facial expressions were controlled through utilising schematic facial expression stimuli; this response advantage was also not susceptible to stimulus artefacts arising from specific features in the happy face stimuli (i.e. upturned mouth line) (Leppänen & Hietanen, 2004). Although in general happy faces are recognised as emotional quicker and more accurately in comparison to negative affect, evidence suggests that the advantage for happy facial expressions observed particularly in studies utilising photographs of real posed expressions of affect may be the result of more low-level facial physical differences that a happy face might display, which might make it more distinctive than neutral or negative faces. For example, when comparing the ability to categorise emotions in blended facial expression stimuli of sad or angry and neutral faces to that between positive (happy) and neutral faces, inability to accurately categorise valence between negative and neutral expressions

tends to be more frequent to that between positive and neutral (Johnston, Katsikitis, & Carr, 2001). On the other hand, negative facial expressions are thought to be more difficult to pose for on demand, therefore suggesting that negative facial expression stimuli may be more heterogeneous amongst posers than those for positive facial expressions (Calvo & Lundqvist, 2008; Juth et al., 2005; Ohman, 1999). It may be the case that the comparison between a happy and a neutral face makes far less attentional demands than a comparison between a negative and a neutral emotional face when participants are required to detect emotion quickly; recognising a happy facial expression quickly and accurately requires the observer to focus on fewer facial features that deviate from a neutral expression (i.e. upturned mouth line) than recognition of a negative face that may require attending to changes in more facial features (i.e. eyebrows, mouth line, teeth) (Adolphs, 2002; Johnston et al., 2001). Before any manipulation of gaze direction has therefore taken place, happy faces are already more likely to elicit quicker and more accurate responses than negative, as the remaining physical manipulation required to portray a smile is comparatively less than that needed to portray an angry expression (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001), therefore resulting in more homogenous sets of positive/happy facial expression stimuli, compared to those portraying angry expressions.

The conceptualisation of angry affect as a form of approach behaviour in studies examining the attentional effects of the direction of gaze has been investigated in terms of their resulting behaviours. Conversely to the response pattern observed for direct gaze happy and angry faces, fearful and sad facial expressions result in quicker and more accurate responses when gaze is averted from the observer (Adams & Kleck, 2003a). For example, Adams and Kleck (2003a) tested this hypothesis in two behavioural experiments, where participants were shown facial expressions of anger and fear (study 1) and joy and sadness (study 2) which were either blended (study 1 only) (i.e. the authors used a morphing algorithm for blending anger and fear expressions in equal levels), or pure expressions (study 1 & study 2) (i.e. only anger, and only fear). The authors manipulated gaze direction to either averted (left vs. right hemifield), or directed to the observer. The facial expression stimuli were presented centrally on the display, and remained on screen until participants provided with a response in terms of whether the displayed face was angry or fearful (study 1), or happy/sad (study 2). The authors also compared the

number of emotion categorisations for the blended expressions utilised in study 1, and found that although participants labelled stimuli as fearful or angry for a roughly equal amount of occurrences when stimuli had direct gaze, categorisation of stimuli as fearful was significantly higher than that of anger when stimuli displayed averted gaze. Response latency findings from the two studies confirmed that correct categorisation of emotion resulted from an interaction between direction of gaze and emotion displayed, whereby both angry and happy faces with a direct gaze were responded to more quickly, and fearful and sad faces with averted gaze were responded to more quickly (Adams & Kleck, 2003a). A subsequent attempt to replicate Adams and Kleck's gaze direction and emotion interactions by Bindermann et al however failed to reproduce the same patterns of behavioural responses (Bindemann et al., 2008). Specifically, two experiments reported by Bindermann et al, which were designed to replicate Adams and Kleck's emotion and gaze direction interactions resulting from pure emotional facial expressions did not find significant differences between angry and fearful, or happy and sad faces as dependent on gaze direction. Bindermann and colleagues suggested that the lack of replication of the gaze-direction and emotion interactions reported by Adams and Kleck (2003a) might be a result of potential stimulus confounds (i.e. artificial vs naturalistic eye gaze manipulation); instead of utilising Adams and Kleck's stimulus set of pure facial expressions where gaze direction was digitally manipulated, Bindermann et al created their own stimulus set where posers displayed natural gaze direction variations (Bindemann et al., 2008). The non-replication of the emotion-specific interactions with direction of gaze might also be attributed to the use of experimental paradigms that allowed stimuli to remain visible until participants provided with a response, in addition to requiring participants to provide an emotion categorisation response (i.e. angry vs. fearful) (Bindemann et al., 2008, 2005). Both the lack of a response time cut-off, and the task requirement to categorise facial expressions in terms of the emotion displayed may have lead to higher-load cognitive demands, and the subsequent recruitment of more complex attentional networks than those employed in speeded detection/reaction tasks (Petersen & Posner, 2012; Posner et al., 1985; Posner & Rothbart, 2007).

Allowance for participant-led stimulus onset-offset times might also offer insight for the lack of replication. In the neuroimaging literature, the network of activated areas in response to fearful-averted gaze faces has been established as being the same

as when responding to general threat (i.e. amygdala, hypothalamus) (Adams et al., 2012; Hadjikhani et al., 2008; van der Zwaag, Da Costa, Zürcher, Adams, & Hadjikhani, 2012). In addition, amygdala responses to fearful gaze-averted faces have been shown to significantly differ depending on stimulus presentation time. For example, rapid (300ms) stimulus duration times have resulted in increased amygdala activation when gaze-averted fearful faces are displayed (Hadjikhani et al., 2008), while when stimulus presentation time is increased to 2000ms, it is fearful gaze-direct faces that elicit heightened amygdala activation (Adams et al., 2003b). In both Adams and Kleck (2003a) and Bindermann et al's (2008) work, stimuli were displayed until participants provided a response; lack of speeded responses might therefore have led to lengthier attentional engagement from participants, whereby any rapid attentional engagement specific to threat might be lost.

Finally, the inclusion of sad facial expressions in studies of gaze manipulation on emotion (Adams & Kleck, 2003a; Bindemann et al., 2008) might further complicate resulting response patterns. Sadness – although a socially relevant, basic emotional stimulus – is difficult to interpret via the approach/avoidance behavioural distinction thought to be the core mediator of any effect gaze direction has on perceiving facial expressions of affect. Differences in gaze direction of sad stimuli cannot be perceived as aiding in the localisation of rapid, biologically-relevant and immediate threat in the same way that angry or fearful faces might. Specifically, gaze-manipulated sad facial expressions might not be expected to elicit similar approach motivation behaviours to those observed with happy/direct gaze faces. Although a sad/direct gaze face might relate to higher-order, lengthier in disambiguation and processing time, and complex emotional states in the observer such as empathy (e.g. Kosonogov, Titova, & Vorobyeva, 2015), it may not tap into the same low-level, rapid-onset attentional engagement a happy face might (N'Diaye, Sander, & Vuilleumier, 2009). Taken together, the above findings seem to suggest that each type of primary facial affect, when paired with manipulated gaze (averted vs. direct), will elicit highly efficient and almost reflex-like behavioural responses that can reflect either to action to avoid, or action to approach.

4.1.3 REFLEX VERSUS REFLECT: RESPONSE PATTERN DIFFERENCES DEPEND ON DURATION OF GAZE-MANIPULATED FACIAL AFFECT

Reflexive responses to negative affect (or any variation of an emotion eliciting action readiness) are more likely to occur following rapid stimulus display times. This is because initial engagement of attention has been found to commence after 50-100ms-long stimulus display times, with displays of 300ms and longer resulting in higher-order attentional engagement (Posner et al., 1985). Additionally, when gaze-manipulated facial expression stimuli are presented peripherally (i.e. either on left or right visual field of a display) instead of centrally, the same early-onset attentional mechanisms have been suggested to be engaged in their processing (Sato, Yoshikawa, Kochiyama, & Matsumura, 2004). Similar rapid engagement of attention has also been reported in tasks utilising rapid alternations between neutral and emotional facial expressions (N'Diaye et al., 2009).

A possible explanation for this comes from the neuroimaging literature, through suggestions that methodological parameters such as rapid display time have been suggested to facilitate processing through the magnocellular pathway by prioritising visual input through it (Adams et al., 2012). The same pathway has been suggested to be involved in reflex-like orientation to potential threat (Adams et al., 2012; Vuilleumier, 2005). Recent work by Adams and colleagues has focused on presentation speed as the potential source of behavioural pattern in response to gaze averted versus gaze direct facial expressions of fear (Adams et al., 2012). The authors compared short (300ms) and long (1s) stimulus display times during passive viewing of fearful, gaze direction-manipulated stimuli, and observed a complete shifting of the amygdalar activation pattern depending on gaze direction. Specifically, in the shorter display times, subjects perceived fearful faces with averted gaze as threatening where increased activation was right-lateralised within the amygdala, whereas when longer presentation times were employed fearful gaze-direct faces were perceived as conveying threat, whereby left-lateralised amygdalar activation was observed (Adams et al., 2012). It could therefore be the case, that in order to observe reflex responses elicited as a direct result of the attentional recruitment in localising potential threat, one must enlist highly speeded stimulus exposure times. Once exposure times go beyond the 100ms threshold for preattentive properties to be elicited (Posner et al., 1985; Posner & Rothbart, 2007), stimuli pass on to

lengthier attentional mechanisms that are not representative of fight or flight reactions.

To summarise, this section has discussed evidence from the behavioural and neuroimaging literatures on the influence of gaze direction has on our ability to quickly and accurately respond to angry and fearful stimuli. Direction of gaze within a facial expression is a powerful manipulation, which has been shown to modulate behavioural patterns of response. When paired with an inherently negative emotion (i.e. anger or fear), gaze direction guides our ability to localise a potential source of impending threat, much like the localisation abilities observed when listening to looming/approaching sounds. Based on this finding and given the additional lateralised attentional benefits the valence hypothesis posits, one could predict a pattern of responses whereby angry faces paired with direct gaze and fearful faces paired with averted gaze will elicit best response efficiency when displayed on the left visual field.

Specifically, motivated by the lack of research emphasis in utilising highly salient, ecologically-valid audiovisual stimuli as modulating factors for how we process and respond to emotion, Experiment 4.2 address hypotheses of gaze direction modulation of responses to negative emotion (angry/fearful), predicted to be further modulated by presence of auditory threat (looming/receding) and visual field location.

4 EXPERIMENT 4.2

OVERVIEW

This experiment was designed to examine the threat localisation benefits gaze direction has been suggested to have on negative (angry and fearful) facial expressions of affect, when the valence of a visual target is further enhanced by the presence of auditory threat (looming sounds). Further, the present experiment will also attempt to confirm whether visual field location of negative stimuli will further enhance response efficiency, based on the valence hypothesis of emotional lateralisation. Therefore, this study hypothesises that left visual field presentations of

angry faces paired with looming sounds when gaze of the face is direct to the observer, and fearful faces with looming sounds when gaze is averted from the observer, will produce higher response efficiency.

4.2.2 METHODS

4.2.2.1 SUBJECTS

Twenty-five right-handed neurologically healthy adults (undergraduate students, Department of Psychology, City University London) took part in this experiment (6 males; mean age: 21.1, SD=2.1). As no participants produced improbable response times (<300ms) or chance accuracy judgements on the majority of trials, no participants were excluded from analysis. Participants were recruited through an advertisement on the University's online experiment participation tool (SONA).

4.2.2.2. APPARATUS

Laboratory setup and apparatus was the same as described in experiment 4.1 in the present chapter.

4.2.2.3. STIMULI

4.2.2.3.1 VISUAL TARGET STIMULI

Experiment 4.2 utilised photographs of angry and fearful facial expressions of varying salience (intensities 1-5), where gaze was manipulated into looking left, ahead, and right. Image processing for manipulating gaze direction was conducted in MATLAB, where all original photograph pupils and sclera were replaced with artificial pupils and sclera, matched for luminance and size. Specifically, for each of the 6 posers whose photographs were selected for inclusion in the present thesis (see Chapter 2 for stimulus selection procedure), control points were defined on the edges of each eye in the highest salience photographs (intensity 5). Corresponding control points were then calculated on the same eye in the same poser's neutral expression photograph (intensity 0), which were used to create a polygon mask to be applied on the eye (Figure 4.8).

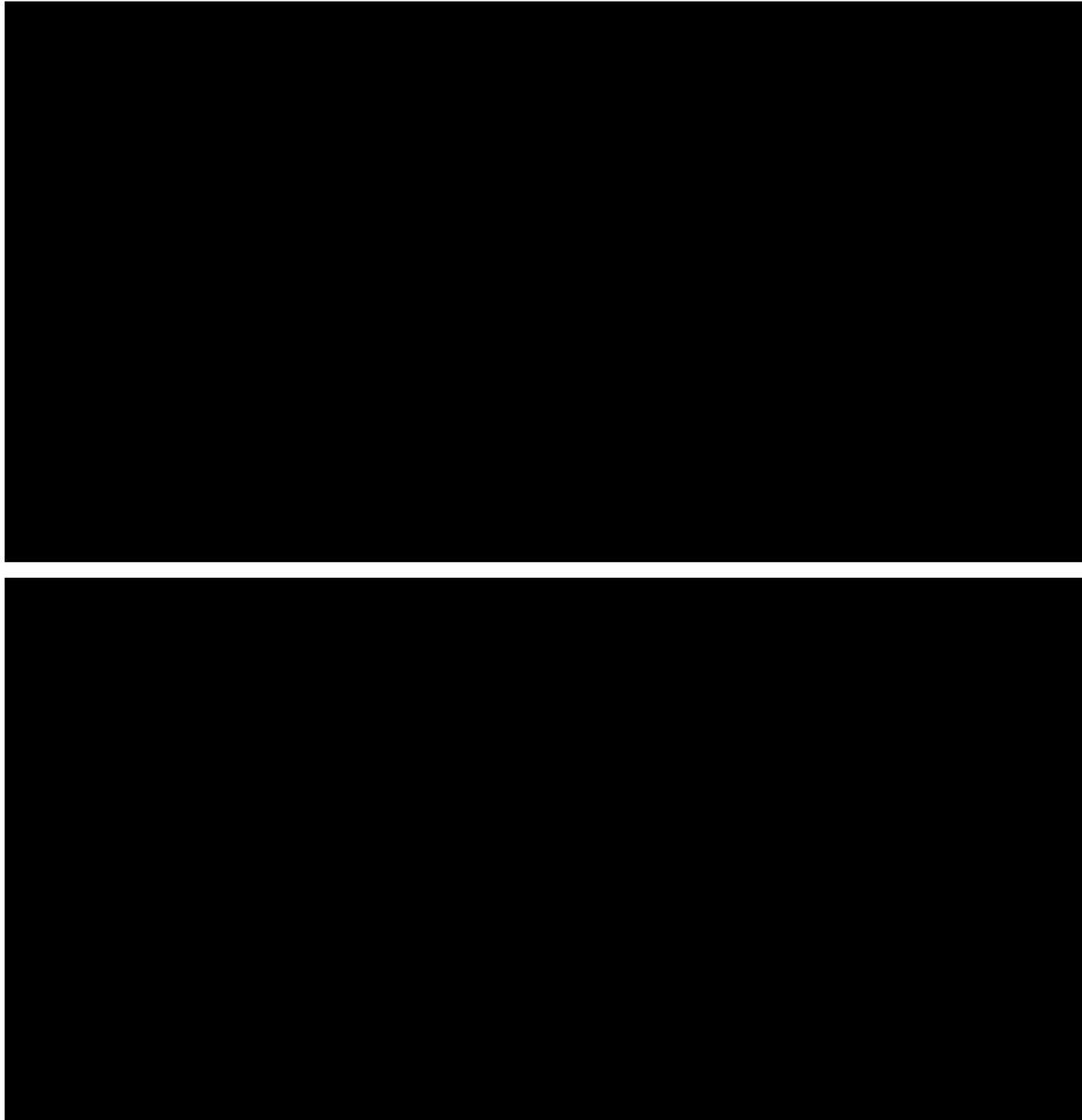


Figure 4.8 Example of eye masking procedure in preparation for manipulating gaze direction. After calculating control points around the edge of the eye in the emotional picture of one poser (bottom right square), a corresponding polygon-shaped mask was applied on the same poser's neutral photograph (bottom left square).

The eye masking procedure was applied to each expression salience intensity separately, by interpolating the control points positions between those defined for emotional and neutral photographs. Based on Calder et al's original interpolation gradations for manipulating expression intensity, the same steps from 0.25 to 1.25 were applied for interpolating control points between emotional and neutral pictures (Calder et al., 1997). The resulting polygon masks were subsequently used to cover the poser's pupil and sclera per intensity, by replacing them with an artificial image of

a dark ellipse on a light grey background which was then shifted towards the left or right (Figure 4.9).



Figure 4.9 Example ellipse on a stimulus photograph. The ellipse could be moved between a number of set points to achieve gaze direction manipulation.

Natural appearance of artificial gaze was achieved by adjusting four parameters within the context of the overall image. Specifically, pupil size was set at 14 pixels, sclera brightness was set to 0.85 (where 1 is white), gaze was offset horizontally by 8 pixels, and a low-pass filter based on a two-dimensional Gaussian kernel with a 5 pixel standard deviation was applied on each image to match it for blurriness relative to the rest of the image (Figure 4.10).

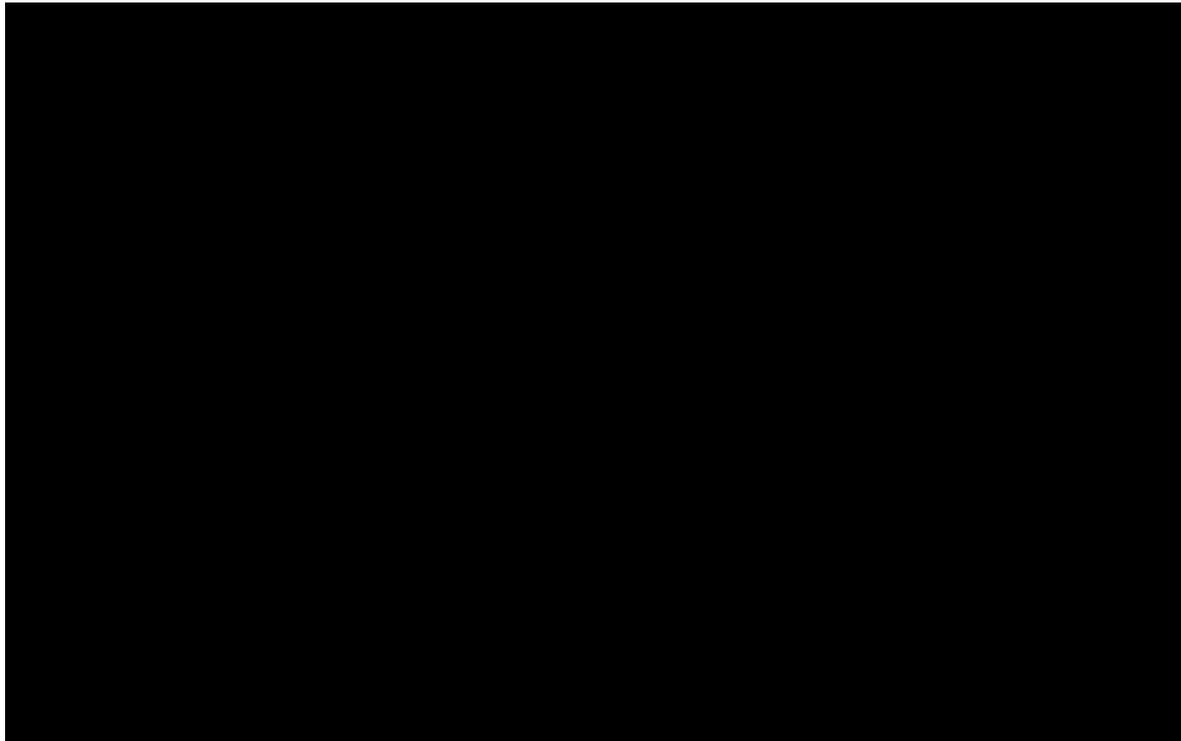


Figure 4.10 Example full set of image intensities and gaze directions from one poser. Each of the five intensities is shown as a separate column, while rows represent the three different gaze directions with gaze ahead on the top, gaze left in the middle, and gaze right in the bottom row.

The gaze manipulation procedure resulted in 15 discrete images for each of the two emotions (angry/fearful) per poser, which accounted for the three gaze directions and five levels of expression intensity. The total number of emotional expression images used was 90, accounting for each of the 6 posers selected for inclusion in the paradigm (total of 180 images for both emotions). As in experiment 4.1, visual stimuli appeared on the screen for 100ms (cf. Posner et al, 1985).

4.2.2.3.2 AUDITORY STIMULI

The looming and receding 100ms-long sounds used in experiment 4.1 were also utilised in the present paradigm, and were administered binaurally to participants via stereophonic headphones.

4.2.2.4. DESIGN

The experiment utilised a 3x2x2x2x5 repeated-measures factorial design, with gaze direction, sound, emotion, visual field, and facial expression intensity as within-subjects factors. Sound (looming/receding), emotion (anger/fear), and visual field (left/right) all had two levels, gaze (leftward/ahead/rightward) had three, and intensity had five (intensities 1-5). The within-subjects factors resulted in a total of 120 possible combinations between gaze direction, sound, emotion, visual field location and expression salience with conditions randomised across participants (total number of trials across testing blocks was 2400). Manual (button press) reaction times (ms) and accuracy scores (% correct) were the two dependent measures collected.

4.2.2.5. PROCEDURE

The testing procedure from experiment 4.1 was also applied to the present study. Each participant was tested individually, and was tasked with making a forced-choice judgement on the visual field location of the emotional face regardless of type of sound, gaze direction, or type of emotional expression (fearful vs. angry). Target location was unpredictable across trials, and participants provided responses via the right and left arrow keyboard keys, whilst the SPACE key was used to initiate stimulus delivery. In the present paradigm, both neutral and emotional photographs were always of the same gaze direction at any given trial (e.g. rightward gaze neutral paired with rightward gaze emotional).

4.2.2.6. DATA PREPARATION AND ANALYSIS

Raw reaction time data were filtered to exclude values from incorrectly responded-to trials in addition to reaction times less or more than 2 standard deviations from the mean. Mean response time (ms) and accuracy scores (% correct) were calculated per condition, per participant using E-Data Aid (E-Prime software suite, Psychology Software Tools, Pittsburgh, MA).

4.2.2.2 RESULTS

4.2.2.2.1 REACTION TIME

A repeated-measures ANOVA was conducted with gaze direction (leftward/ahead/rightward), sound (looming/receding), emotion (fearful/angry), visual field location (left/right) and expression salience intensity (1-5) as within-subject factors on the reaction time data. The analysis produced a significant main effect of sound [$F(1,24)=38.5$, $p=.001$, partial $\eta^2=.7$], where receding sounds resulted in quicker response times (mean=478, SE=24) than looming sounds (mean=495, SE=24). A further significant main effect of gaze direction was produced [$F(1.8, 45)=2.9$, $p=.05$, partial $\eta^2=.1$], where gaze ahead stimuli were responded to quicker (mean=485, SE=24) than leftward gaze (mean=490, SE=23.1) and rightward gaze (mean=487, SE=24), although gaze direction did not interact with any of the remaining factors (Fig. 4.11). The analysis also revealed a significant main effect of emotion [$F(1,24)=13.2$, $p=.001$, partial $\eta^2=.4$], with angry faces producing quicker response times (mean=480, SE=23) than fearful (mean=492, SE=23). A final significant main effect of expression salience intensity was also found [$F(1.7, 41)=5.8$, $p=.009$, partial $\eta^2=.2$].

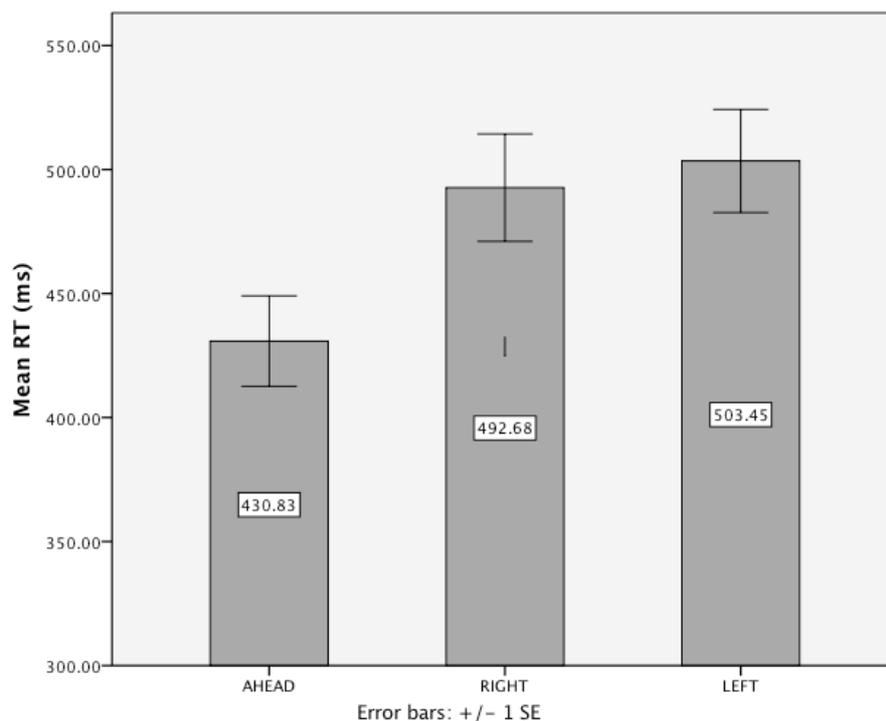


Figure 4.11 Bar chart depicts mean RT per gaze direction (ahead, right, left).

A marginally-significant interaction between sound (looming/receding) and emotion (fearful/angry) was produced [$F(1,24)=4.4$, $p=.05$, partial $\eta^2=.2$] (Figure 4.12), whereby faces paired with receding sounds produced the quickest response times, which were quicker still for angry faces. Post-hoc paired samples t-tests revealed significant differences within the same emotion in terms of looming or receding sounds for both angry [$t=3.01$, $df=24$, $p=.006$] and fearful [$t=4.5$, $df=24$, $p=.001$], with angry faces paired with the receding sound achieving quicker response times (mean=488, SE=20.5) than when paired with the looming sound (mean=497, SE=20.9). Similarly, fearful faces paired with the receding sound were responded to quicker (mean=492, SE=22) than when paired with the looming sound (mean=507, SE=22). Post-hoc analysis also revealed differences between angry and fearful stimuli when paired with the looming sound [$t=-3.51$, $df=24$, $p=.002$], whereby angry faces with looming sound were responded to quicker (mean=495, SE=21) than fearful faces paired with looming sound (mean=508, SE=21.6). However, no differences were found between angry and fearful stimuli when both were paired with the receding sound ($p=.2$).

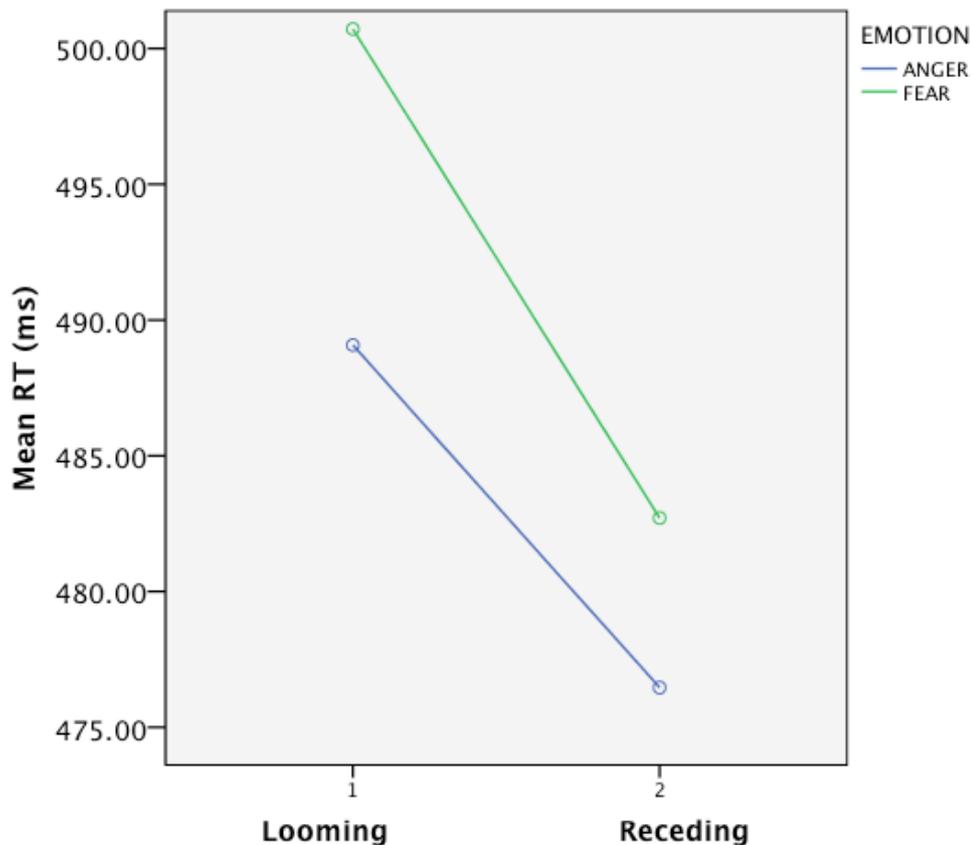


Figure 4.12 Line graph depicts mean reaction times for angry (blue line) and fearful (green line) stimuli plotted in terms of looming or receding audio stimulus pairing.

A further significant interaction between emotion (fearful/angry) and visual field location (left/right) was observed [$F(1,24)=4.4$, $p=.04$, partial $\eta^2=.2$] (Figure 4.13), whereby right visual field presentations of target stimuli were responded to quicker, which were quicker still for angry stimuli. Post-hoc paired samples t-tests revealed significant differences between angry and fearful faces when both were displayed on the left visual field [$t=-5.53$, $df=24$, $p=.001$], with angry faces resulting in quicker response times (mean=477, SE=20.2) than fearful faces (mean=500, SE=21.1). Similarly, significant differences were found when comparing angry and fearful faces when both were displayed on the right visual field [$t=-3.1$, $df=24$, $p=.005$], whereby angry faces were again responded to quicker (mean=489, SE=21) than fearful (mean=500, SE=22). No differences were observed when comparing angry faces in terms of left and right visual field presentations ($p=.2$), and similarly for fearful faces ($p=.94$).

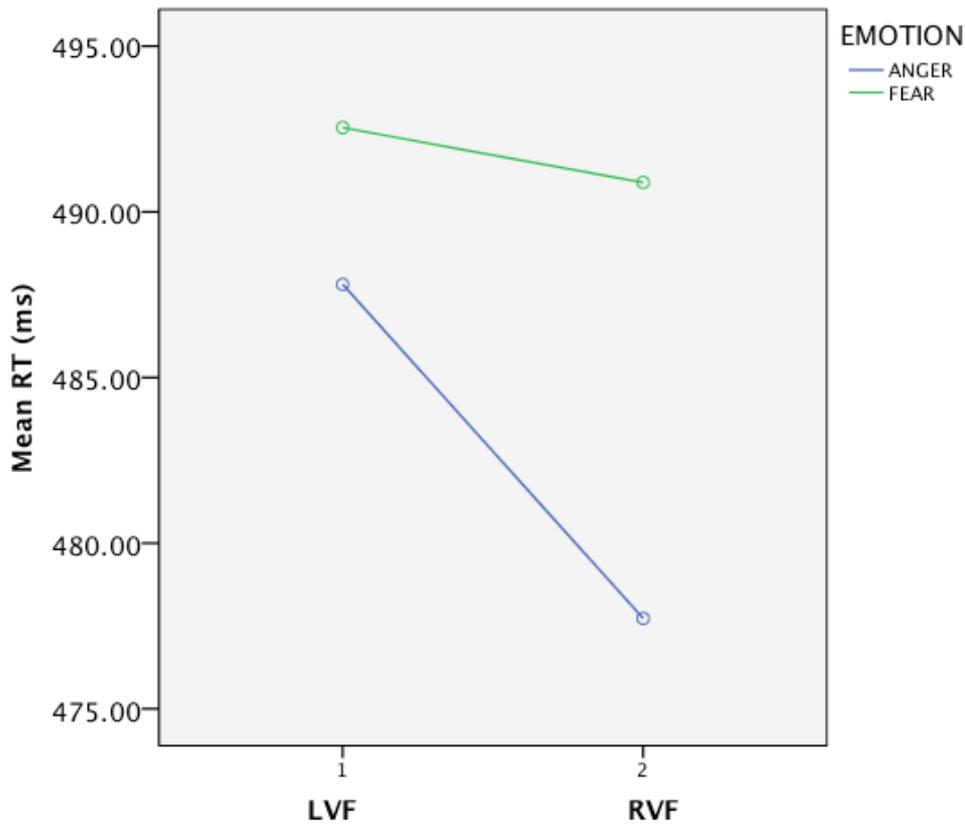


Figure 4.13 Line graph depicts mean reaction times for angry (blue line) and fearful (green line) stimuli plotted in terms of left visual field (LVF) and right visual field (RVF) visual target stimulus presentation.

4.2.2.2.2 ACCURACY

A repeated-measures ANOVA with the within-subjects factors of gaze direction (leftward/ahead/rightward), sound (looming/receding), emotion (fearful/angry), visual field location (left/right), and expression intensity (1-5) was conducted for the dependent measure of mean % correct scores. The analysis produced a significant main effect of emotion [$F(1,24)=52, p=.001, \text{partial } \eta^2=.7$], with angry faces resulting in higher accuracy scores (mean=.75, SE=.03) than fearful faces (mean=.66, SE=.02). A further significant main effect of expression intensity was found [$F(2,39)=72, p=.001, \text{partial } \eta^2=.7$].

A significant interaction between emotion (angry/fearful) and expression intensity (1-5) was also found [$F(4, 81)=11, p=.001, \text{partial } \eta^2=.3$] (Figure 4.14), whereby angry stimuli achieved overall higher accuracy across intensities. Post-hoc paired samples t-tests revealed significant differences between angry and fearful faces for

all expression intensities, with angry faces scoring higher accuracy at all intensities overall (Table 4.5).

| Intensity | Stimulus | Mean | SE | t | df | Sig. |
|-----------|----------|------|------|------|----|-------|
| 1 | Angry | .61 | .02 | 7.05 | 24 | .000* |
| | Fearful | .47 | .045 | | | |
| 2 | Angry | .71 | .11 | 6.8 | 24 | .000* |
| | Fearful | .6 | .09 | | | |
| 3 | Angry | .78 | .15 | 4.04 | 24 | .000* |
| | Fearful | .70 | .11 | | | |
| 4 | Angry | .82 | .16 | 4.2 | 24 | .000* |
| | Fearful | .76 | .14 | | | |
| 5 | Angry | .84 | .15 | 4.3 | 24 | .000* |
| | Fearful | .8 | .16 | | | |

Table 4.5 Table lists comparisons between angry and fearful stimuli across all 5 expression intensities. Significant differences were found at each intensity (denoted by *).

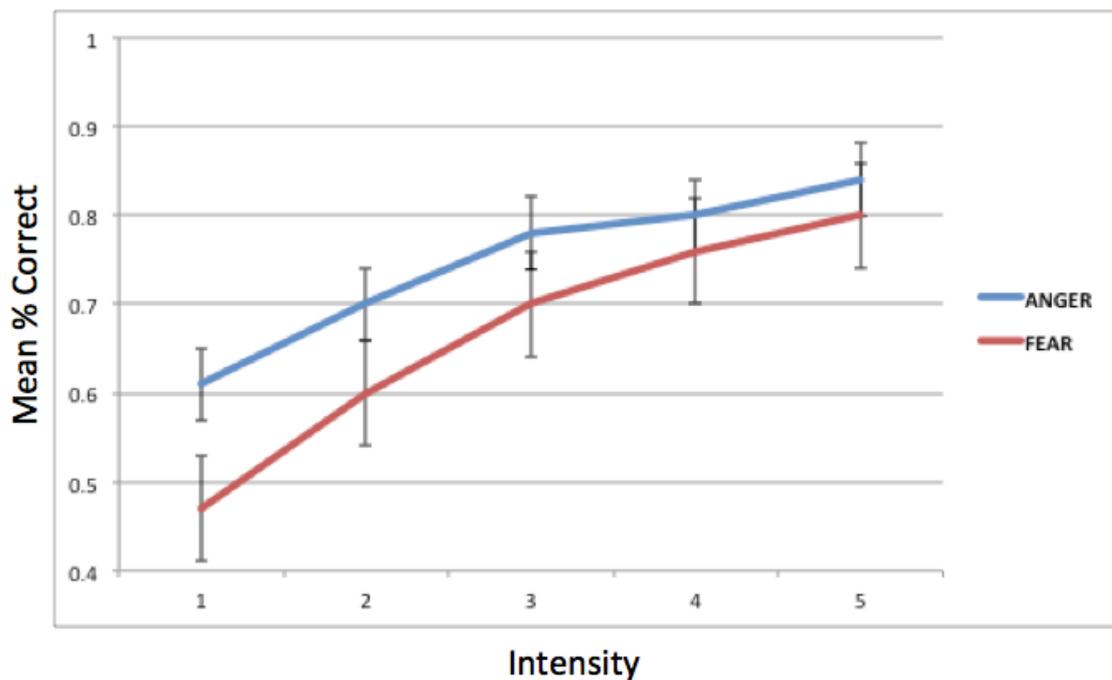


Figure 4.14 Line graph depicts mean accuracy scores for angry (blue line) and fearful (red line) faces respectively, plotted as a function of expression intensity. Error bars represent Cousineau-corrected +1 within-subjects error.

The analysis also produced a significant interaction between sound (looming/receding), gaze direction (leftward/ahead/rightward) and emotion (fearful/angry) [$F(2,45)=5.14$, $p=.01$, partial $\eta^2=.2$] (Figure 4.15), showing that looming sounds benefit left angry faces and right fearful faces, while receding sounds have the opposite effect.

When angry faces were paired with the receding sound, rightward gaze also showed higher accuracy similar to gaze-ahead faces. Fearful stimuli on the other hand displayed lower accuracy overall, with no significant accuracy advantage for averted gaze stimuli, aside from when paired with receding sounds. Unpacking of the interaction with post-hoc paired samples t-tests comparing gaze direction and emotion pairs per sound, revealed significant differences between looming angry and looming fearful stimuli for gaze ahead [$t=7.06$, $df=24$, $p=.001$], gaze right [$t=6.5$, $df=24$, $p=.002$] and gaze left [$t=8.3$, $df=24$, $p=.001$], with best accuracy for angry faces with direct gaze (mean=.77, SE=.022) as opposed to fearful (mean=.66, SE=.02), followed by angry faces with gaze-right (mean=.75, SE=.029) as opposed to fearful (mean=.67, SE=.02), and finally by angry faces with gaze-left (mean=.74, SE=.026) as opposed to fearful (mean=.65, SE=.10). Similarly, significant differences were found between receding angry and receding fearful stimuli for gaze ahead [$t=3.7$, $df=24$, $p=.001$], gaze right [$t=6.5$, $df=24$, $p=.001$] and gaze left [$t=5.7$, $df=24$, $p=.001$], whereby best accuracy was achieved by angry faces with gaze-right (mean=.77, SE=.02) as opposed to fearful (mean=.65, SE=.02), followed by angry faces with gaze-ahead (mean=.75, SE=.02) as opposed to fearful (mean=.66, SE=.02), and finally angry faces with gaze-left (mean=.74, SE=.02) as opposed to fearful (mean=.66, SE=.02). However, when comparing across sounds but within gaze and emotion, no significant differences were observed. Specifically, no differences were found between looming angry and receding angry gaze ahead faces ($p=.13$), gaze right ($p=.25$) or gaze left ($p=.2$). Additionally, no differences were found between looming fearful and receding fearful gaze ahead faces ($p=.64$), gaze right ($p=.7$), and gaze left ($p=.06$).

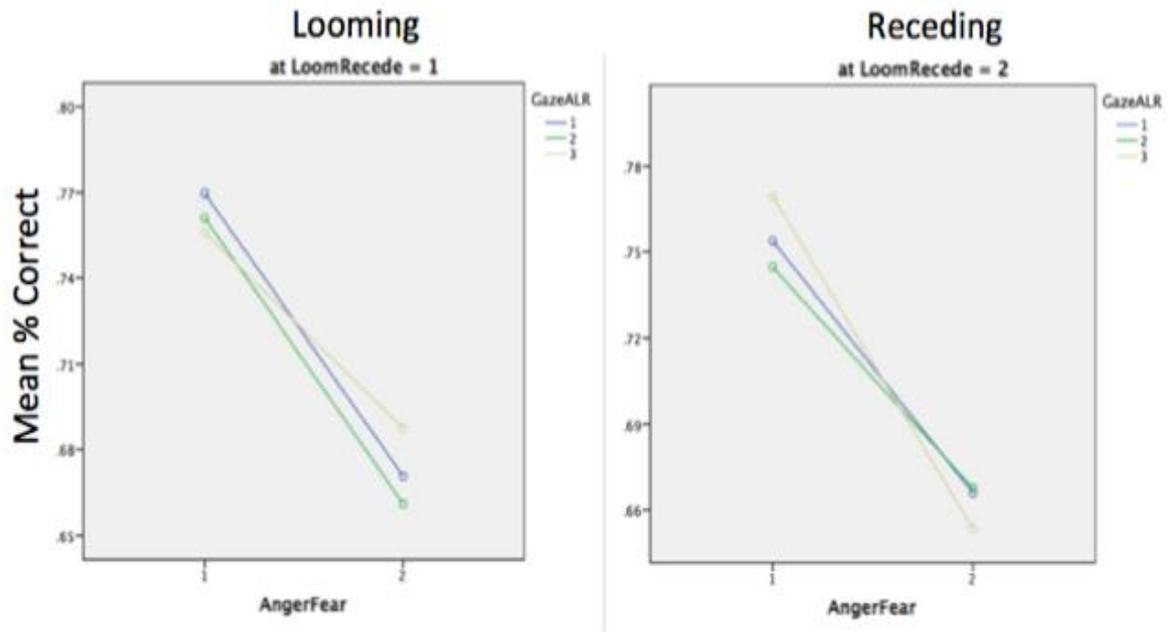


Figure 4.15 Plots display mean accuracy scores for gaze ahead (blue), gaze left (green) and gaze right (beige) to angry (x-axis 1) and fearful (x-axis 2) faces, plotted by Looming (left graph) and Receding (right graph) sounds separately.

No further significant interactions were found for the accuracy data.

4.2.3 EXPERIMENT 4.2 SUMMARY

Results from experiment 4.2 provided evidence that confirmed predictions of the modulating properties of additional, contextual factors such as auditory threat and gaze on response efficiency. For manual response times, a similar effect of sound to that observed in experiment 4.1 was found, whereby receding sounds were overall preferentially responded to. However, this was contrary to the predicted directionality of a sound effect, originally hypothesizing looming sounds as increasing response efficiency. Gaze was also found to play a modulating role for response times, whereby gaze-ahead stimuli consistently resulted in quicker response times than leftward or rightward gazing faces, regardless of emotion or additional auditory threat. In terms of emotion-based modulation, angry faces were overall responded to quicker than fearful. Hypotheses on the interplay between added threat-enhancing contextual factors and emotional facial expressions as indicative of distinctly

lateralised responses were also confirmed but only for angry faces, whereby angry faces on the right visual field elicited the quickest responses.

Accuracy analysis confirmed the angry face advantage observed in the response time data, with angry faces achieving overall more accurate responses than fearful; this effect was maintained across all expression intensity levels. Further support for the influencing role of gaze and sound onto response accuracy was also observed, as looming sounds appeared to confer an advantage for angry faces with ahead or leftward gaze compared to rightward gaze, and the reverse advantage for fearful faces with rightward gaze compared to leftward or gaze ahead. Receding sounds resulted in the opposite pattern, conferring an advantage for angry faces with rightward gaze, and for fearful faces with leftward or gaze ahead.

4.3 GENERAL DISCUSSION

Findings from the two tasks in the present chapter are the first to demonstrate distinct patterns in the modulation of behavioural responses to primary affect, when the valence of a facial expression is combined with two ecologically valid and biologically significant valence-enhancing factors; auditory threat and gaze direction. Across two methodologically comparable tasks, the modulatory effects of auditory threat were examined first independently of, and secondly in conjunction to, gaze direction in terms of their influence on response efficiency.

Albeit contrary to the original directionality of the present chapter's predictions that were based on the literature on auditory threat, receding sounds (instead of looming) were shown to significantly influence response latency overall in the sound-only experiment. Additionally, the visual field location of the target stimuli produced a right visual field bias in terms of response speed for both types of affect; for participants' accuracy however, a left visual field bias was observed but only for negative affect (angry), which was unaffected by the presence of a looming or receding sound.

The same receding sound response speed advantage was observed when the gaze-direction manipulation was introduced in the second experiment that only utilised negative facial expressions (angry vs. fearful). In this study, gaze influenced the speed of responses, whereby stimuli with direct gaze consistently resulted in quicker response times than leftward or rightward gazing faces. In terms of emotion-

based modulation, angry faces were overall responded to quicker overall than fearful. Gaze for fearful faces appeared to be depended on sound; this offers some support for the hypothesis that angry faces should benefit more from looming sounds combined with direct gaze, and fearful from averted gaze; receding sounds have the opposite effect as if they suck attention away from the self, and towards the surrounding environment. It appears as though the implied motion that receding sounds may carry drives attention away from the visual stimulus, in an attempt to localise where the potential threat may be. In this case, the averted gaze may be considered a visual cue (looking right vs. looking left) towards the site of an aggressor that is causing the stimulus fear. The right visual field bias for response speed found in Exp. 4.1 was replicated in Exp. 4.2 but only for angry faces, whereas fearful faces showed a sizeable looming advantage for rightwards gaze vs left/ahead.

Taken together, these results provide new evidence for the modulatory role that auditory threat and gaze direction may play on the behavioural responses to facial expressions of emotion. The following sections will first discuss the novel finding of receding sounds benefiting response efficiency from a methodological perspective, and will then focus on the combined modulatory benefits of receding sounds and gaze direction on response efficiency to anger.

4.3.1 METHODOLOGICAL CONSIDERATIONS

Best response efficiency was consistently observed for receding sounds, conversely to hypotheses favouring looming sounds. Evidence from the literature would suggest that looming sounds – aside from being ecologically valid stimuli due to their inherent ability to localise threat (e.g. Bach et al., 2015; Romei et al., 2009)– should facilitate a looming bias in participant responses (e.g. Neuhoff, 2001). However, present findings exhibit a different bias, present in both the sound-only study (negative vs. positive affect), and in the study combining auditory threat with direction of gaze (negative affect only). A preliminary interpretation might attribute this finding to a potential stimulus artefact. The two auditory stimuli were constructed from the same sound wave, with the only changing factor being dB intensity; to create the looming sounds intensity was rapidly increased and for the receding

sound intensity was rapidly decreased. Subsequently, due to the rapid decrease in sound intensity utilised to create the effect of a receding sound, a click or crashing-like sound effect was audible as a result. Research utilising the looming/receding manipulation combined with neutral visual stimuli recommends the addition of a 10ms stimulus onset rapid ramp-up prior to administering the auditory stimulus in an attempt to diminish the click-like sound effect caused by reversing the temporal profile of the looming sound so as to sound as receding (Leo et al., 2011). This could be incorporated in future work examining the effects of looming and receding sounds on emotional visual stimuli. On the other hand, it could be that the sudden click-like crashing sound effect in the receding sound used may have created a stronger alerting effect than the looming sound stimulus used. The resulting receding sound advantage observed in both studies therefore could be the product of an increase in vigilance, regardless of the presence of click-like sound effects. In the sound-only experiment (4.1), the presence of receding sounds enhanced the overall bias to happy faces, which was further accentuated by a right visual field bias for response accuracy. Therefore, receding sounds in this case could be seen as having played an alerting role that strengthens the right visual field lateralisation of response efficiency to happy stimuli. In the second experiment (4.2), when the valence comparison was only focused on negative affect (angry vs. fearful), receding sounds specifically benefited response efficiency to angry faces which again were lateralised to the right visual field, and were further enhanced by the presence of direct gaze. If angry and happy affect is interpreted as states that may elicit action-readiness (or even approach) behaviours, then receding sounds in this case appear to significantly facilitate preparation to act, by acting as vigilance enhancers. A final possibility however may also be that the strong effect receding sounds were seen to have on response efficiency is in fact a real phenomenon; it could be that the receding sound is perceived as signalling safety to the observer, as the auditory threat it may carry is perceived as moving away from the subject's location. This could be therefore seen as a response equivalent to the robust happy-face advantage observed in chapters 2 and 3; in this light, receding sounds could be perceived as 'safe', and therefore interpreted as positively valenced when processed through rapid attentional filters. Such an interpretation may potentially mean that across chapters 2 to 4, a strong positivity bias is observed, across the visual and auditory modalities.

4.3.2 ALERTING SOUNDS AND DIRECT GAZE MODULATE LATERALISATION OF RESPONSES TO POTENTIAL THREAT

An overall attentional advantage for threatening stimuli (be those visual or auditory) has been observed in a variety of cognitive domains. For example, a threat-advantage for angry and fearful faces has been observed in numerous visual perception tasks (Bushman & Anderson, 2001; Duncan & Barrett, 2007; Horstmann, 2007; Horstmann & Bauland, 2006), while a threat-advantage has also been found in visual perception studies using words or scenes (e.g. Fox, Russo, & Dutton, 2002; Koster, Crombez, Damme, & Verschuere, 2004; Yiend, 2010) and in studies of working memory (e.g. Jackson, Linden, & Raymond, 2014; Thomas, Jackson, & Raymond, 2014). Similarly, in studies of auditory perception, looming sounds consistently bias responses to neutral target stimuli (e.g. Altenmüller et al., 2002; Mitchell et al., 2003; Noulhiane et al., 2007; Sutherland et al., 2014). Both experiments in the present chapter provided evidence for lateralised responses that are specific to anger. In the sound-only study (exp4.1) increased accuracy was observed for left visual field angry faces. In the gaze-direction and sound study (exp4.2), angry faces on the right visual field were responded to quicker, while fearful face response times were equivocal across visual field locations, regardless of face-gaze. Angry facial expressions, regardless of presence of additional emotion-enhancing contextual information, have resulted in evidence for the preferential engagement of the right hemisphere (therefore left visual field advantage, given the contralateral nature of the visual system) (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz, & Davidson, 1981).

Given that in the present Chapter auditory stimuli were attached to an additional emotional load of varying intensity (angry/happy facial expressions), a possibility might be that receding sounds created an effect of a missed threat. Although the literature provides with examples of looming sounds biasing visual perception and acuity for neutral visual stimuli such as flashes (e.g. Grèzes, Adenis, Pougà, & Armony, 2012), point-light walkers (e.g. Schouten et al., 2011), and Gabor-patches (e.g. Leo et al., 2011), the presence of valenced visual stimuli where expression salience is gradated may require more complex processing, due to the potential additional perceptual demands necessary for their disambiguation. For example, facial expressions presented within the rapid attention threshold window (50-100ms

as ctd. in Posner et al, 1985) may result in increased alertness, as the observer would not have had sufficient time to disambiguate the valenced stimulus. Resulting responses therefore appear to be hastened, and are perhaps more representative of a rushed startle reflex. Conversely, looming sounds paired with emotional expressions usually signal danger that has not yet arrived, thus allowing the observer more time to firstly localise the source of threat, for which looming sounds are particularly helpful, and secondly prepare for action. This remains a preliminary interpretation however, as to the author's knowledge there is presently no other work utilising the looming/receding manipulation combined with the gradated valence of facial expressions.

Hastened responses for receding/emotional stimuli were found for both happy and angry faces, with happy faces being quicker overall. The happy advantage is in line with a number of cases from the literature where happy faces are consistently recognised, identified as emotional, and responded to quicker than any other type of primary affect, possibly due to the smaller number of facial feature changes that observers would need to attend to, that are present in happy facial expressions (i.e. upturned mouth lines) compared to feature changes required to depict negative facial expressions (i.e. frowning of eyebrows, showing of teeth etc.) (e.g. Fabre-Thorpe et al., 2001; Johnston et al., 2001). Focusing on the effects observed in the negative facial expressions used (anger/fear) might be more informative however. In the study examining the combined effects of gaze direction and auditory threat, the effect the receding sound had on angry faces was less pronounced to that for fearful faces, shown as quicker responses for fearful faces with receding sounds as opposed to angry. It could therefore be the case that a small looming advantage does in fact exist for anger, which is superimposed on the more general advantage from the receding sound.

When combining looming and receding sounds with manipulated gaze direction and two different negative facial expressions, receding sounds once again elicit hastened responses, which are quicker still for faces with direct gaze. This gaze effect which in the literature has usually been found to elicit quicker responses when specifically paired with angry facial expressions (Adams et al., 2003; Adams & Kleck, 2003; Marsh, Adams, & Kleck, 2005) now appears to not be influenced by the nature of observed emotion, but instead is influenced by the possibly stronger bias and increased vigilance induced by receding sounds. Specifically for anger, evidence

from Exp. 4.2 in the present chapter show that the combination of angry faces with direct gaze only enhances participants' accuracy when paired with receding sounds, with a similar benefit for fearful faces paired with averted gaze (Fig. 4.14 & 4.15). Perhaps the increase in vigilance caused by the receding sound helps disambiguate the significance of threat posed by a negatively valenced visual stimulus in a more direct way than gaze direction alone might in the absence of any auditory cues. Further research examining the effect of gaze direction in the context of a methodologically-controlled, speeded response task utilising stimuli of varying salience but without the inclusion of auditory threat would be needed however, to confirm hypotheses of a gaze direction effect that is specific to different types of valenced stimuli.

4.3.3 CONCLUSION

The present chapter has introduced novel evidence for the way in which facial expressions of affect combined with additional valence-enhancing factors interact in terms of observable behaviour. This Chapter suggests that so far, investigations on the role that auditory threat and gaze direction have on perception may have been limited either in terms of task demands (i.e. reflective versus reflex/startle responses, usage of neutral visual stimuli), or in terms of consideration of how threat naturally occurs in our environment (audiovisual information versus solely audio or solely visual). The findings presented here have provided new evidence for the influence auditory threat and gaze direction may have on the behavioural responses to facial expressions of emotion, that manifest as rushed, startled responses. These findings lead to new, testable hypotheses on how the interplay between gaze and startling sounds may affect rapid and accurate detection of emotional visual stimuli.

5 CHAPTER 5: INDIVIDUAL VARIABILITY IN ANXIETY MODULATES LATERALISED RESPONSES TO AFFECT

5.1 INTRODUCTION

The present thesis has examined lateralised behavioural patterns resulting from rapid engagement of emotional attention, and their dependence on specific perceptual and contextual emotional attention-manipulating factors, such as monocular viewing conditions (nasotemporal hemifield asymmetries), presence of auditory threat (looming vs. receding sound), and gaze direction (direct vs. averted gaze) of emotional facial expressions. Evidence from experiments in the present thesis so far suggest that lateralised behavioural responses to the detection of facial expressions of basic affect resemble rapid, reflexive reactions. This suggestion contributes to our understanding of the lack of consistent replication of patterns of lateralisation found in the behavioural literature (see Ch.1 for a discussion). Usually, behavioural investigations of emotional perception have measured participants' subjective categorisation, labelling and interpretation of emotional stimuli (e.g. Carver, 2004; Eder, Hommel, & De Houwer, 2007; Fox, Russo, & Dutton, 2002), which in their majority point to right-hemisphere unilateral engagement (Rolls, 1990), instead of preferentially engaging the right or left hemisphere depending on the nature of the emotional stimulus observed (Reuter-Lorenz, & Davidson, 1981). However, by utilising a speeded target location identification task that can elicit rapid, reflexive responses, experiments in the present thesis have established a dynamic lateralisation pattern that has been found to be prone to modulation by contextual elements incorporated in the presentation of stimuli.

One additional potentially modulating factor that might influence lateralisation of response efficiency is that of individual differences, and more specifically variability in terms of individual anxiety levels. Until now, research on individual variation and emotional perception has predominantly focused on either clinical or high comorbidity sub-clinical populations by investigating the underpinning biology of disordered behaviour and perception (i.e. schizophrenia, alexithymia, depression, bipolar disorder) (e.g. Bediou et al., 2007; Berthoz et al., 2002; Graham & Labar,

2012; Gray, 2001; Helzer, Connor-Smith, & Reed, 2009; Liotti et al., 2000; Reker et al., 2010), or has utilised secondary, social emotions (see Ch. 1 for a definition) and personality variables (i.e. empathy, extroversion, introversion etc.) (e.g. Canli et al., 2001; Duncan & Barrett, 2007; Gruzelier & Phelan, 1991; Kosonogov, Titova, & Vorobyeva, 2015; Singer et al., 2004) that reflect higher-order, complex cognitive functions. However, very little work has been conducted in investigating the relationship between non-clinical behaviour (i.e. high-anxiety individuals) and the ability to efficiently detect basic emotion by looking at how this relationship might translate into observable behaviour. Across the few examples from the literature that have investigated individual variation based on personality traits and basic emotional perception, the methodologies applied typically utilise median split participant groupings, that potentially fail to partial out individual micro-differences that might have otherwise influenced the pattern of findings, and often task participants with the passive viewing of valenced stimuli therefore not considering resulting effects on behaviour, or with the subjective classification of affect which does not optimally engage pre-attentive processes (e.g. Grèzes, Adenis, Pouga, & Armony, 2012; Pouga, Berthoz, De Gelder, & Grèzes, 2010). Individual variability that is often dismissed as noise in the data might –in the case of rapid, early-onset emotional perception – be of key importance in our understanding of human behaviour and responses to emotional stimuli at a very basic, ontologically old level. Furthermore, the link between detection and response to primary affect, and the suggested rapid attentional engagement initiated by facial expressions of primary affect may be more readily detectable when looking at personality traits that stem from a similar increase in arousal, vigilance, and startle responses such as anxiety. The final experimental chapter in the present thesis will therefore focus on the effects of individual anxiety variability on response efficiency, as a modulating factor in the complex, dynamic process of behavioural lateralisation resulting from rapid exposure to facial expressions of primary affect. In the following sections, the present chapter will first review the literature reporting on the influence of individual variability on emotional perception overall, and will also consider the neurological correlates of emotion-driven individual variability. The chapter will then review the evidence for the influence of anxiety on the way we perceive and respond to emotional stimuli, and will finally consider how individual anxiety variability may manifest in lateralised behaviour.

5.1.1 INDIVIDUAL VARIABILITY AND EMOTIONAL PERCEPTION

Historically, both neuroimaging and behavioural bodies of research on emotional perception have produced inconsistent results regarding neuronal activation and behavioural response patterns during the processing of basic affect. A number of explanatory arguments have been brought forward in an attempt to account for the divergence in findings. Specific to the neuroimaging emotional perception literature for example, one argument suggests that it is the difference in spatial and temporal resolution between different neuroimaging techniques (e.g. fMRI, PET etc.) in addition to differences between each technique's sensitivity that might account for the lack of consistent reporting of the same activation networks during emotional perception (Eugène et al., 2003; Schneider & Kastner, 2005). Another argument addresses the somewhat heterogeneous participant populations recruited for experimental studies; for example, there are a number of studies highlighting gender differences in emotional perception as the primary cause for result pattern discrepancies (e.g. George, Ketter, Parekh, Herscovitch, & Post, 1996; Lane et al., 1997; Wager, Tor, Phan, Luan, Liberzon, & Taylor, 2003), although there is some reservation as to whether gender differences are enough to fully justify the divergence between results, as there have been a number of gender differences studies using similar methodology and same-sex samples but have still resulted in different patterns of results (Eugène et al., 2003). A final suggested argument is that of the difference between artificially inducing the emotion under investigation to participants (i.e. via the watching of valenced films or photographs) and that of inducing a subjective, actual experiencing of the emotion to participants. Either task requirement can prove to be somewhat problematic; for example, studies where participants were asked to experience an emotion usually require participants to think back to an autobiographical event of the same valence (i.e. think back to a happy occasion so as to elicit happy affect during testing) (e.g. Damasio et al., 2000; Liotti et al., 2000) had been suggested to tap into a slightly different emotional neurological substrate to that reported in studies using artificial evocation of an emotion through film excerpts or photographs (Reiman et al., 1997). Such big methodological differences offer an explanation for the discrepancies in findings. Nonetheless, this is where individual differentiation in personality traits might play a key role; given that individual differences in neuronal activation when perceiving

affect have been consistently reported in a number of neuroimaging studies (e.g. Canli et al., 2001; Canli, Desmond, Zhao, Glover, & Gabrieli, 1998; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002), it might be the case that individual variation can be considered as an additional modulatory factor responsible for the inconsistencies in emotional perception and response findings.

Perception and behaviour vary across individuals. Aside from being adaptive to the type and self-relevance of environmental stimulation experienced, to a great extent they are also shaped by our own unique individual personality characteristics. One's decision to fight or flee in the presence of danger, the detection speed and accuracy of emotional information, the ability to manage impulses, and the regulating and control of emotional reactions can be influenced by a number of personality traits (i.e. extroversion, introversion); at the point where these traits surpass the level where they do not severely impact day-to-day social interaction, perception can become distorted, and behaviour can become disordered. The relationship particularly between emotion regulation and symptomatology has been well documented in the clinical diagnostic literature. For example, symptoms such as inappropriate affect, avoidance, and lack of emotion regulation have been found to be prevalent in individuals with emotional deregulation resulting from generalised anxiety disorder or depression (Cole, Michel, & Teti, 1994).

Aside from clinically diagnosed cases of personality and mood disorders however, it is possible that sub-clinical behaviour can still be susceptible to variability, depending on the prevalence of certain personality traits. Although individual variation is usually filtered out (through averaging) from analyses as it is thought to constitute noise in the data, more recently a small proportion of research has utilised individual differences data to study the underlying basis of basic cognitive functions such as perception (e.g. Gaser & Schlaug, 2003; Maguire et al., 2000; Sluming et al., 2002; Whitford et al., 2011), motor control (e.g. Johansen-Berg, Della-Maggiore, Behrens, Smith, & Paus, 2007; van Gaal, Scholte, Lamme, Fahrenfort, & Ridderinkhof, 2011), and decision making (e.g. Forstmann et al., 2008; Ivanoff, Branning, & Marois, 2008). The influence of individual differences in the behaviour of atypical individuals has been investigated in a variety of perceptual and behavioural domains. For example, research from the behavioural neuroscience literature has suggested that personality traits might predict differential hemispheric engagement in the visual domain, which translates as enhanced performance depending on visual

field presentation of stimuli (Heller, 1993; Levy, 1983). The assumption that individual personality differences are closely associated with visual field asymmetries is not new. For example, research investigating stable personality characteristics and cognitive performance has provided evidence showing distinct cerebral engagement asymmetries as dependent on personality, whereby increased cognitive performance from the left visual field correlated with participant extraversion and optimism, while increased performance from the right visual field correlated with participant introversion and pessimism (Heller, 1993). Levy and colleagues provided evidence for participants with pessimistic personality traits showing better performance in the right visual field, while participants with optimistic personality traits elicited better performance in the left visual field (Levy, 1983). In the EEG literature, asymmetries based on individual personality differences have also been reported in terms of lateralised activity and emotion regulation. For example, Jackson and colleagues reported results from a study tasking participants to view valenced and neutral stimuli where startle probes were presented after each visual stimulus presentation. The authors found that participants who showed increased left-lateralised anterior activation, also displayed increased startle magnitude following the display of negative stimuli (Jackson et al., 2003). Altogether, the above cited work points to the importance individual variability in personality traits has not only on emotional perception, but potentially as a modulating factor in the lateralisation of observable responses. The following section will therefore focus on the neurological basis of individual variability during the processing of affect, as a segue to drawing parallels between anxiety and responses to emotional stimuli.

5.1.1.1 NEURAL UNDERPINNINGS OF INDIVIDUAL DIFFERENCES IN EMOTIONAL ATTENTION

Individual differences have been investigated in studies looking to identify sensory discrimination thresholds (Andrews, Halpern, & Purves, 1997), as well as in measurements of structural differences in early-onset sensory processing pathways (i.e. lateral geniculate nucleus and primary visual cortex) (Westlye, Grydeland, Walhovd, & Fjell, 2011). Findings from such investigations point to a neuroanatomical link between individual variability, and differences in size of subcortical structures, grey matter volume, and magnitude of cortical activation during basic sensory processing (Kanai & Rees, 2011). Studies focusing on grey-

matter volume individual differences utilise MRI techniques such as voxel-based morphometry (VBM) to correlate grey matter volume differences to differences in perception (e.g. Forstmann et al., 2008; van Gaal et al., 2011). This methodology is not however without its limitations. Specifically, the cellular foundation of alterations in grey matter volume has not as of yet been fully established, and the cellular variations that may cause volume increases whilst being detectable and measurable through MRI are not fully understood (Kanai & Rees, 2011). Additionally, VBM studies attempting to correlate behavioural individual differences to brain structure would require very large numbers of participants, and the resulting correlations would need to be particularly strong for any inferences between structure and function to be made (Kanai & Rees, 2011).

The relationship between grey matter volume and perception stretches to studies on attention. For example, by using the attention network test (ANT) to investigate orienting, alerting, and attentional control, studies have provided evidence for changes in cortical thickness in brain regions associated with control and alerting (e.g. Westlye et al., 2011). Other examples from this portion of the attention literature have linked individual differences to genetic variations; when combined with individual social experience, genetic variability produces significant differentiation in attentional network activity (Petersen & Posner, 2012).

Individual differences have also been found to significantly influence aspects of emotional perception, including emotional attention, emotional responses, and subjective experience. For example, early behavioural work by Tucker and colleagues noted that individual variability in emotional state produced significant differences in the operation of attentional arousal (Tucker, 1981). Although the majority of conclusions on the loci of neuronal activity involved in emotional perception comes from group analyses that partial out specific individual variability, the subjective emotional experience, perception, and reaction time have been found to be subject to elements of one's unique personality traits (Hamann & Canli, 2004; Schaefer et al., 2002). This research domain has provided evidence for strong correlations between variability in personality, and activity in prefrontal and limbic brain regions during processing of emotional information (Hamann & Canli, 2004). Work by Schaefer and colleagues showed that when participants were tasked with maintaining their negative emotional experience following exposure to negatively-valenced photographs, participants who reported high negative affect also exhibited

equivocally high amygdala activation (Schaefer et al., 2002). Additionally, based on data from two fMRI studies, Canli and colleagues reported increased amygdala activation in high extroversion participants following exposure to happy facial expression stimuli, while also reporting strong correlations between neuroticism and extroversion and amygdalar activation as a function of exposure to positively and negatively valenced facial expression stimuli (Canli et al., 2001; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002).

Individually variable responses have also been found in studies of higher-order, and more socially complex affect such as empathy. For example, when comparing activated areas during self-experienced pain and those activated during empathic reactions for a loved one experiencing pain, Singer and colleagues reported that the activation level in areas for self-experienced pain such as anterior cingulate cortex and insula, strongly correlated with the level of individual empathy (Singer et al., 2004). Lastly, evidence from studies in activation resulting from arousal in sub-clinical populations such as alexithymics (i.e. alexithymia has been defined as an impairment of the ability to identify and communicate one's emotional state) have reported less left-lateralised hemispheric activation displayed by alexithymic participants when viewing negative, high-arousal stimuli, whereby less activation in the left mediofrontal cingulate cortex was observed, comparatively to the control group (Berthoz et al., 2002). During high-arousal positive stimulus presentation however, alexithymic participants displayed increased activation in anterior cingulate, mediofrontal cortex and in the medial frontal gyrus compared to non-alexithymic participants (Berthoz et al., 2002).

5.1.2 ANXIETY AND EMOTIONAL PERCEPTION

Anxiety has featured prominently in the behavioural literature of emotional perception. As a physiological state with direct manifestations in observable behaviour, anxiety has been shown to influence our attention, emotional and physiological arousal in response to self-relevant environmental stimuli, aspects of memory processing, and reasoning (Beck, Emery, & Greenberg, 2005). Specifically in the emotional perception literature, anxiety has been often utilised as a modulating factor in the eliciting of a suggested attentional bias for threatening stimuli (e.g.

Bradley, Mogg, & Millar, 2000; Mogg, Bradley, Williams, & Mathews, 1993; Mogg, Bradley, De Bono, & Painter, 1997). The attentional bias that threat-related stimuli are suggested in inducing (Horstmann & Bauland, 2006), translates as a propensity to preattentively perceive threat, potentially before the stimuli inducing are past the detection threshold; this effect would be further accentuated when individuals with high anxiety levels respond (Mogg et al., 1993). The suggestion of a preattentive processing of threat has also been identified independently to correlations with individual anxiety (e.g. Horstmann & Bauland, 2006; Horstmann, 2007). It may therefore be the case that anxiety would further promote threat-processing by automatically drawing attention towards threatening environmental information (Mathews & Wells, 1999; Mogg, Garner, & Bradley, 2007).

The relationship between individual anxiety and threat perception has been investigated in the neuroimaging literature, which has reported a wide variety of results regarding relative subcortical activation. For example, one study examining amygdala activation specific to threat perception that has utilised participant anxiety groupings (high, medium, low) reports bilateral dorsal amygdala activation specific to angry facial expressions that was however only specific to male participants with high anxiety (Carré, Fisher, Manuck, & Hariri, 2012). An earlier fMRI study also looking at relative amygdalar activation during threat perception reported that high anxiety participants, regardless of gender, showed increased activity during exposure to fearful faces (Bishop et al., 2004). Evidence for the influence of a possible attentional bias relating to threatening stimuli that also correlates with anxiety have also been reported in studies using valenced word stimuli. For example, in a study using a valenced version of the Stroop task, Van Strien and Valstar reported evidence for high anxiety female participants showing left visual field-lateralised interference resulting from positively valenced words and right visual field-lateralised interference resulting from negatively valenced words (Van Strien & Valstar, 2004).

Similar to the criticisms of the behavioural literature on emotional lateralisation the present thesis posits in previous chapters, research on the potential advantageous processing of threatening stimuli in relation to individual anxiety is prone to similar kinds of methodological limitations. For example, although the theoretical suggestion of preattentively processing threat requires an almost automatic processing of negative stimuli, the majority of neuroimaging studies investigating this claim either

display stimuli until participants supply a response, or set the response cut-off point to range from 4 to 10 seconds (e.g. Bishop et al., 2004; Carré et al., 2012; Cooper, Rowe, & Penton-Voak, 2008), whereby usually the threshold for rapid attentional engagement which would be expected to be at play during exposure to emotional, environmentally-relevant stimuli ranges between 50-100ms (Posner et al., 1985). Additionally, current investigations in this field require participants to subjectively classify emotional expressions for the stimuli observed (e.g. Bishop et al., 2004; Cooper et al., 2008), or to passively observe negative, positive or neutral pictorial stimuli (e.g. Carré et al., 2012), whereas the preattentive and near-automatic rapid processing of such valenced stimuli would potentially necessitate the rapid engagement of localising attentional networks as opposed to passive perception or subjective classification with no incentive to respond – an effect which should be even larger in magnitude once high anxiety levels are taken into account. Lastly, although theoretically informative, current research correlating anxiety to cognitive function and subsequent response overwhelmingly relies on participant anxiety groupings, therefore not considering the wide differentiation that individual anxiety levels show in the data. This is an often overlooked but important aspect of human differentiation that is often attributed to outlier/extreme values in a dataset and filtered to present with more normally distributed sample scores; disregard of micro-differences in emotional perception and response however ultimately takes away from the overall psychological significance of results reported based on generalised effects.

5.1.3 MIGHT INDIVIDUAL DIFFERENCES IN ANXIETY LEVELS PREDICT PATTERNS OF RESPONSE EFFICIENCY?

Participant anxiety levels have been shown to significantly influence activation of the neural network responsible for the processing of threat (Mogg et al., 2007). When examining the orientation of gaze towards angry and fearful faces where salience and stimulus face gaze direction were manipulated between a high-anxiety and low-anxiety sample sub-groups, the authors observed that high anxiety participants tended to direct their gaze towards high-salience angry expressions compared to low anxiety participants, with no differences found across groups for fearful expressions (Karin Mogg et al., 2007). Early evidence from the neuroscience literature highlights the significant influence that individual emotional states can have

on activation of attentional arousal and vigilance (Tucker, 1981). More recent work examining the effects of individual differences in social anxiety as well as individual sensitivity for generalised anxiety on the processing of facial expressions of affect has provided evidence of differential neural activation in emotion-processing brain regions for high anxiety participants, particularly in the amygdala and insula (Ball et al., 2012). Specifically, the authors observed that an increase of connectivity between brain areas (amygdala and insula) during general emotional face processing manifested as a function of social anxiety, whereas conversely decreased activity in response to positively valenced facial expressions was predominantly associated with individual subjective negative affect (Ball et al., 2012). However, in another study recruiting participants diagnosed with generalised anxiety disorder and attempting to link high levels of anxiety to amygdalar dysfunction Prater and colleagues report the converse pattern. Specifically, they reported decreased connectivity between amygdala, anterior cingulate cortex, and dorsolateral prefrontal cortex for fearful facial expressions, a pathway which has been predominantly linked with the processing of threat (Prater, Hosanagar, Klumpp, Angstadt, & Phan, 2013). One possibility might be that the use of fearful (instead of angry) stimuli in Prater et al's work reversed the activation pattern originally hypothesised. It could therefore be the case that fearful and sad stimuli do not necessarily represent a strong social signal. Anger however, has been suggested as positing a strong social signal, particularly from evidence of recent work in the working memory domain; for instance, angry faces have been shown to enhance working memory aspects (i.e. encoding) (Jackson, Linden, & Raymond, 2014; Nakashima, Langton, & Yoshikawa, 2012; Thomas, Jackson, & Raymond, 2014). Chapter 4 in the present thesis has also provided evidence that show that fearful facial expressions are not responded to as efficiently as angry expressions, especially when threat-enhancing elements such as auditory threat and manipulated gaze direction have been added to facial expression stimuli. Additionally, seeing as Prater et al utilised participant groupings through median split (generalised anxiety disorder vs controls) (Prater et al., 2013), it could be the case that micro-differences in individual anxiety levels and their manifestation into threat processing subcortical network activation have been filtered out, therefore subject to the caveat reported by Kanai and Rees (2011) suggesting that it is these micro-differences that potentially modulate the type and pattern of response. Recently, neuroimaging and behavioural studies have started to gradually

move away from groupings-based generalisations regarding the perception and response to stimuli, and have stressed the importance of looking at response and perception patterns at an individual level (see Kanai & Rees, 2011 for a review). This move towards individual micro-differences in perception and response seems particularly appropriate for the study of basic emotional attention and perception. Given the historical variation in results – which also seems to be heavily tied to methodological and experimental design aspects – regarding emotional perception, it might be the case that the main reason underlying this disparity is the lack of consideration of the strong modulating role individual personality variability might play in this sensory processing domain.

5.1.4 SUMMARY

The present chapter has discussed the importance and value that individual variability in anxiety might place on how we perceive and respond to basic emotional stimuli. The chapter also discussed the ability of the physiological condition of anxiety to rapidly engage attentional resources in the face of potentially threatening, negative emotional stimuli. Despite the large body of literature looking at correlating anxiety and emotional perception, particularly through neuroimaging methodologies, a wide divergence in results has been reported and attempts at replication often fail to produce the original patterns of results. Given the emerging importance of individual variability – which is often overlooked or filtered out as data noise – on all sensory modalities, perception and resulting behaviour, there is an overall lack of focus on how one's anxiety state might determine the preferential processing of some basic emotions more than others. The first of three experiments described in the following sections was designed to address this gap, by hypothesising that individual anxiety scores per participant will induce distinct attentional engagement, which will be additionally subject to visual field attentional biases depending on the positioning of target stimuli. This experiment also takes into account theoretical recommendations regarding the timing required for the rapid engagement of attention, with stimuli however always remaining detectable and suprathreshold. The two additional experiments designed for this chapter seek to further explore the modulatory role of individual anxiety by incorporating two factors that have been

suggested to manipulate primary emotional processing; auditory threat in the form of looming or receding sounds when paired with positive or negative expressions of affect, and a gaze-direction manipulation for two distinct types of negative affect (anger and fear). Specifically, Experiment 5.2 hypothesizes that quicker and more accurate responses will be elicited by angry faces paired with a looming sound, when these are presented in the left visual field. Happy faces are expected to produce quicker and more accurate responses when paired with a looming sound and presented on the right visual field. Additionally, participants' individual anxiety is expected to significantly influence participant responses depending on the nature of audiovisual emotion received, whereby response time and accuracy will significantly decrease as a function of anxiety, and will be quicker and more accurate still when the audiovisual stimulus is comprised of either angry faces paired with a looming sound, presented on the left visual field, or happy faces paired with a looming sound, presented on the right visual field. Finally, Experiment 5.3, hypothesises that angry faces with direct gaze and fearful faces with averted gaze will elicit quicker and more accurate responses when presented on the left visual field, with participants' individual anxiety further enhancing response speed and accuracy.

5 EXPERIMENT 5.1

5.2.1 METHODS

5.2.1.1 SUBJECTS

Twenty-three neurologically healthy adults (Undergraduate students, Department of Psychology, City University London) took part in this study (3 males; mean age: 22.3, SD: 2.1). Participants were recruited through online advertisements on the University's online experiment participation tool (SONA). Poor quality data from one further participant were omitted from analyses due to improbable reaction times (<300ms). All participants were right-handed with normal or corrected to normal vision and had given written consent prior to testing.

5.2.1.2 APPARATUS & MATERIALS

Laboratory setup and apparatus were the same as described in Experiment 2.1, chapter 2. In addition, the 20-item State Anxiety form taken from Spielberger's State-Trait Anxiety Inventory, Y Form (STAI) (Appendix A) was administered as a self-report measure of state anxiety (Spielberger, 2010). The combined STAI form is commonly used to differentiate between anxiety and depressive symptoms in clinical diagnoses, although its original development was specifically for assessing anxiety within non-clinical populations for research purposes (Bieling, Antony, & Swinson, 1998). In the present chapter, only the State Anxiety 20-item form was used, based on evidence suggesting that the Trait Anxiety scale assesses depression in addition to anxiety; the State scale has not been suggested to measure states other than anxiety (Bieling et al., 1998). Each item on the 20-item State Anxiety form is rated on a 4-point Likert scale ranging from "almost never" to "almost always", with overall higher scores indicating higher anxiety levels.

5.2.1.3 STIMULI & PROCEDURE

Visual target stimuli used in practice and test experimental blocks were the same as those used in Experiment 2.1, Chapter 2. The computer-based paradigm used in Experiment 2.1 was also used in the present study, with the procedural addition of the completion of the State Anxiety scale (Spielberger, Gorsuch, & Lushene, 1970) by each participant prior to commencing the computer-based task. Number of experimental conditions and total number of experimental trials collected were the same as in Experiment 2.1, chapter 2.

5.2.1.4 DESIGN

Experiment 5.1 employed a 2x2x5 repeated measures factorial design, with emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors. The factors of emotion and visual field location had two levels, while the factor of intensity had five. Two dependent measures of response efficiency were collected, in the form of manual response times (button press, measured in ms), and accuracy scores (% correct).

5.2.1.5 DATA PREPARATION & ANALYSIS

Raw reaction time data (ms) were filtered to exclude values from incorrectly responded to trials, as well as response times less or more than 2 standard deviations from the mean. Mean reaction times (ms) and mean accuracy scores (% correct) were calculated per experimental condition, per participant using E-Data Aid (E-Prime, Psychology Software Tools, Pittsburgh, MA). Questionnaire scores were aggregated per participant, and mean-centred prior to inclusion in subsequent analyses. 'Centred Qscore' in the following results sections denotes the mean-centred questionnaire scores, as in all subsequent experiments reported in the present chapter (Expt. 5.2 & 5.3). Centred questionnaire scores were manually transformed by subtracting the raw covariate values by the centre. This procedure was deemed appropriate as when using behavioural data, the assumption of obtaining exact measurements of the covariate without error is often violated; as such, utilising the raw scores may cause inconsistent results due to estimation errors in the covariate. Analyses reported in the following results section have all been Greenhouse-Geisser – corrected. Function fits were calculated with MATLAB PSIGNIFIT toolbox (R2013). Significant covariate interactions have been further analysed using Spearman's Rho.

5.3.1 RESULTS

5.3.1.1 REACTION TIME

A repeated-measures ANOVA was conducted using emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors on the reaction time data. The analysis produced a significant main effect of emotion [$F(1, 23)=20.9, p<.001, \text{partial } \eta^2= .56$], whereby happy faces (mean=480, SE=10.2) were responded to quicker than angry (mean=490, SE=10.9). The analysis also showed a significant main effect of visual field location [$F(1, 23)=20.1, p<.001, \text{partial } \eta^2= .47$], whereby left visual field targets (mean=472, SE=10.9) were responded to quicker than right visual field targets (mean=499, SE=11.01). A final significant main effect of intensity was found [$F(4, 92)=32.5, p<.001, \text{partial } \eta^2= .59$], where Bonferonni-corrected multiple pairwise comparisons revealed significant differences across intensities 2-5. The main effects observed in the present experiment replicate those of Exp. 2.1, Ch. 2 which utilized the same paradigm (without the inclusion of the anxiety questionnaire).

The analysis produced a significant interaction between emotion (angry/happy) and expression salience intensity (1-5) [$F(4, 92)=2.9, p=.02, \text{partial } \eta^2= .11$], whereby happy faces were responded to quicker overall, aside when target stimuli were ambiguous (intensity 1) (Fig. 5.1).

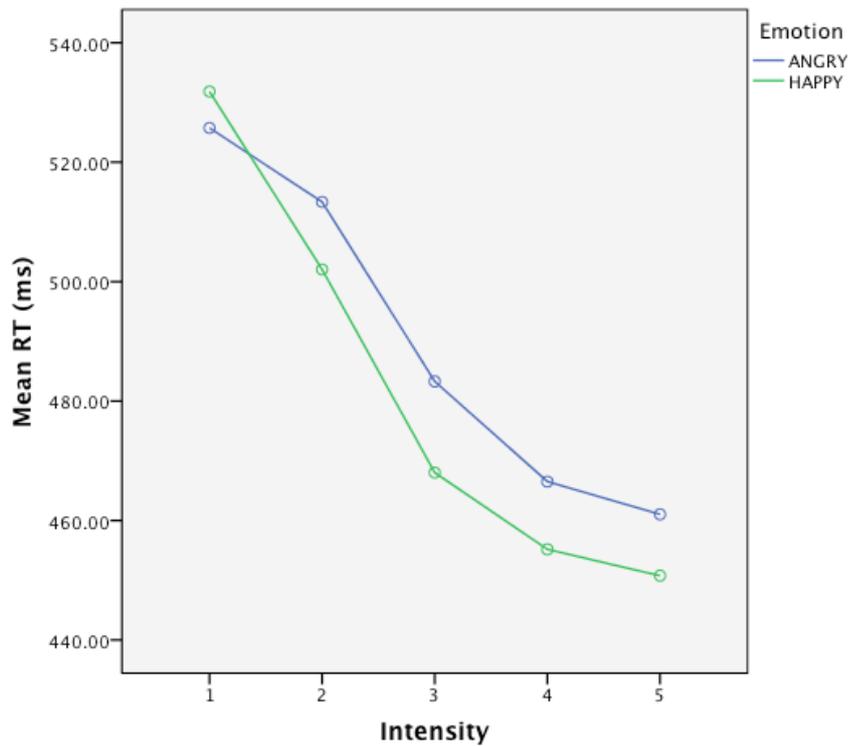


Figure 5.1. Line graph plots mean RTs for angry (blue line) and happy (green line) target stimuli as a function of expression salience intensity (1-5).

A further significant interaction was found between visual field location (left vs. right) and expression salience intensity [$F(4, 92)=2.62, p=.03, \text{partial } \eta^2= .10$], whereby left visual field targets were responded to quicker across intensities, as opposed to right visual field targets (Fig. 5.2). Post-hoc paired-samples t-tests confirmed that visual field differences were significant across salience intensities (Table 5.1).

| Visual Field comparison | <i>t</i> | df | Sig. |
|-------------------------|----------|----|-------|
| LVF Int.1 / RVF Int.1 | -4.3 | 22 | .000* |
| LVF Int.2 /RVF Int.2 | -3.7 | 22 | .001* |
| LVF Int.3 / RVF Int.3 | -3.4 | 22 | .002* |
| LVF Int. 4 /RVF Int. 4 | -3.7 | 22 | .001* |
| LVF Int. 5 /RVF Int. 5 | -2.9 | 22 | .008* |

Table 5.1. Table reports post-hoc t-test statistics for VF comparisons across the five intensities. Significant comparisons are denoted by *.

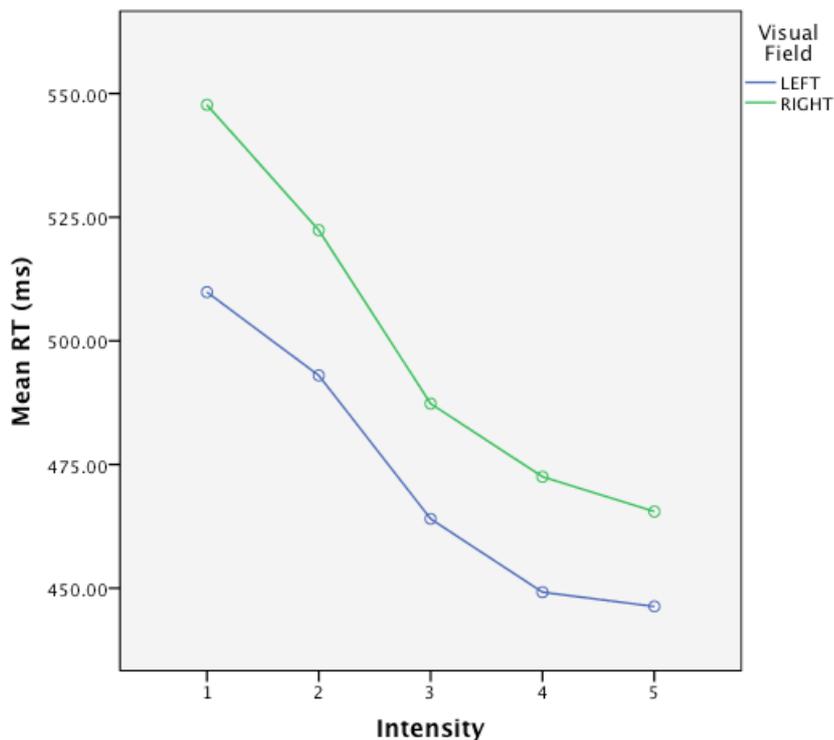


Figure 5.2. Line graph plots mean RTs for LVF (blue line) and RVF (green line) target stimuli as a function of expression salience intensity (1-5).

Importantly, the three-way interaction between emotion, visual field, and intensity initially observed in Exp. 2.1, Ch. 2 was not replicated in the present data. There were no further interactions in the ANOVA for the reaction time data.

A repeated-measures ANCOVA was conducted using emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the reaction time data. A significant interaction was found between emotion (angry/happy) and anxiety score [$F(1,22)=6.2$, $p=.02$, partial $\eta^2=.3$]. In unpacking the interaction, the difference between happy and angry faces was calculated by subtracting angry from happy. This resulted in a range of difference RT scores from negative to positive values, relative to the anxiety scores. Post-hoc Spearman's Rho test confirmed that as anxiety increases, RTs to angry faces decrease relative to happy faces, resulting in positive values for happy-minus-angry (Figure 5.3).

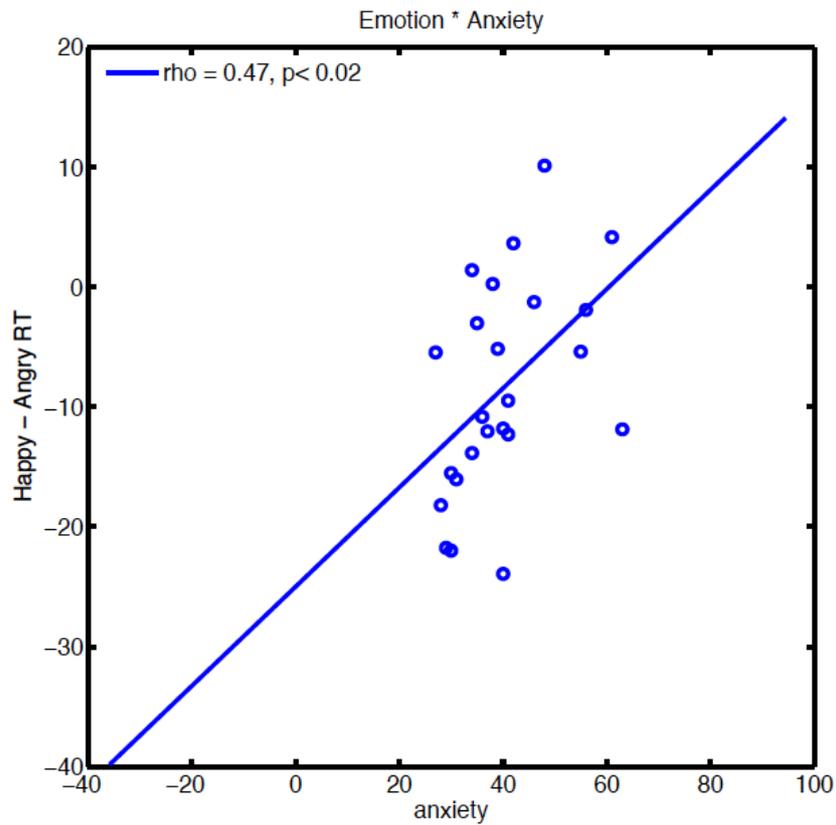


Figure 5.3. Graphic displays the difference in RT between angry and happy faces (y-axis) and anxiety scores (x-axis).

A further significant interaction between anxiety score and expression salience intensity was found [$F(4,88)=7$, $p=.001$, partial $\eta^2=.3$], where post-hoc Spearman's Rho tests revealed a significant positive relationship only for intensity 1 faces [$\rho=0.53$, $p<.01$] (Figures 5.4-5.8). In this interaction, it seems that highly ambiguous faces (int. 1), result in increased response latency for participants with higher anxiety scores. As anxiety increases, so does response speed, but only for the non-salient facial expressions, regardless of type of emotion.

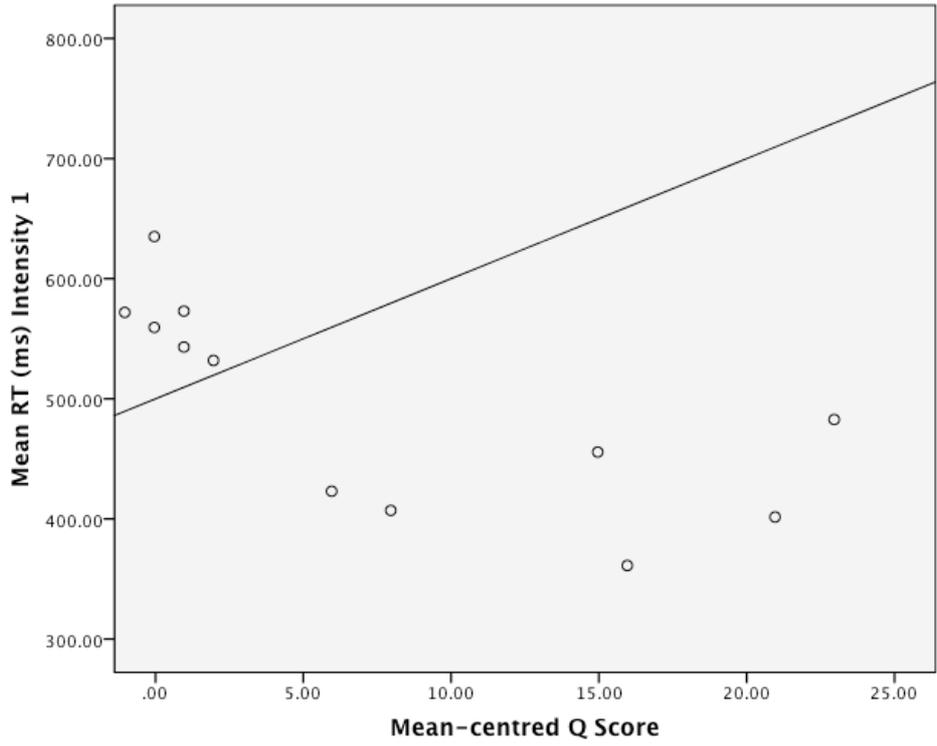


Figure 5.4. Graph displays the mean RT distribution for Intensity 1, plotted as a function of centred Q scores

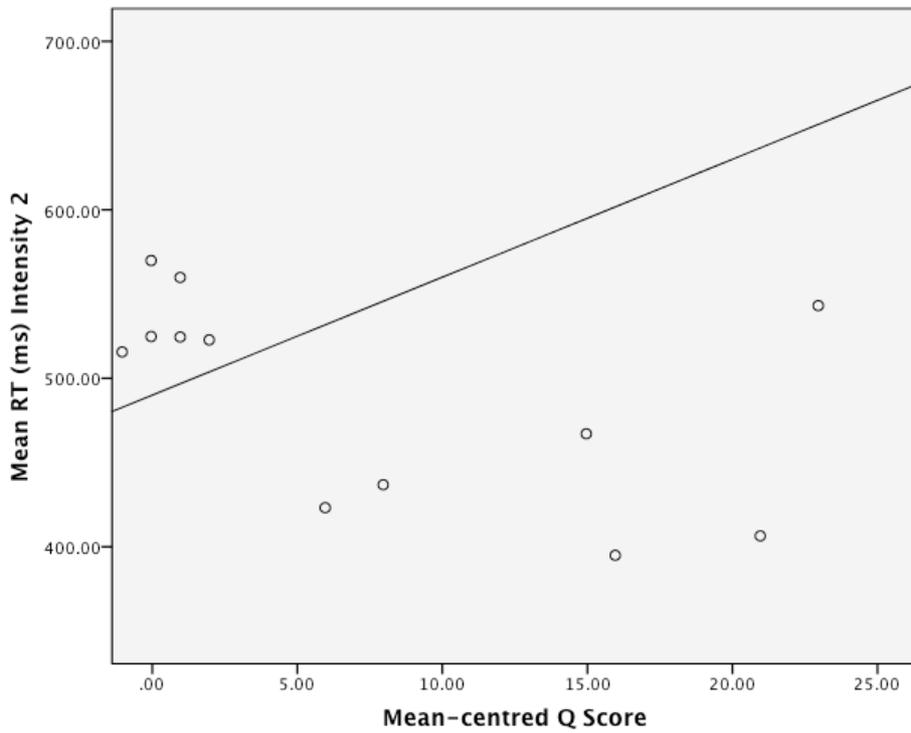


Figure 5.5. Graph displays the mean RT distribution for Intensity 2, plotted as a function of centred Q scores

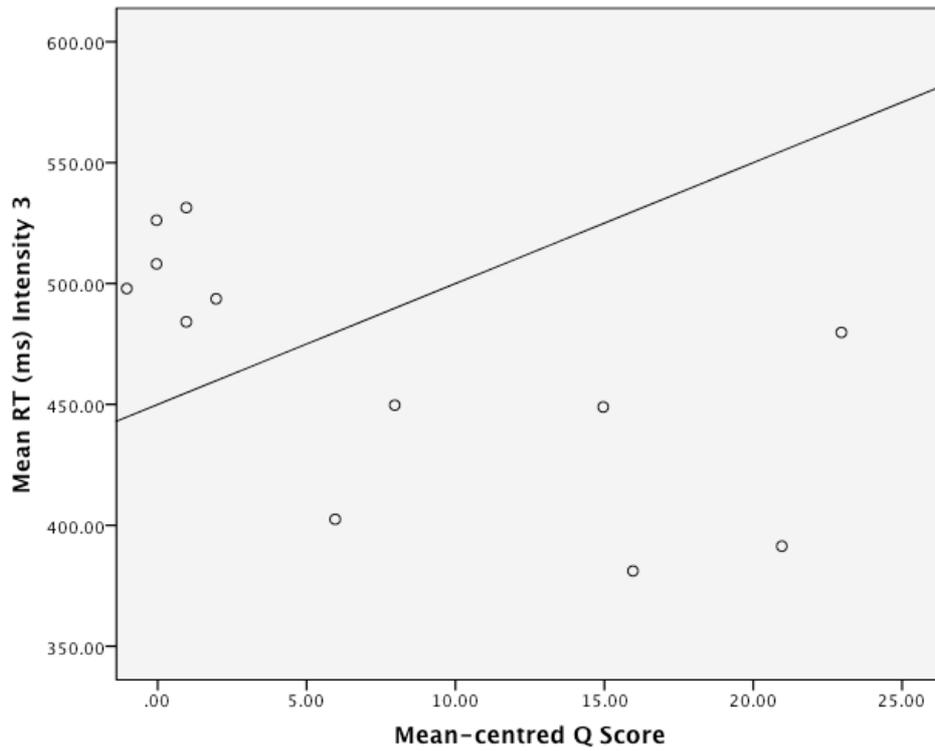


Figure 5.6. Graph displays the mean RT distribution for Intensity 3, plotted as a function of centred Q scores

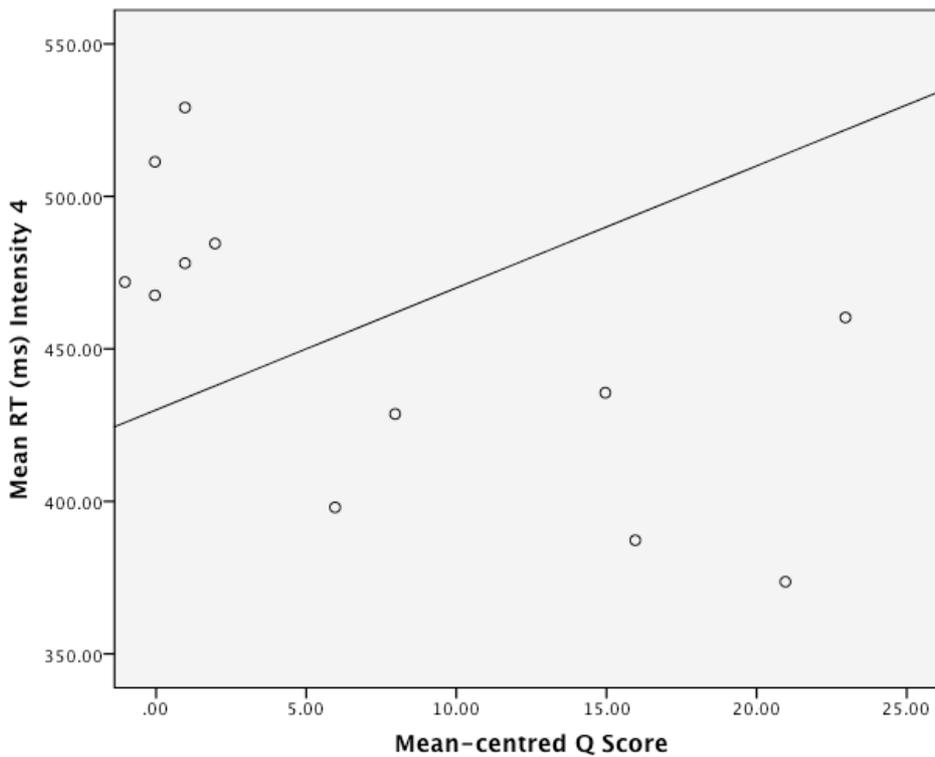


Figure 5.7. Graph displays the mean RT distribution for Intensity 4, plotted as a function of centred Q scores

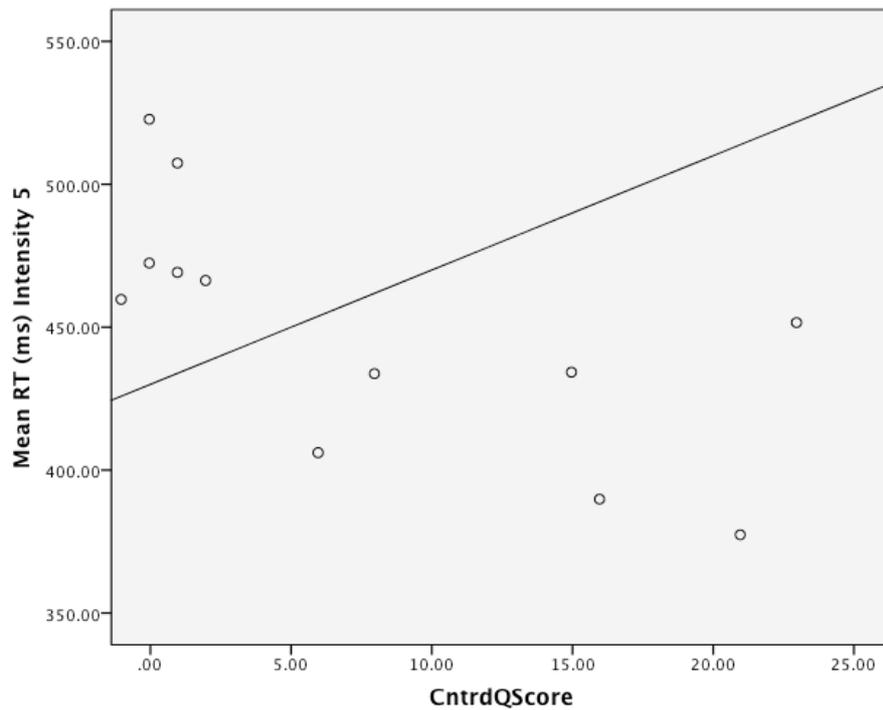


Figure 5.8. Graph displays the mean RT distribution for Intensity 5, plotted as a function of centred Q scores

A 3-way significant interaction between emotion, expression salience intensity and anxiety score was found [$F(4,88)=4$, $p=.001$, partial $\eta^2=.13$], where post-hoc correlational analysis showed significant positive relationships only between intensity 1 happy-angry RT and anxiety scores (Figure 5.9).

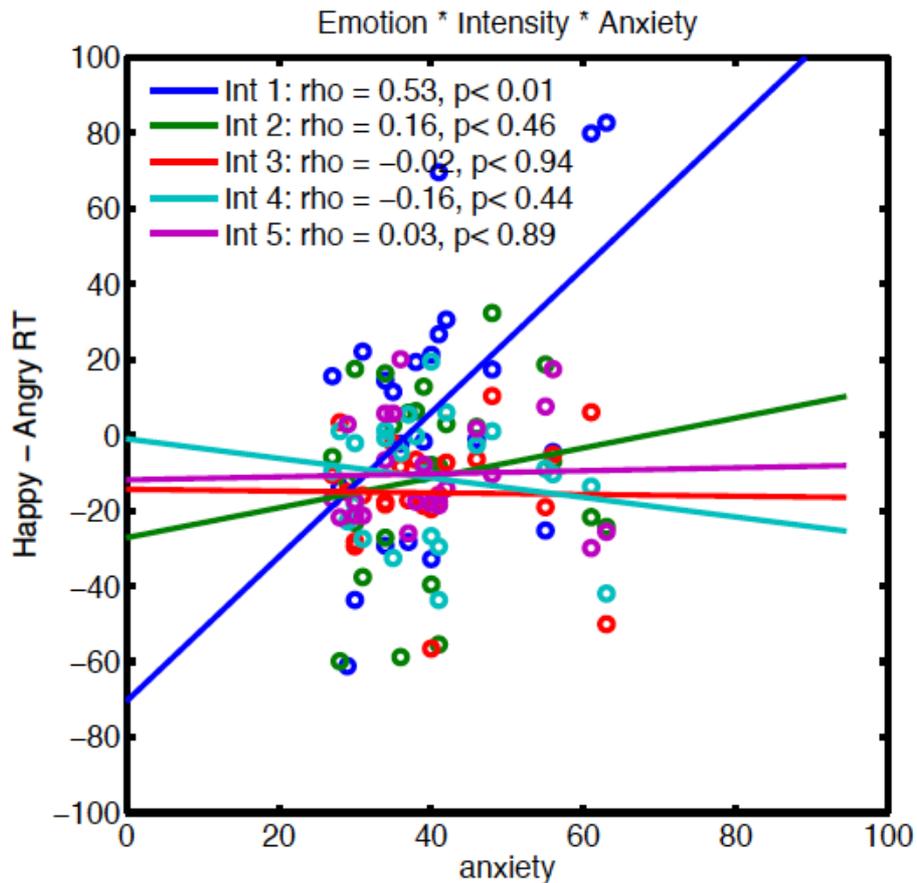


Figure 5.9. Graphic displays the significant, moderate positive relationship between response times only to intensity 1 emotional stimuli (y-axis) and anxiety scores (x-axis). The higher the anxiety, the quicker response times become, but only for highly ambiguous emotional faces.

Post-hoc correlational analyses for response times to the two emotions (angry/happy) as a function of anxiety, specifically for intensity 1 stimuli, revealed significant negative relationships between both emotions and response latency (Figure 5.10). This relationship potentially shows that anxious subjects subliminally sense the presence of angry faces faster than happy even if they don't know where they are; but more likely, perhaps angry faces are actually harder to see than happy, and anxious subjects are faster to make a random guessing response compared to when happy faces are visible, while non-anxious subjects are more cautious about guessing.

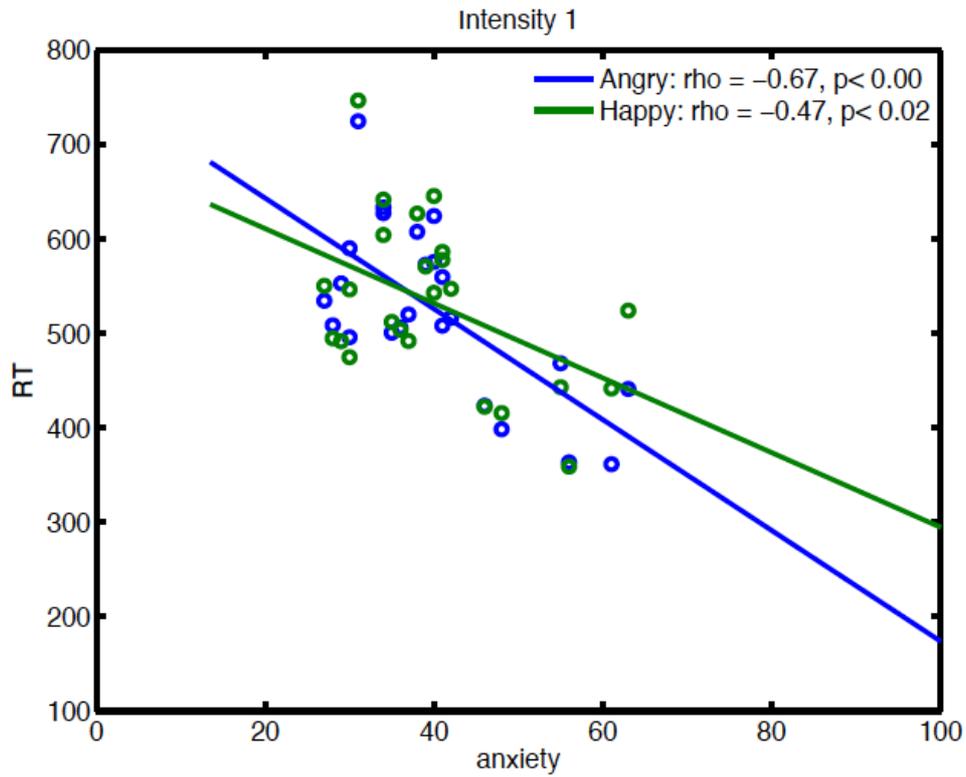


Figure 5.10. Graphic displays the significant, moderate negative relationship between angry stimuli (blue line) and response times as a function of anxiety. Significant negative correlations were found for both angry (blue line) and happy (green line) facial expressions, at expression salience intensity 1.

There were no further significant interactions for the reaction time data.

5.3.1.2 ACCURACY

A repeated-measures ANOVA was conducted with emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors for the accuracy data. Similarly to the main effects found in Exp. 2.1, ch.2, the analysis showed a significant main effect of emotion [$F(1,23)=48.2$, $p<.001$, partial $\eta^2= .71$], whereby happy faces elicited higher accuracy (mean=.80, SE=.1) than angry faces (mean=.75, SE=.01). The analysis also showed a significant main effect of visual field location [$F(1,23)=18.51$, $p<.001$, partial $\eta^2= .51$], whereby left visual field presentations elicited higher accuracy (mean=.82, SE=.01) than right visual field presentations (mean=.74, SE=.01). A final significant main effect of intensity was found [$F(4,92)=464.3$, $p<.001$, partial $\eta^2= .95$], where Bonferonni-corrected multiple pairwise comparisons showed significant differences across all intensity pairs (1-5).

The interaction between emotion and expression salience observed in ch.2 was replicated in these data. Specifically, the ANOVA revealed a significant interaction between type of emotion (angry/happy) and expression salience intensity (1-5) [$F(4,92)=12.5$, $p<.001$, partial $\eta^2= .35$], whereby happy faces achieved overall higher accuracy than angry across intensities 2-5. At intensity 1, accuracy for both angry and happy faces was at chance level (Fig. 5.11).

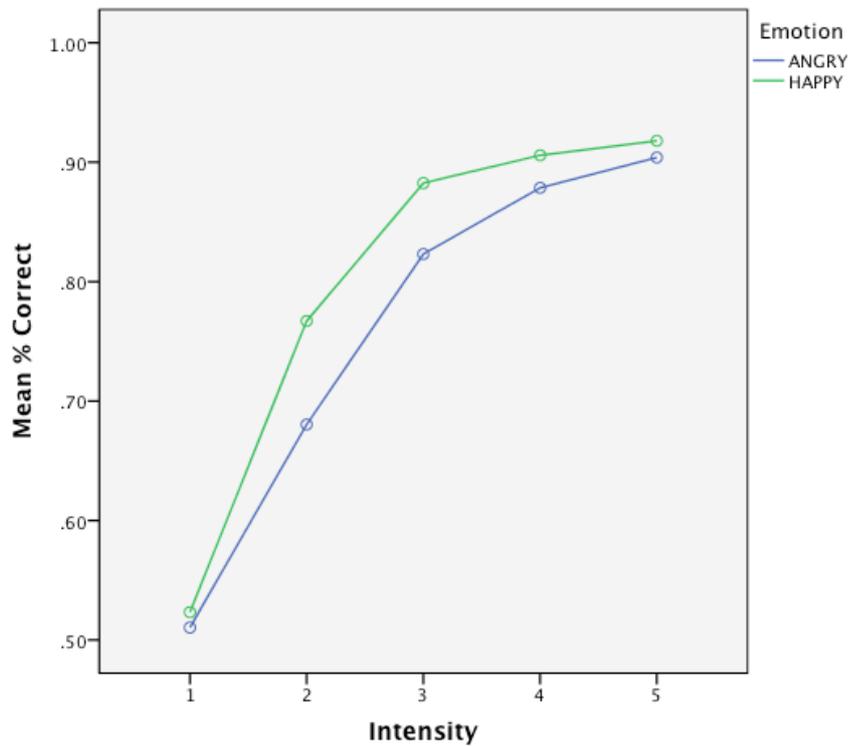


Figure 5.11. Line graph plots mean accuracy scores for angry (blue line) and happy (green line) stimuli as a function of expression salience intensity.

Again similarly to the interaction between visual field and expression salience first observed in ch.2, the present data resulted in a significant interaction between visual field location (left/right) and expression intensity [$F(4, 92)=3.83, p=.006, \text{partial } \eta^2=.15$]. In this interaction, left visual field presentations elicited overall higher accuracy than right visual field presentations, across all expression salience intensities (1-5). This interaction suggests that expression salience modulates the overall left advantage, with subjects guessing when responding to ambiguous stimuli; as salience intensifies, subjects' accuracy for happy is enhanced, before responses reach ceiling responses for both angry and happy at the highest salience intensities (Fig. 5.12).

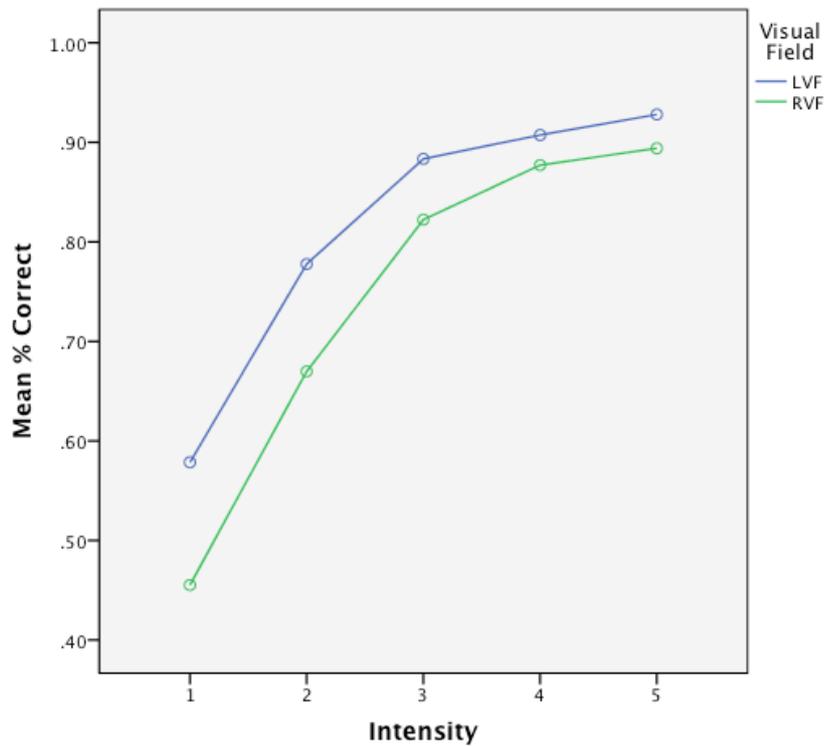


Figure 5.12. Line graph plots mean accuracy scores for LVF (blue line) and RVF (green line) target stimuli as a function of expression salience intensity.

Importantly, the interaction between emotion and visual field location observed in ch.2 was not replicated in the present data. The ANOVA revealed no further significant interactions for the accuracy data.

A repeated-measures ANCOVA was conducted using emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the accuracy data. A significant interaction between expression salience intensity and anxiety score was also observed [$F(4,88)=3.8$, $p=.007$, partial $\eta^2=.2$]. In unpacking the interaction, the difference between happy and angry faces was calculated by subtracting angry from happy. This resulted in a range of difference accuracy scores from negative to positive values, relative to the anxiety scores. Post-hoc Spearman's Rho analyses revealed that accuracy increases as a function of anxiety, but only for intensity 1 (Figure 5.13).

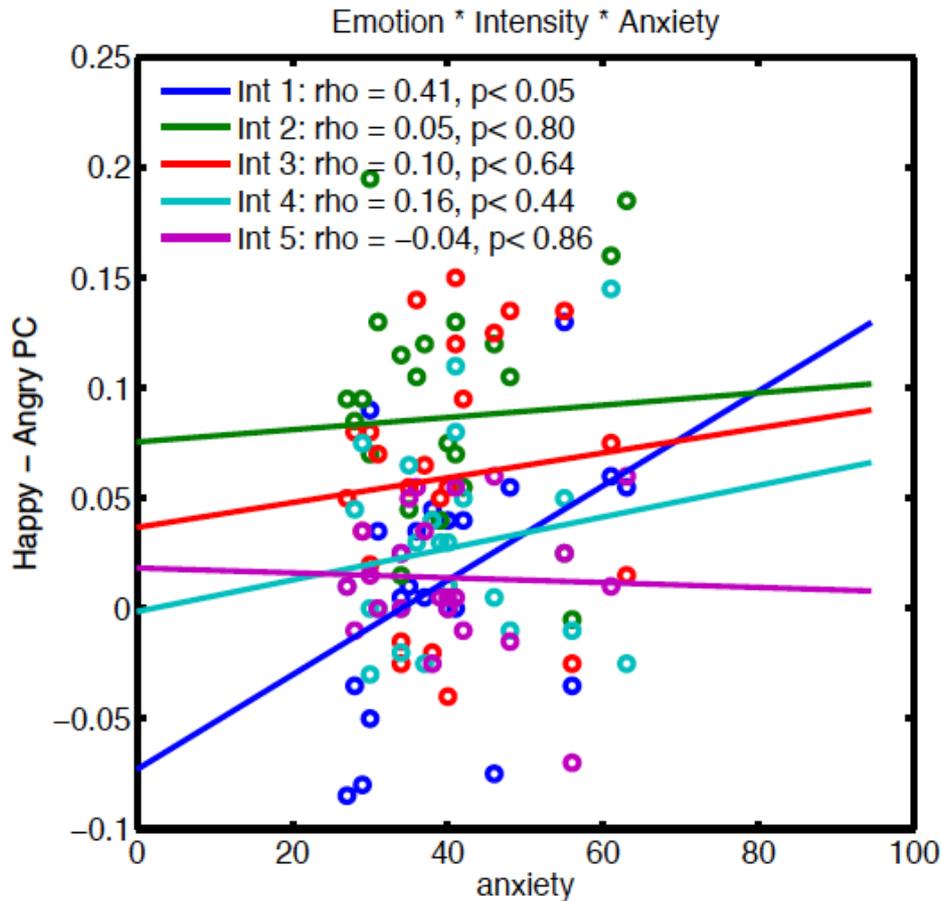


Figure 5.13. Graphic displays the significant, moderate positive relationship between accuracy scores only to intensity 1 emotional stimuli (y-axis) and anxiety scores (x-axis).

On further post-hoc investigation of the correlation between anxiety score and intensity 1 faces, Spearman's rho analyses at expression salience intensity 1 for angry and happy faces revealed a significant negative relationship between anxiety and angry faces, but a non-significant relationship between anxiety and happy faces (Figure 5.14), whereby for angry stimuli, an increase in anxiety reflects a decrease in response accuracy for highly ambiguous facial expressions (intensity 1). Accurate responding to happy stimuli does not appear to be influenced by level of state anxiety.

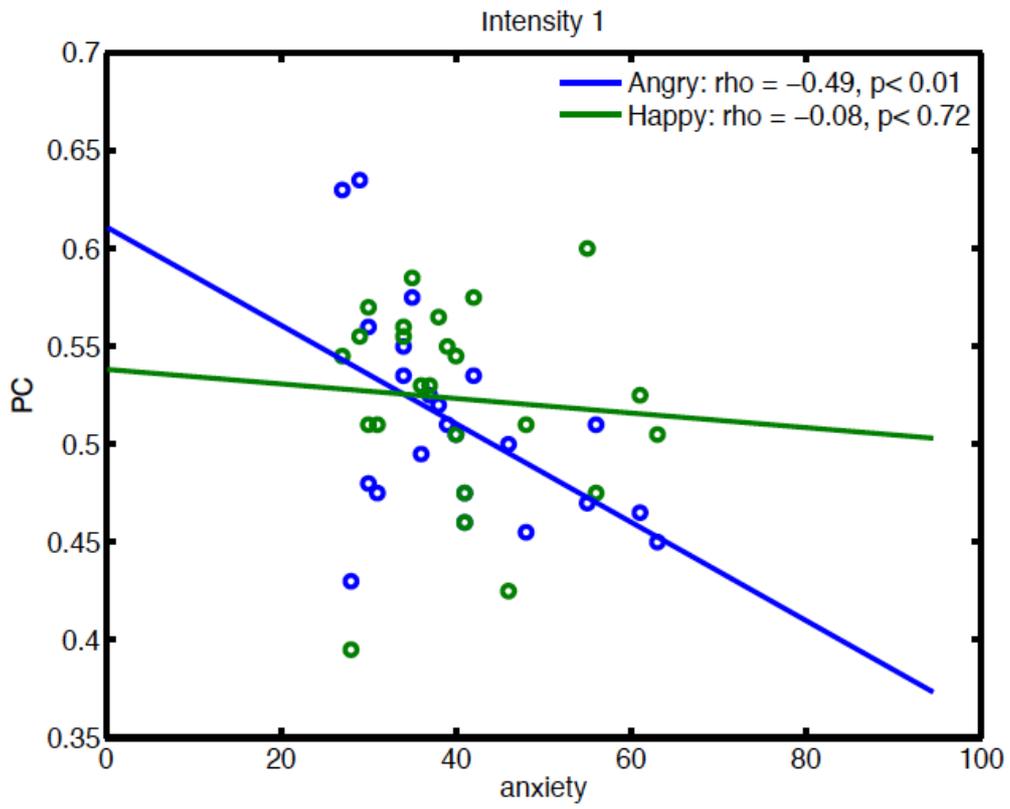


Figure 5.14. Graphic displays the significant, moderate negative relationship between angry stimuli (blue line) and accuracy scores as a function of anxiety.

5.3.1.3 THRESHOLDS

Individual functions between anxiety score and mean accuracy were fit per participant to calculate discrimination thresholds, that denote the intensity required for participants to correctly identify the emotional expression at 75% accuracy (for the methodology of calculations, see Ch. 2, Exp. 2.1).

Thresholds were correlated to angry and happy expression stimuli separately as functions of anxiety, with significant positive relationships resulting for each type of affect (Figure 5.15).

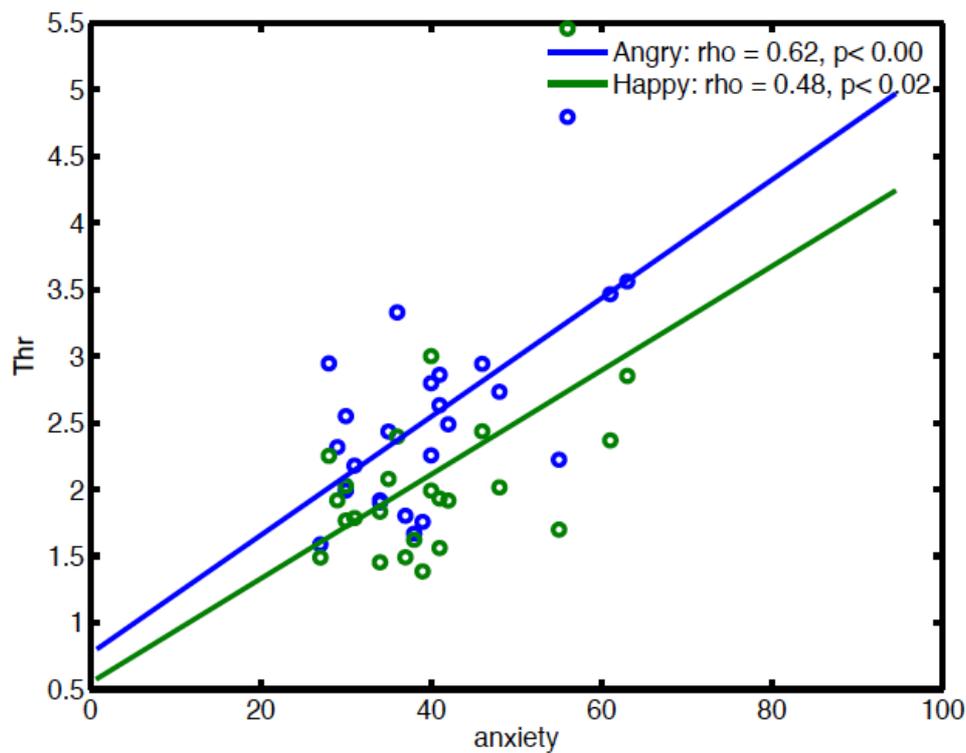


Figure 5.15. Graphic displays significant relationships between angry (blue line) and happy (green line) stimuli to detection thresholds (y-axis) as a function of anxiety (x-axis). Correlations are significant for both emotions, with the angry correlation being stronger than that for happy.

Comparison of thresholds per emotion as a function of level of state anxiety revealed a borderline significant difference between the two types of emotional expression (Figure 5.16). It appears that thresholds for angry faces increase relative to happy as a function of increasing anxiety (i.e. they become relatively less sensitive to angry features compared to happy).

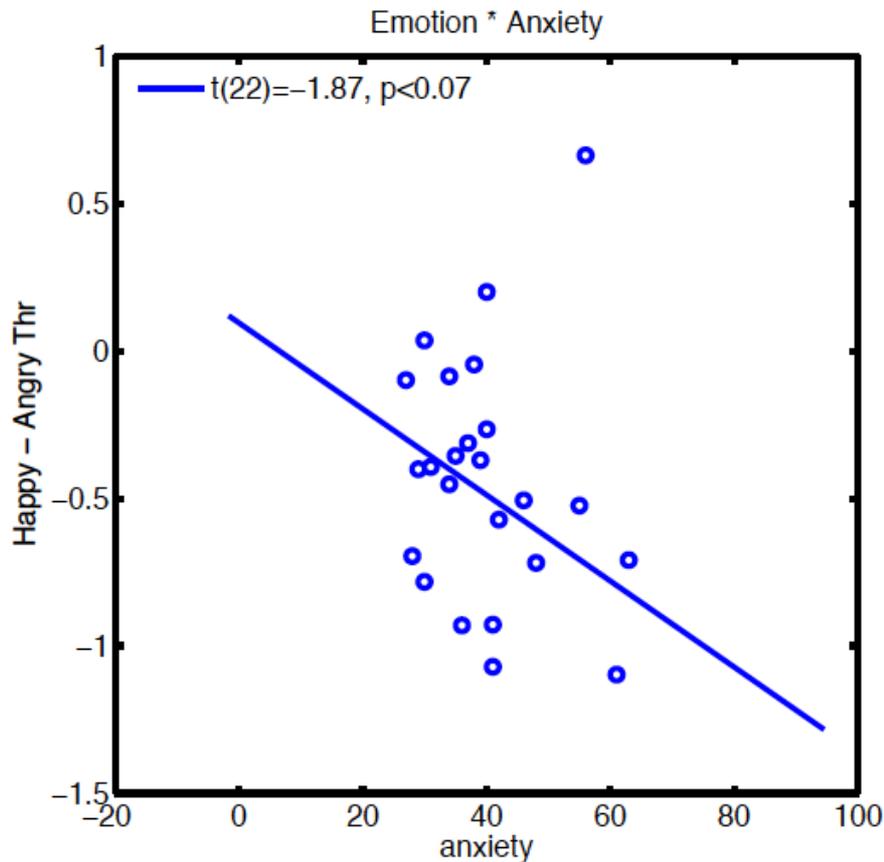


Figure 5.16. Graphic illustrates the difference for thresholds for angry faces relative to happy as a function of increasing anxiety.

The speed-accuracy trade off was calculated for present data. This measure quantifies how the threshold accuracy covaried with response latency, across experimental conditions (Heitz, 2014). For this calculation, the mean response speed and mean accuracy rates were fitted as functions per participant and for each condition using the PSIGNIFIT function in MATLAB (R2013). The average fits were then plotted as a function of the covariate (mean-centred anxiety scores). Finally, rho values for the correlation of RT with % correct scores for each intensity was plotted as a function of anxiety (Fig. 5.17), showing that higher anxiety correlates with a decrease in the strength of the correlation towards zero, whereby participants with low anxiety tend to trade off speed for sensitivity, while for participants with high anxiety sensitivity is not related to response time.

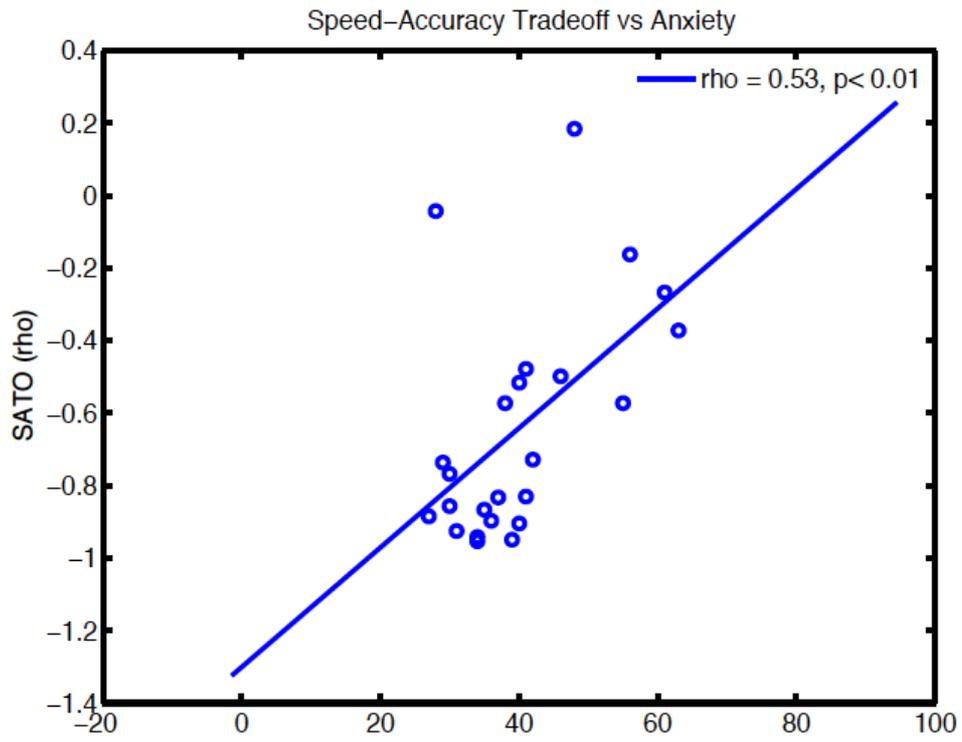


Figure 5.17. Graphic plots the speed-threshold accuracy trade off (SATO) (y-axis) for threshold faces as a function of anxiety. The higher the anxiety score, the higher SATO becomes for responses to emotional faces.

5.3.1.4 EXPERIMENT 5.1 SUMMARY

Both response time and accuracy data were firstly analysed without utilizing the anxiety covariate. Findings from these preliminary analyses showed a left visual field bias for both measures, with happy faces eliciting quicker and more accurate responses overall. The present results partially replicated the findings from experiment 2.1, chapter 2, without however managing to replicate the emotion and visual field interactions for response latency and accuracy. When including participants' anxiety scores in the analysis, findings from the present experiment revealed the significant influence of state anxiety in responses to ambiguous facial expressions of affect. For response latency, the higher anxiety that participants reported, the more speeded responses were to emotional expressions. Responses were quicker still for the most ambiguous of stimuli (intensity 1). Although the relationship between expression intensity and anxiety was true for both types of affect (angry/happy) at intensity 1, angry faces elicited even quicker responses as state anxiety levels increased. As the response time data reflected values from correctly responded-to trials, this finding may indicate the existence of a subliminal effect of the facial emotion; it may be the case that participants are indeed processing the emotions observed instead of blindly guessing the location of the target. Alternatively, they are less likely to hesitate from making a fast guess when the stimuli are nearly or completely indistinguishable.

The accuracy data reinforced the influence of stimulus ambiguity on response efficiency. Again it was ambiguous stimuli (intensity 1) that in this case elicited decreasing accuracy scores as a function of increasing state anxiety scores. When inspected for each emotion separately, angry intensity 1 faces showed a decrease in accuracy as state anxiety levels increased. The accuracy data showed that accuracy for happy faces remains roughly constant, but decreases for angry faces (even more so as expression salience for angry decreases). Although the accuracy of responses to happy stimuli does not appear to be influenced by the level of participants' anxiety, for ambiguous (int. 1) angry faces, participants' increase in anxiety reflects a decrease in accuracy.

Calculation of detection thresholds confirmed the speed-accuracy trade-off for high ambiguity facial expressions. Although this was evident for both types of affect, angry thresholds decreased relative to happy when state anxiety levels increased.

5 EXPERIMENT 5.2

OVERVIEW

The second experiment in this chapter seeks to further examine the role of individual anxiety in influencing response efficiency for positive and negative facial expressions of varying salience, when facial expressions are paired with threatening auditory stimuli (looming vs. receding sounds). This experiment hypothesizes that quicker and more accurate responses will be elicited by angry faces paired with a looming sound, when these are presented in the left visual field. Happy faces are expected to produce quicker and more accurate responses when paired with a looming sound and presented on the right visual field. Participants' individual anxiety is expected to significantly influence participant responses depending on the nature of audiovisual emotion received. Specifically, it is hypothesized that response time and accuracy will significantly decrease as a function of anxiety, and will be quicker and more accurate still when the audiovisual stimulus is comprised of either angry faces paired with a looming sound, presented on the left visual field, or happy faces paired with a looming sound, presented on the right visual field.

5.2.2 METHODS

5.2.2.1 SUBJECTS

Twenty-four neurologically healthy adults (Undergraduate students, Department of Psychology, City University London) took part in this study (4 males; mean age: 22.3, SD: 2.1). Participants were recruited through online advertisements on the University's online experiment participation tool (SONA). Poor quality data from a further two participants were omitted from analyses due to improbable reaction times (<300ms. All participants were right-handed with normal or corrected to normal vision and had given written consent prior to testing.

5.2.2.2 APPARATUS & MATERIALS

Laboratory setup and apparatus was the same as in Experiment 4.1, with the addition of Spielberger's 20-item State Anxiety scale (Spielberger et al., 1970).

5.2.2.3 STIMULI & PROCEDURE

Visual target stimuli, and auditory looming and receding stimuli used in practice and test experimental blocks were the same as those used in Experiment 4.1, Chapter 4. The computer-based paradigm used in Experiment 4.1 was also used in the present study, with the procedural addition of the completion of the State Anxiety scale (Spielberger, Gorsuch, & Lushene, 1970) by each participant prior to commencing the computer-based task. Number of experimental conditions and total number of experimental trials collected were the same as in Experiment 4.1, chapter 4.

5.2.2.4 DESIGN

Experiment 5.2 employed a 2x2x2x5 repeated measures factorial design, with sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors. The factors of emotion and visual field location had two levels, while the factor of intensity had five. Two dependent measures of response efficiency were collected, in the form of manual response times (button press, measured in ms), and accuracy scores (% correct).

5.2.2.5 DATA PREPARATION & ANALYSIS

Raw reaction time data were filtered to exclude values from incorrectly responded to trials, as well as response times less or more than 2 standard deviations from the mean. Mean reaction times (ms) and mean accuracy scores (% correct) were calculated per experimental condition, per participant using E-Data Aid (E-Prime, Psychology Software Tools, Pittsburgh, MA). Questionnaire scores were aggregated per participant, and mean-centred prior to inclusion in subsequent analyses. Analyses reported in the following results section have all been Greenhouse-Geisser – corrected. Significant covariate interactions have been further analysed using Spearman's Rho.

5.3.2 RESULTS

5.3.2.1 REACTION TIME

A repeated-measures ANOVA was conducted using sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors on the reaction time data. The analysis showed a significant main effect of emotion [$F(1,23)=23.3$, $p<.001$, partial $\eta^2= .50$], whereby happy faces were responded to quicker (mean=522, SE=13.1) than angry faces (mean=532, SE=14.5). A further significant main effect of sound was observed [$F(1,23)=23.4$, $p<.001$, partial $\eta^2= .50$], whereby receding sounds elicited quicker responses (mean=518, SE=13.6) than looming sounds (mean=536, SE=14.2). A final significant main effect of expression salience intensity was found [$F(1,27)=30.1$, $p<.001$, partial $\eta^2= .61$], where Bonferonni-corrected multiple pairwise comparisons found significant differences across intensities 2 to 4. These main effects replicate the effects observed in Exp. 4.1, ch.4.

Unlike findings from Exp. 4.1, ch.4 which did not observe an interaction between visual field and emotion, the ANOVA on the present data showed a significant interaction between emotion and visual field location [$F(1,23)=3.9$, $p=.05$, partial $\eta^2= .15$], where happy faces on the RVF were responded to quicker than when on the LVF, and angry faces on the LVF were responded to quicker than when on the RVF (Fig. 5. 18).

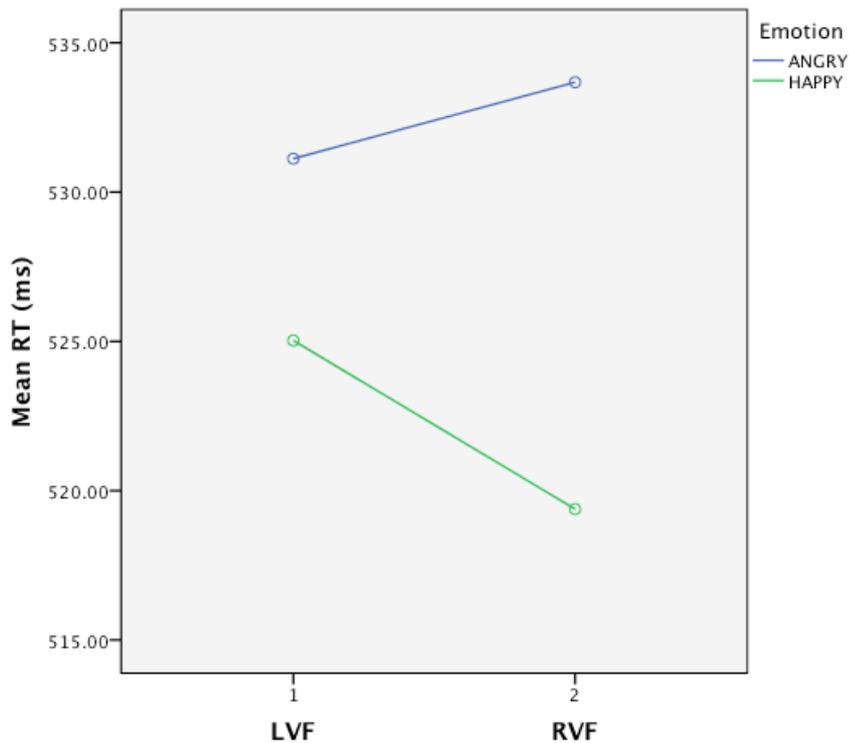


Figure 5.18 Line graph plots mean RT for angry (blue line) and happy (green line) when on the left and right visual field respectively.

Similarly to the interaction between visual field and expression salience observed in Exp. 41, ch.4 the present data revealed a further significant interaction between visual field location and expression salience intensity [$F(4,92)=3.3$, $p=.02$, partial $\eta^2= .12$], whereby for the more ambiguous intensities (1-2) target stimuli on the left visual field elicit quicker responses; this pattern is however reversed for the salient intensities (3-5), where right visual field presentations elicit quicker responses (Fig. 5.19).

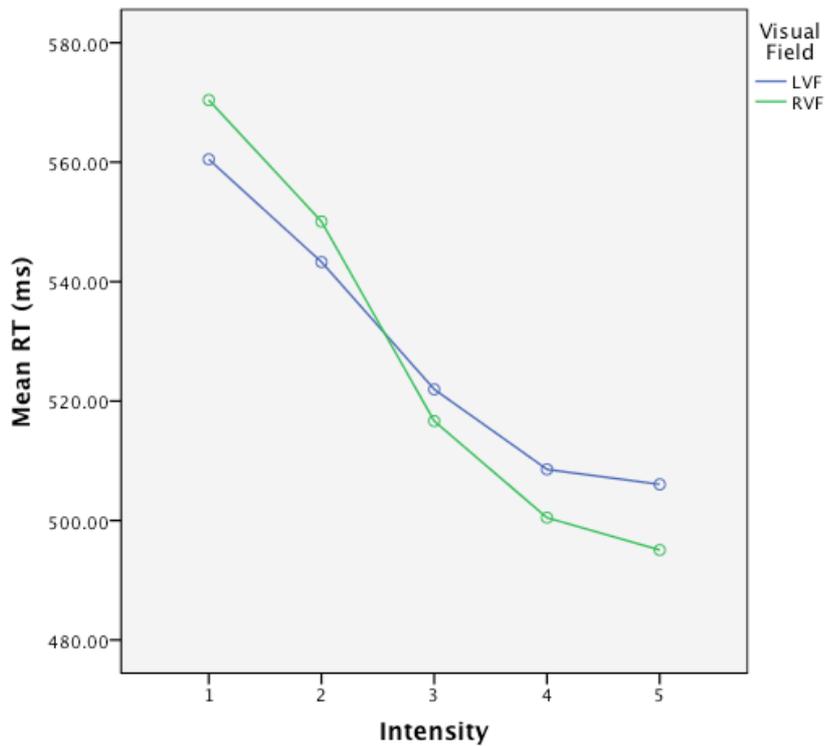


Figure 5.19 Line graph plots mean RT for left visual field (blue line) and right visual field (green line) presentations of target stimuli as a function of expression salience intensity.

The ANOVA revealed no further significant interactions for the response time data, and did not replicate the three-way interaction between emotion, sound and expression salience intensity observed in Exp. 4.1, ch.4.

A repeated-measures ANCOVA was conducted using sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the reaction time data. A significant interaction between visual field location and state anxiety score was found [$F((1,22)=8, p=.009, \text{partial } \eta^2=.6)$] (Figure 5.20),]. In unpacking the interaction, the difference between LVF and RVF target location was calculated by subtracting LVF RTs from RVF RTs. This resulted in a range of difference response time scores from negative to positive values, relative to the mean-centred anxiety scores. Post-hoc Spearman's Rho analyses revealed a significant negative relationship between visual field and anxiety scores [$\text{Rho}=-.5, p=.01$], suggesting that as anxiety increases, participants became less reliant on a dominant visual field for locating the target.

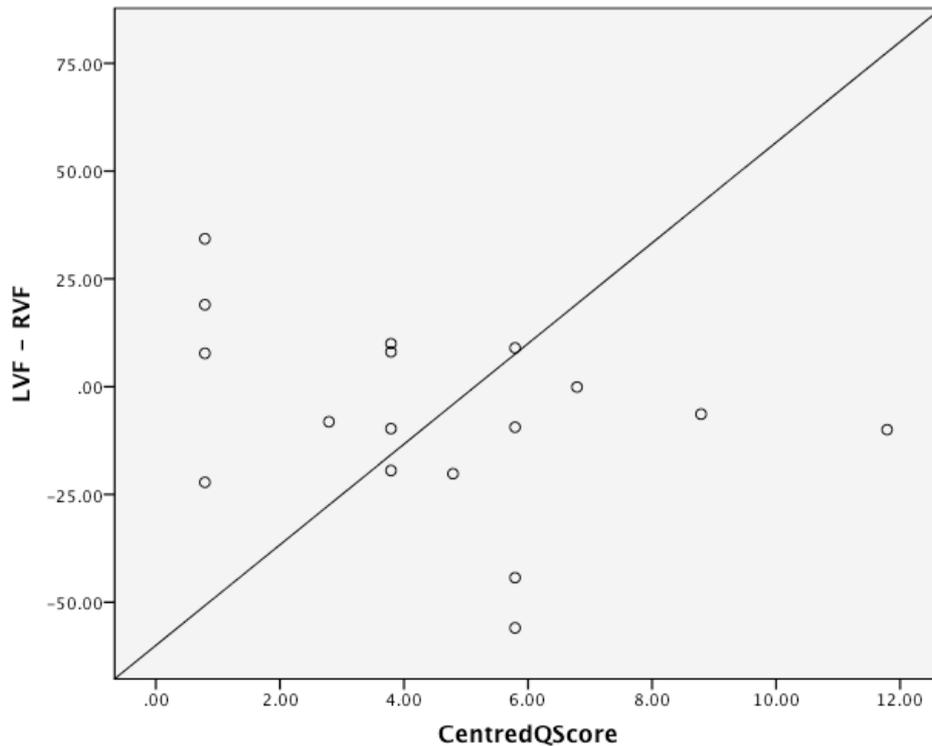


Figure 5.20 Scatterplot shows the relationship between the calculated VF difference (LVF-RVF) as a function of mean-centred questionnaire score (anxiety).

5.3.2.2 ACCURACY

A repeated-measures ANOVA was computed using sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) on the accuracy data. Replicating the effects observed in Exp. 4.1, ch.4, the analysis produced a significant main effect of emotion [$F(1,23)=42.1$, $p<.001$, partial $\eta^2= .64$], with happy faces eliciting higher accuracy (mean=.80, SE=.01) than angry faces (mean=.75, SE=.01). A further significant main effect of sound was found [$F(1,23)=16.4$, $p<.001$, partial $\eta^2= .41$], with looming sounds eliciting higher accuracy (mean=.78, SE=.01) than receding sounds (mean=.76, SE=.01). A significant main effect of visual field location was also found [$F(1,23)=4.5$, $p=.04$, partial $\eta^2= .16$], with left visual field presentations producing higher accuracy (mean=.79, SE=.01) than right visual field presentations (mean=.75, SE=.01). A final significant main effect of intensity was found [$F(2,42)=294$, $p<.001$, partial $\eta^2= .92$], with Bonferonni-corrected multiple pairwise comparisons showing significant differences across intensities 1 to 4.

The ANOVA replicated the interaction observed in Exp. 4.1, ch.4, by revealing a significant interaction between type of emotion and visual field location [$F(1,23)=6.3$, $p=.02$, partial $\eta^2= .22$], where both angry and happy faces elicited higher accuracy when displayed on the left visual field (Fig. 5.21). Post hoc paired-samples t-tests revealed significant differences between angry and happy faces, across visual field locations (Table 5.1)

| | t | df | Sig. |
|--------------------------|----------|-----------|-------------|
| Angry L / Angry R | 2.5 | 23 | .002* |
| Happy L / Happy R | -9.4 | 23 | .001* |
| Angry L / Happy L | 18.5 | 23 | .001* |
| Angry R / Happy R | -6.2 | 23 | .001* |

Table 5.1. Table reports t-test statistics for each paired comparison unpacking the visual field and emotion interaction. Significant pairs are denoted by *.

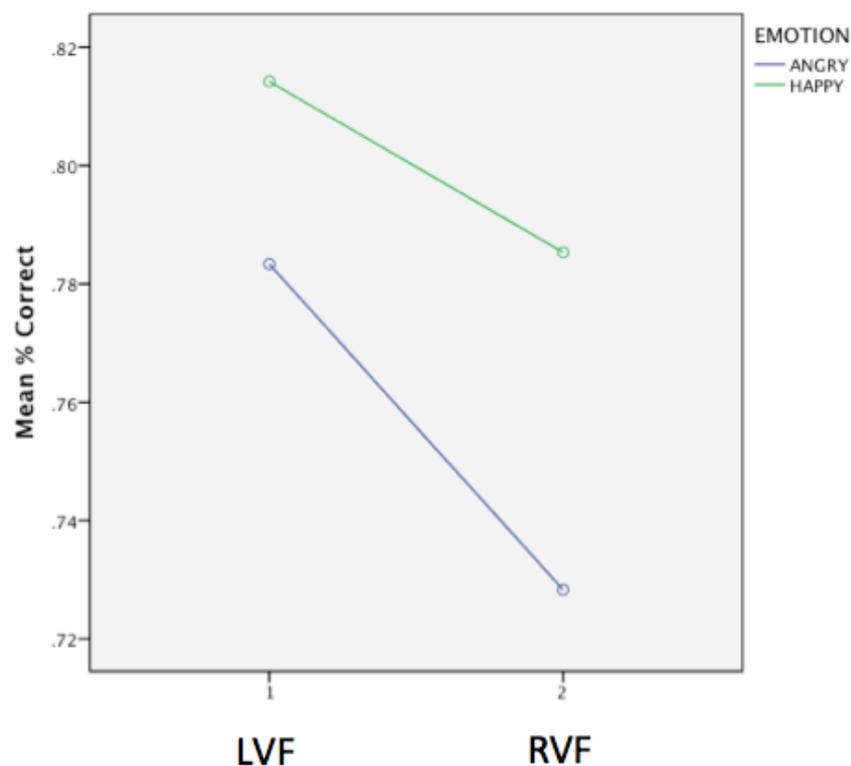


Figure 5.21 Line graph displays mean accuracy scores for angry (blue line) and happy (green line) stimuli when presented on the left and right visual field respectively.

A further significant interaction between type of emotion and expression salience intensity was found [$F(3,67)=9.5$, $p<.001$, partial $\eta^2= .3$], whereby happy faces

elicited consistently higher accuracy for intensities 2-5. In intensity 1, accuracy scores for both types of emotion were at chance level (Fig. 5.22). Post hoc paired-samples t-tests revealed significant differences between angry and happy faces, across for intensities 2-5, with no significant differences observed at intensity 1 (Table 5.2).

| | t | df | Sig. |
|--------------------------|----------|-----------|-------------|
| Angry 1 / Happy 1 | -0.02 | 23 | .9 |
| Angry 2 / Happy 2 | -5.1 | 23 | .001* |
| Angry 3 / Happy 3 | -5.9 | 23 | .001* |
| Angry 4 / Happy 4 | -3.8 | 23 | .001* |
| Angry 5 / Happy 5 | -5.6 | 23 | .001* |

Table 5.2. Table reports t-test statistics for each paired comparison unpacking emotion and intensity interaction. Significant pairs are denoted by *.

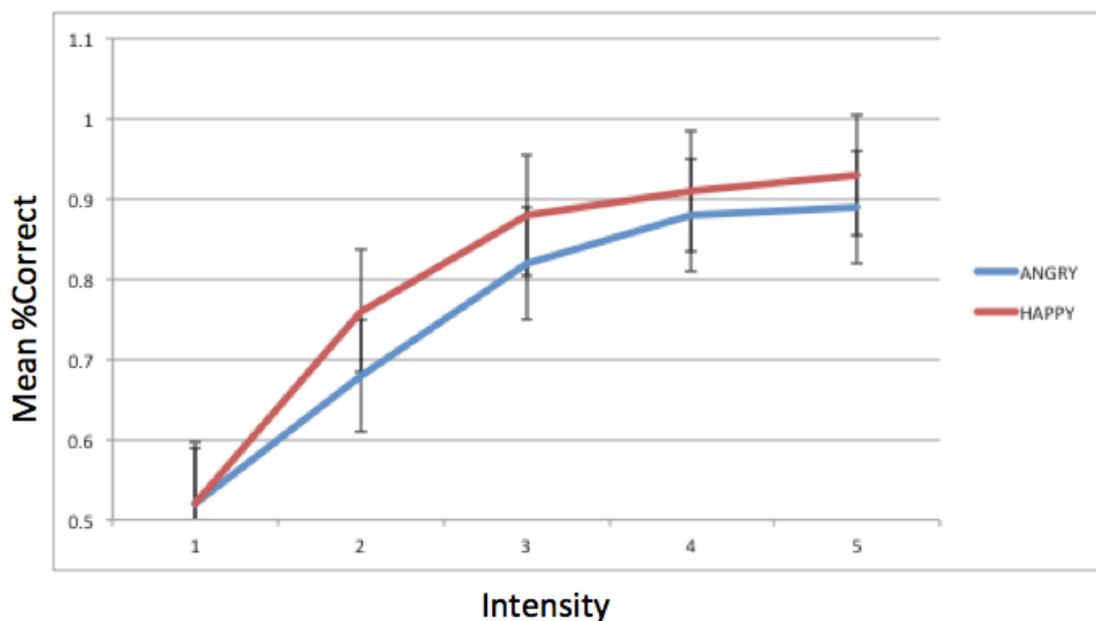


Figure 5.22 Line graph displays angry (blue line) and happy (red line) mean accuracy scores as a function of expression salience intensity. Error bars represent Cousineau-corrected within-subjects ± 1 SE of the mean.

Unlike Exp. 4.1, ch.4, the ANOVA on the present data showed a significant 3-way interaction between type of emotion (angry/happy), visual field location (left/right), and expression salience intensity [$F(2.9, 67.3)=2.9, p=.04, \text{partial } \eta^2= .11$], whereby happy faces produce overall higher accuracy, which is higher still when they are presented on the LVF for the ambiguous intensities, and the RVF for the salient intensities. Angry faces on the LVF produce consistently higher accuracy scores than when on the RVF, regardless of expression intensity. It appears that there could

be a response bias for hitting 'left' when subjects are guessing; in this case, it may be informative to measure false alarm rates (i.e. signal detection theory) to derive a bias-free measure of accuracy. (Fig. 5.23). Post hoc paired-samples t-tests revealed significant differences between angry and happy faces, for both visual fields and across intensities (Table 5.3).

| Visual Field | Intensity | Emotion Pair | t | df | Sig. |
|--------------|-----------|------------------|-------|----|-------|
| LVF | 1 | Angry / Happy | -.44 | 23 | .66 |
| | 2 | Angry / Happy | -1.8 | 23 | .07 |
| | 3 | Angry / Happy | -3.9 | 23 | .001* |
| | 4 | Angry / Happy | -2.1 | 23 | .041* |
| | 5 | Angry / Happy | -2.8 | 23 | .009* |
| RVF | 1 | Angry / Happy | .6 | 23 | .55 |
| | 2 | Angry / Happy | -6.4 | 23 | .001* |
| | 3 | Angry / Happy | -4.8 | 23 | .001* |
| | 4 | Angry / Happy | -3.06 | 23 | .005* |
| | 5 | Angry / Happy | -4.7 | 23 | .001* |

Table 5.3. Table reports t-test statistics for each paired comparison unpacking emotion, visual field, and intensity interaction. Significant pairs are denoted by *.

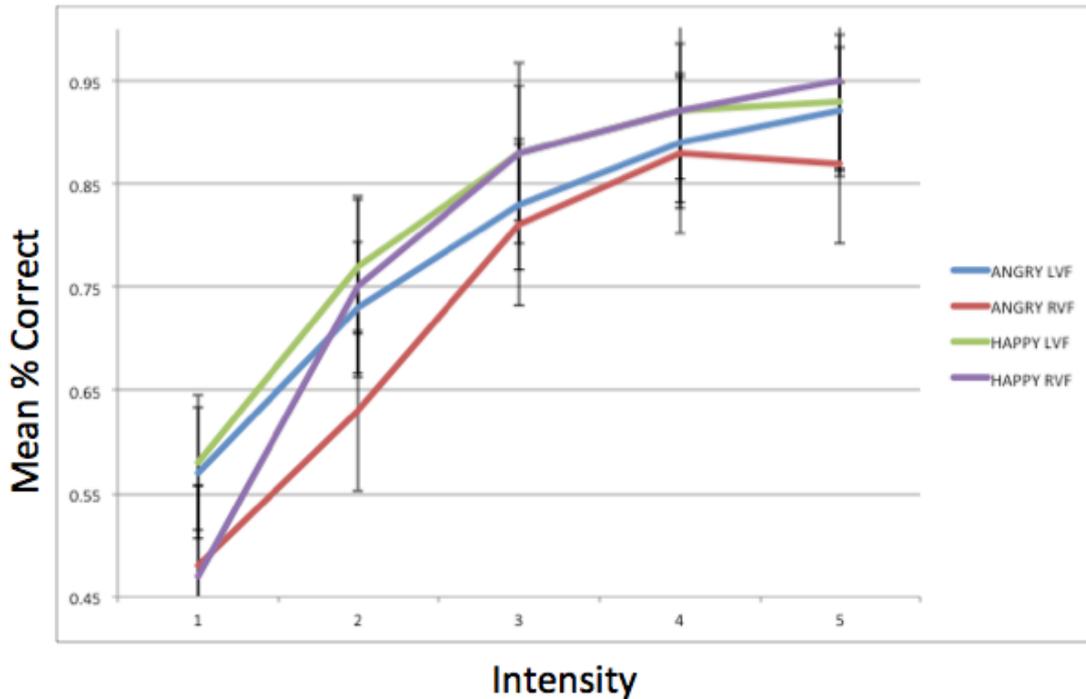


Figure 5.23 Line graph displays mean accuracy scores for each emotion/visual field location condition as a function of expression salience intensity. Error bars represent Cousineau-corrected within-subjects ± 1 SE of the mean.

The ANOVA showed no further interactions for the accuracy data.

A repeated-measures ANCOVA was conducted using sound (looming/receding), emotion (angry/happy), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the accuracy data. A significant interaction between state anxiety score and visual field location was also found for the accuracy data [$F(1,22)$, $p=.04$, partial $\eta^2=.2$], whereby correlational analyses showed a significant positive relationship between left visual field-presented stimuli, and a significant negative relationship between right visual field-presented stimuli and state anxiety levels. Here, as anxiety increases, accuracy increases for left visual field stimuli, whereas the opposite pattern is observed for right visual field stimuli. (Figure 5.24). In unpacking the interaction, the difference between LVF and RVF target location was calculated by subtracting LVF RTs from RVF RTs. This resulted in a range of difference response time scores from negative to positive values, relative to the mean-centred anxiety scores. Post-hoc Spearman's Rho analyses revealed a marginally significant relationship between visual field and anxiety scores [$Rho=-.32$,

p=.05], suggesting that as anxiety increases, participants become less reliant on a dominant visual field for accurate target identification.

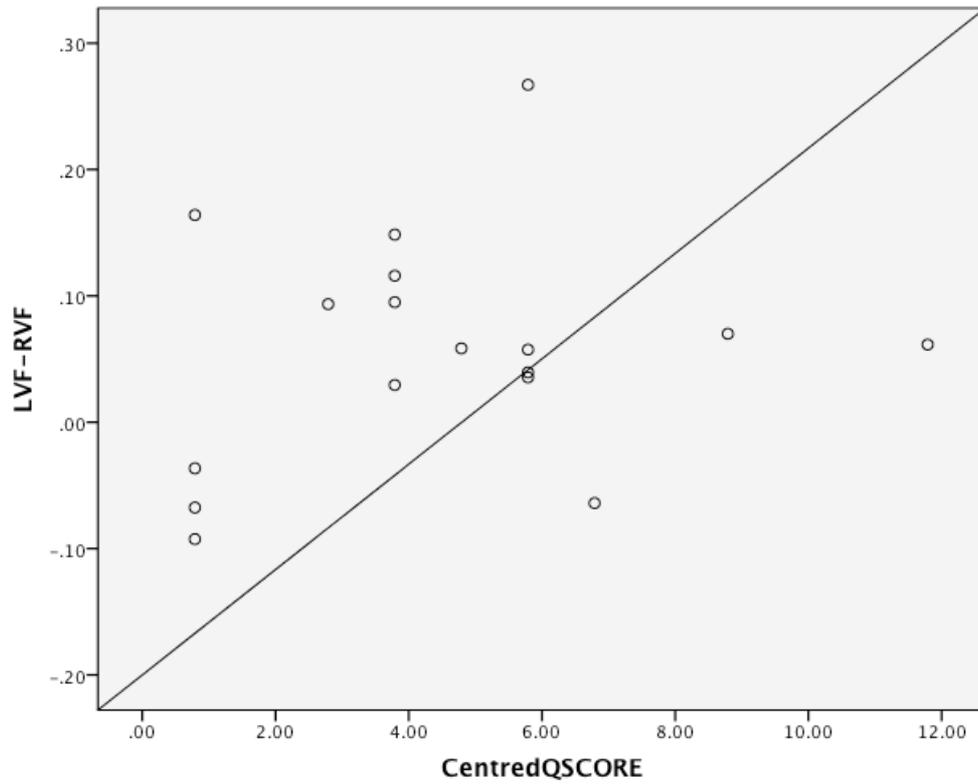


Figure 5.24 Scatterplot shows the relationship between the calculated VF difference (LVF-RVF) as a function of mean-centred questionnaire score (anxiety).

5.3.2.3 EXPERIMENT 5.2 SUMMARY

Findings from the present experiment not only replicate the core interactions shown in Expt. 4.1, chapter 4 for both response speed and accuracy, but also reveal further, more complex relationships across factors and in terms of the covariate. Preliminary ANOVAs in the present experiment showed an RVF response speed advantage for happy faces and an LVF response speed advantage for angry faces. Visual field location of target stimuli appeared to modulate response speed regardless of type of affect, with ambiguous stimuli eliciting quicker responses when on the LVF, and salient stimuli eliciting quicker responses when on the RVF. In terms of accuracy, showed an overall LVF advantage for both angry and happy faces regardless of sound, with happy faces receiving more accurate responses overall. Ambiguity of expression appeared to modulate response accuracy for happy faces, whereby ambiguous happy faces on the LVF were more accurately responded to, as were happy faces on the RVF. Although sound did not interact with emotion, visual field location or salience, receding sounds consistently elicited quicker and more accurate responses overall.

Findings from the present experiment provided evidence for the modulatory role of state anxiety in responses to facial expressions of affect when paired with additional auditory threat (looming and receding sounds). State anxiety in the present study was found to interact with the visual field location of target stimuli, regardless of the nature of the emotion observed (angry vs. happy).

For response latency, significant relationships between visual field location (left vs right) and state anxiety showed left visual field stimuli eliciting decreased response latency as a function of increasing anxiety, whereas right visual field stimuli revealed the opposite pattern (increased response latency as anxiety scores increased). For detection accuracy, it was again visual field location that interacted with state anxiety, whereby left visual field stimuli showed increased accuracy as a function of increasing state anxiety and right visual field stimuli elicited decreased accuracy as state anxiety increased. Emotion appeared to play an additional modulatory role to that of anxiety and visual field location in terms of successful visual target detection accuracy in the form of accuracy differences between the two emotions only for post detection threshold intensities (2 and above), repeating the pattern of higher

accuracy for happy affect over angry observed in previous experiments in the present thesis (experiments 2.1, 3.1, 4.1).

Findings from the present experiment suggest that in the presence of additional, auditory threat acting as a localizer of the source of potential danger, it is response efficiency based on visual field location of target stimuli (facial expressions) that is the most affected when individual state anxiety is taken into consideration.

5 EXPERIMENT 5.3

OVERVIEW

The present experiment focused on two types of negative affect (anger/fear), in an attempt to examine the modulatory role of gaze direction (direct vs. averted), visual field location, salience intensity and anxiety on participants' response efficiency. Based on suggestions that angry faces paired with direct and fearful faces paired with averted gaze should elicit quicker and more accurate responses, this study hypothesises that angry faces with direct gaze and fearful faces with averted gaze will elicit quicker and more accurate responses when presented on the left visual field, with participants' individual anxiety further enhancing response speed and accuracy.

5.2.3 METHODS

5.2.3.1 SUBJECTS

Twenty-five neurologically healthy adults (Undergraduate students, Department of Psychology, City University London) took part in this study (2 males; mean age: 20.1, SD: 2.3). Participants were recruited through online advertisements on the University's online experiment participation tool (SONA). Poor quality data from a further three participants were omitted from analyses due to improbable reaction times (<300ms). All participants were right-handed with normal or corrected to normal vision and had given written consent prior to testing.

5.2.3.2 APPARATUS & MATERIALS

Laboratory setup and apparatus was the same as in Experiment 4.2, chapter 4, with the addition of Spielberger's 20-item State Anxiety scale (Spielberger et al., 1970).

5.2.3.3 STIMULI & PROCEDURE

Visual target stimuli used in practice and test experimental blocks were the same as those used in Experiment 4.2, Chapter 4 (i.e. gaze direction manipulated facial expressions of fearful and angry affect of varying expression salience). The computer-based paradigm used in Experiment 4.2 was also used in the present study, without however the inclusion of the auditory (looming/receding) sounds originally used in experiment 4.2. The sole procedural addition was that of the State Anxiety scale (Spielberger, Gorsuch, & Lushene, 1970) administered to each participant prior to commencing the computer-based task. Subsequently, participants were tested under a total of 60 experimental conditions (totalling 3600 experimental trials), so as to incorporate each level of the 4 factors (gaze direction, type of emotion, visual field location, and expression salience intensity).

5.2.3.4 DESIGN

Experiment 5.3 employed a 3x2x2x5 repeated measures factorial design, with gaze direction (ahead, gaze-left, and gaze-right), emotion (angry/fearful), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors. Two dependent measures of response efficiency were collected, in the form of manual response times (button press, measured in ms), and accuracy scores (% correct).

5.2.3.5 DATA PREPARATION & ANALYSIS

Raw reaction time data were filtered to exclude values from incorrectly responded to trials, as well as response times less or more than 2 standard deviations from the mean. Mean reaction times and mean accuracy scores (% correct) were calculated per experimental condition, per participant using E-Data Aid (E-Prime, Psychology Software Tools, Pittsburgh, MA). Questionnaire scores were aggregated per participant, and mean-centred prior to inclusion in subsequent analyses. Analyses reported in the following results section have all been Greenhouse-Geisser corrected.

5.3.3 RESULTS

5.3.3.1 REACTION TIME

A repeated-measures ANOVA was computed utilising gaze direction (ahead/left/right), emotion (angry/fearful), visual field location (left/right), and expression intensity (1-5) as within-subjects factors on the reaction time data. The analysis produced a significant main effect of emotion [$F(1,24)=19.2$, $p<.001$, partial $\eta^2= .45$], whereby angry faces were responded to quicker (mean=519, SE=16.1) than fearful faces (mean=530, SE=17.5). A further significant main effect of expression intensity was found [$F(4, 96)=14.3$, $p<.001$, partial $\eta^2= .43$], where Bonferonni-corrected multiple pairwise comparisons revealed significant differences across all intensity pairs. The main effects observed in these data replicate those found in Exp. 4.2, ch. 4. Analysis of the reaction time data did not reveal any significant interactions, and did not replicate the interactions between emotion and sound, and that of emotion and visual field that were found in the Exp. 4.2 RT data.

Repeated-measures ANCOVA was conducted using gaze direction (ahead, gaze-left, gaze-right), emotion (angry/fearful), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the reaction time data. This analysis yielded no significant interactions between the factors and the covariate.

5.3.3.2 ACCURACY

A repeated-measures ANOVA was computed utilising gaze direction (ahead, left, right), emotion (angry/fearful), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors on the accuracy data. The analysis produced a significant main effect of emotion [$F(1, 24)=51.5$, $p<.001$, partial $\eta^2= .47$], whereby angry faces elicited higher accuracy (mean=.76, SE=.02) than fearful faces (mean=.66, SE=.01). A further significant main effect of expression intensity was found [$F(4, 96)=97.4$, $p<.001$, partial $\eta^2= .80$], where Bonferonni-corrected multiple pairwise comparisons revealed significant differences across all intensity pairs.

Unlike the accuracy data findings in Exp. 4.2, ch.4, the ANOVA on the present accuracy data revealed a significant interaction between visual field location and gaze direction [$F(2, 48)=9.3, p<.001, \text{partial } \eta^2= .31$], whereby a left visual field accuracy bias was observed for faces gazing ahead and left, with a right visual field accuracy bias for faces with right gaze (Fig. 5.25).

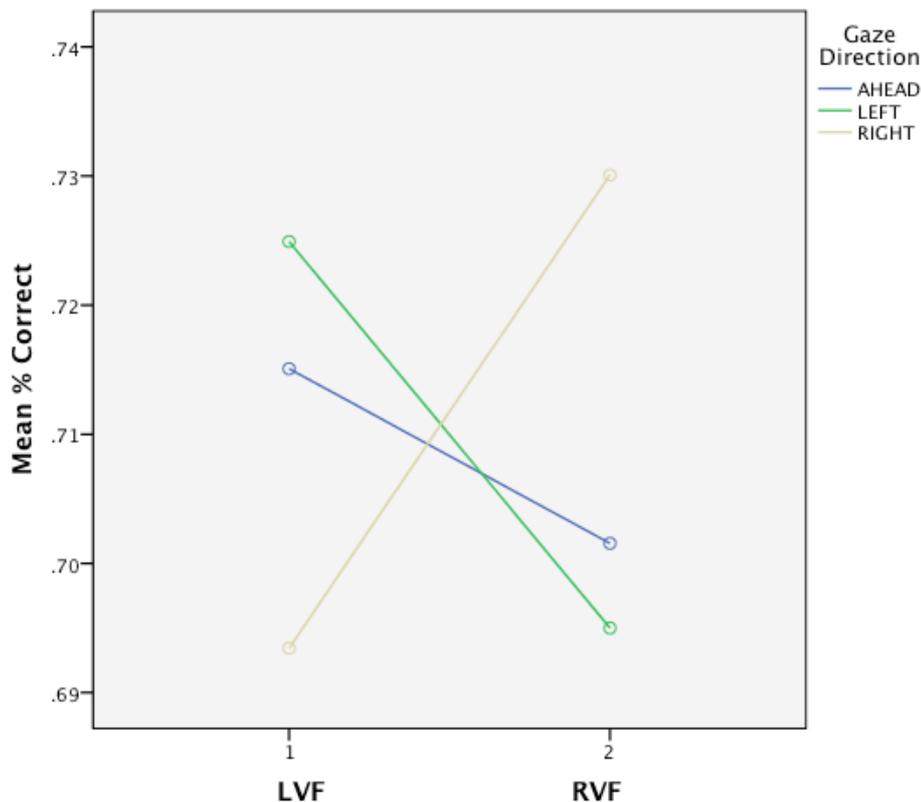


Figure 5.25 Line graph illustrates the three levels of gaze manipulation (gaze ahead=blue line, gaze-left=green line, and gaze-right=beige line) across the two visual fields respectively for the accuracy data.

Replicating the emotion and expression intensity interaction found in the Exp 4.2, ch.4 accuracy data, the ANOVA revealed a further significant interaction between emotion and expression intensity in the present study [$F(4, 96)=8.80, p<.001, \text{partial } \eta^2= .31$], with angry faces achieving overall higher accuracy across expression intensities. In this case, accuracy for fearful ambiguous faces was evidently at chance, with a gradual increase as salience intensified until reaching ceiling for the highest salience expression. This pattern was significantly better for angry faces, where participants accurately responded to angry even for the most ambiguous intensities (Fig. 5.26).

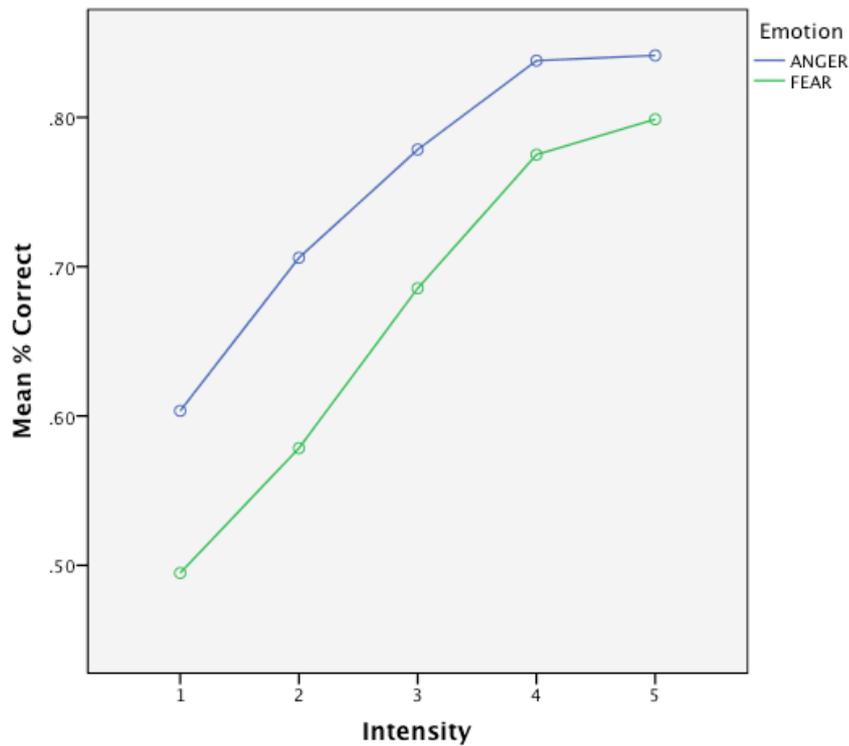


Figure 5.26 Line graph illustrates mean accuracy scores for angry (blue line) and happy (green line) faces as a function of expression intensity (1-5).

The three-way interaction between gaze, sound, and emotion originally found in the accuracy data of Exp. 4.2, ch.4 was not replicated here. Instead, the present ANOVA revealed a significant 4-way interaction between emotion, gaze direction, visual field location, and expression salience intensity [$F(8,192)=2.20$, $p=.03$, partial $\eta^2=.08$] (Fig. 5.26). In this interaction, whereby angry faces receive more accurate responses than fearful overall, accuracy responses to angry faces of ambiguous expression intensity (int. 1) appear to benefit from leftward gaze, with a stronger attentional cueing effect when target stimuli appear on the visual field congruent to gaze (LVF). There is no specific benefit of direct over averted gaze for the angry faces of salient intensities (int. 3-5). Gaze manipulation in fearful stimuli did not produce an accuracy advantage of averted over direct gaze, regardless of the salience of facial expression.

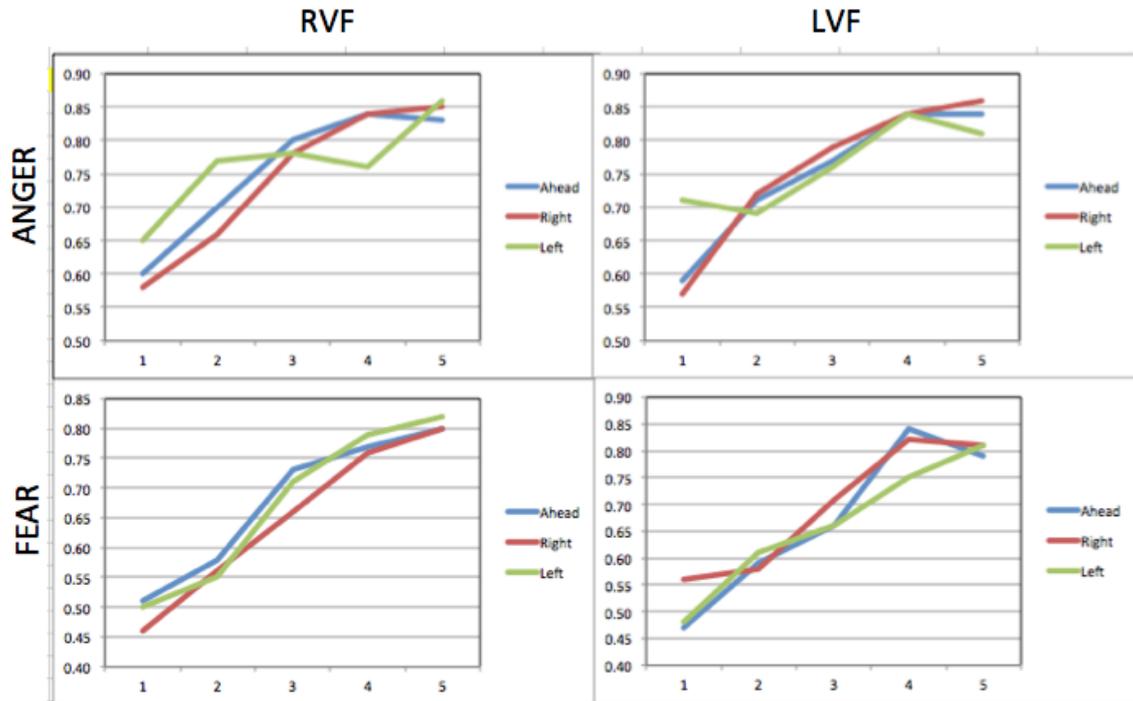


Figure 5.26 Plots display mean accuracy scores for angry (top) and fearful (bottom) faces in terms of ahead (blue), rightward (red), and leftward (green) gaze direction, as a function of expression salience intensity, and per visual field location (RVF = left plots / LVF = right plots).

The ANOVA produced no further interactions for the accuracy data.

Repeated-measures ANCOVA was conducted using gaze direction (ahead, gaze-left, gaze-right), emotion (angry/fearful), visual field location (left/right), and expression salience intensity (1-5) as within-subjects factors and mean-centred State Anxiety scores used as a covariate, on the accuracy data. No significant interactions were found between the factors and the covariate were observed for these data.

5.3.3.3 EXPERIMENT 5.3 SUMMARY

This experiment employed gaze direction (ahead, leftward and rightward) on two negative types of affect (anger/fear) to test the assumption of a possible modulatory relationship between individual levels of state anxiety and response efficiency. Aside from the addition of the anxiety scale, the paradigm employed here was a direct replication of Exp. 4.2, chapter 4. Surprisingly, the response speed data did not replicate any of the original interactions (i.e. sound * emotion, and emotion * visual field) found in Exp. 4.2. Specifically, preliminary ANOVA analyses for the response time data did not reveal an interaction of gaze and visual field location as originally hypothesized. Instead, the speed of participant responses appeared to be biased towards angry faces overall, regardless of visual field location, direction of gaze, or expression salience. Analysis of the accuracy data however, did partially replicate findings from Exp. 4.2; the original interaction between emotion and expression salience was also present in the 5.3 data, but the three-way interaction across sound gaze and emotion seemed to now disappear. Instead, the preliminary ANOVA for the accuracy data however showed a significant interaction across all four factors (gaze, emotion, location, intensity), whereby the most ambiguous angry faces elicited higher accuracy when displaying leftward gaze, and presented in the left visual field. Salient angry stimuli did not reveal a particular advantage for direct vs. averted gaze. For fearful faces, there was no effect of averted vs. direct gaze for any of the expression intensities.

When including individual anxiety scores as an analysis covariate, findings from the present experiment did not reveal a modulatory role for individual state anxiety levels on response efficiency. Instead, participant responses were predominantly guided by a combination of gaze direction and visual field location for both types of affect. Responses were quicker and more accurate for angry faces overall, with accuracy being optimum when a rightward gaze and right visual field visual target presentation were combined. In the present experiment, and given that all stimulus properties were bound to the visual domain, participants relied predominantly on gaze direction as a type of attentional cue for overall response efficiency, with type of emotion only influencing speed of responses.

5.4 DISCUSSION

Across three experiments, the present chapter investigated the modulatory effects of individual perceived state anxiety levels on response efficiency. This suggested modulation was investigated by utilizing specific factors, each of which had previously been found to influence the rapid engagement of emotional attention, and combines both visual and auditory emotion-manipulating contextual information.

Experiment 5.1 focused on the core distinction between positive and negative basic affect by employing angry and happy facial expressions of varying expression intensity in a speeded bilateral presentation target detection task, in addition to individual participant state anxiety scores. Findings from this experiment provided evidence for a speed-accuracy threshold trade off specific to high-ambiguity (intensity1) facial expressions; this trade-off was stronger for the less anxious participants, whereas for participants with higher anxiety, response accuracy depended less on response time, although high anxiety participants tended to provide faster and less accurate responses overall. Both positive and negative affect were subject to this speed-accuracy trade off, however angry faces in particular resulted in even quicker and less accurate responses for the highest in ambiguity facial expression stimuli. Happy stimuli on the other hand, did not exhibit the same decrease in accuracy for highly ambiguous facial expressions.

Experiment 5.2 investigated the modulating properties of anxiety in responses to audiovisual threat by using a combination of visual emotional angry and happy facial expressions paired with looming or receding sound stimuli. In this case, and given the strong localizing benefits that looming and receding sounds have been shown to elicit, visual field target location rather than emotion type significantly interacted with individual anxiety. It could be that in this case, the response bias that type of emotion was originally expected to elicit was replaced by the presence of sounds, and more specifically receding sounds which produced both a response speed and accuracy advantage. Left visual field stimuli produced quicker and more accurate responses as a function of increasing anxiety, possibly as a product of right hemisphere attentional engagement due to the additional auditory threat present; this assumption cannot be confirmed however, as in Exp. 5.2 the factor of sound did not interact with type of emotion. Whether the emotion displayed was positive or negative appeared to influence responses in terms of accuracy for stimuli past the discrimination

threshold (intensities 2 and over), whereby higher overall accuracy was achieved for happy expressions. It is possible that with the addition of threatening sounds, the response bias produced by visual field location of emotional stimuli might depend on individual anxiety; for this to be considered a true response bias, it should be independent of the location of the emotional target, which is the case in Exp. 5.2. In this experiment, it looks like there is a general bias towards hitting the left key when the stimuli are highly ambiguous, while accuracy remains very close to chance. The interaction accuracy and visual field was more prominent for the angry facial expressions, which resulted in more accurate responses when presented on the left visual field, potentially due to a preferential engagement of the right hemisphere in the processing of negative or threatening stimuli.

The final experiment (5.3) in the present chapter focused on the vision-only domain, by manipulating gaze direction of two types of negative facial expressions (fearful and angry) so as to observe the modulating properties of individual anxiety on response efficiency. When considering the accuracy of participant responses without including individual participant anxiety levels, a strong response bias specific to ambiguous angry faces with leftward gaze when presented on the left visual field results. When individual micro-differences in anxiety are included in the analysis, this relationship disappears, even though no significant relationship between state anxiety levels and overall performance was found. Instead, with individual anxiety included, gaze-direction proved to be a particularly strong visual attentional cue, guiding responses to the visual field congruent to target face location, regardless of type of emotion or salience of the expression. One possible interpretation might be that strong directional attentional cues such as gaze direction overtake any effect individual anxiety variability or nature of the emotion observed might have had in its absence. Interestingly, the benefits of gaze direction observed when gaze was combined with auditory threat (i.e. experiment 4.2, chapter 4), or when anxiety is not used as a covariate in the analysis (i.e. experiment 5.3, Fig. 5.26) diminish completely when sound is not included as an emotional contextual factor.

The present chapter has produced novel evidence for the dynamic influencing role of individual anxiety on response efficiency. An initial conclusion could be that anxious subjects are less hesitant at making a guess response when the stimuli are indistinguishable, and angry faces are always harder to distinguish than happy. On the one hand, the extent to which anxiety influences our responses appears to be

dependent on the nature of the emotion observed as it is primarily driven by negative affect, which is enhanced if the visual stimuli benefit from the localizing properties of auditory threat (i.e. in terms of correct target detection). However, when two types of negative affect include additional attentional cues of gaze direction, anxiety does not appear to influence response efficiency; instead, the location priming effects of face-gaze take over the modulation of responses.

5.4.1 AUTOMATICITY OF RESPONSES TO BASIC AFFECT DEPENDS ON INDIVIDUAL ANXIETY

Individual state anxiety was found to significantly influence both speed and accuracy of responses in the first two experiments of the present chapter. When participant anxiety levels were taken into consideration, the observable response resulting from exposure to short bursts of positive or negative facial expressions of affect that also varies in expression salience intensity manifests as a distinct speed-accuracy trade-off between response latency and accuracy of visual target detection. The stimulus display times of facial expressions utilised in the present Chapter's experiments included 50 (Exp. 5.1 & 5.3) and 100ms durations (Exp. 5.2); this resulted in behaviours that closely resemble startle-like reactions (Posner & Rothbart, 2007) that for each participant proved to be closely linked to the amount of behavioural arousal their individual anxiety level induced. The paradigms used in this chapter took advantage of the established relationship between anxiety, attention, and response to potential danger in the environment (Bradley et al., 2000; Mogg et al., 1993; Mogg et al., 1997, 2007), combined with the additional attention-grabbing benefits factors such as auditory threat (Leo et al., 2011; J. G. Neuhoff, 2004; Riskind, Kleiman, Seifritz, & Neuhoff, 2014; Romei et al., 2009; Sutherland et al., 2014) and face gaze-direction (Adams, Ambady, Macrae, & Kleck, 2006; Adams, Gordon, Baird, Ambady, & Kleck, 2003; Adams & Kleck, 2003; N'Diaye, Sander, & Vuilleumier, 2009; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004) have been shown to elicit. By examining these relationships in terms of the efficiency and directionality of observable behaviours that they are thought to inform, the change in response patterns depending on which emotion-manipulating factors were present became evident.

Some support for a preattentive processing of threatening (negative) affect as a function of anxiety was obtained when positive and negative facial expressions of affect were compared in terms of response speed and accuracy. When faces were highly ambiguous, individual differences in participant anxiety dictated what aspect of the behavioural response dominates. For instance, the more anxious participants were, the less accurate but quicker their responses to target stimuli were, albeit their responses showed a weaker correlation between response times and accuracy. Participants with low anxiety levels on the other hand showed a tendency to trade off speed for lower accuracy, whereby their slower responses allowed for better accuracy. One possible interpretation may be that whenever the stimulus is ambiguous, highly anxious participants resort to snap decisions that are on the one hand fast, but on the other very low in accuracy, as opposed to low-anxious participants that take longer overall to provide with a response. This may appear to happen more for angry faces, as they generally tend to be more ambiguous than happy facial expression stimuli. An alternative interpretation might be that the finding of highly ambiguous angry expressions resulted in a larger in magnitude effect of speed accuracy trade-off which further corroborates theoretical suggestions of an almost automatic processing of threat. The literature so far has provided examples of such automatic responses resulting from preattentive processing of threatening environmental stimuli (e.g. Bradley et al., 2000; Mogg et al., 1993; Mogg et al., 2007); in the case of the present chapter findings, similar automatic responses, potentially enhanced by the perceived threat of angry faces, were observed for visible, suprathreshold stimuli which were however ambiguous as to their emotional load. This could mean that when presented with ambiguous threat, highly anxious individuals tend to sacrifice accurate disambiguation in favour of speeded, reflex-like reactions. Interestingly, this pattern of the speed accuracy trade-off was not maintained when additional emotion-enhancing elements were added to the facial expressions. For instance, adding auditory threat translated into highly anxious participants relying on the enhanced cueing effects of visual field location, due to the heightened vigilance the threat-localising benefits of auditory threat pose on perception (i.e. Fig. 5.16 & 5.23). On the other hand, when focusing on the visual domain only by adding a gaze-direction manipulation on different types of negative facial expression, anxiety does not appear to influence participant responses,

perhaps due to the stronger visual attentional bias gaze direction induces on perception.

There are numerous examples in the literature suggesting that negative affect elicits startle-like responses in individuals that self-report high levels of anxiety. The individual physiological experience of anxiety has been shown to result in divergent activation patterns at a neuronal level during the perception of affect in a number of studies from the neuroimaging literature (e.g. Canli et al., 2001, 1998; Canli et al., 2002). Most of these examples however, are either based on findings from group comparisons (i.e. high vs low anxiety), which have been criticised as they are thought to exclude micro-differences between participants as noise, or utilise predominantly masked, unconsciously perceived emotional stimuli. Findings from the present chapter have demonstrated how modulated response patterns can occur from visible facial expressions of affect, and that this modulation is determined by the ambiguity of the facial expression as a function of individual anxiety. In the case of the presence of auditory threat, present findings demonstrate how the attentional urgency of disambiguating an ambiguous threatening facial expression is no longer modulating response efficiency as a result of increased participant anxiety. In this case, it is possible that the combined effects of sound and attentional bias of visual field location overtake any near automatic reactions that might have otherwise been produced. In the case of manipulated gaze direction, differences in individual anxiety levels did not modulate responses at all. Instead, angry faces with rightward gaze that were presented on the right visual field resulted in best accuracy – responses to fearful faces trended towards the conversely lateralised pattern, although this did not reach statistical significance (Fig. 5.27). A possible explanation for the lack of anxiety modulation in this case could be that the attentional advantage that peripheral presentation of gaze direction-manipulated stimuli have been shown to elicit and has been suggested to tap into the same early-onset attentional mechanisms recruited during processing of threat (e.g. Sato et al., 2004), is stronger than the vigilance-increasing properties produced by high, sub-clinical anxiety. Taken together, findings from all three experiments in the present chapter point towards the dynamic and adaptive modulating properties of anxiety, which appear to be either recruited or inhibited depending on the presence or absence of stronger attention-engaging cues.

5.4.2 CONCLUSION

To the author's knowledge, findings from the present chapter are the first to demonstrate individual anxiety dependent modulation across three methodologically comparable paradigms specifically designed to investigate the rapid engagement of attentional resources in response to basic facial expressions of affect. By utilising speeded target detection tasks as opposed to the typically used speeded or free-response emotion identification/classification paradigms, as well as by being the first series of experiments utilising individual anxiety scores instead of anxiety groupings comparisons in relation to basic affect, the present chapter illustrates the dynamic modulation imposed by anxiety on behavioural response efficiency. These novel findings suggest that the influence of anxiety translates into a speed accuracy response trade-off when the task requires participants to distinguish between positive and negative affect, and is particularly prone to highly ambiguous expression salience intensities that is further intensified for negative affect. A similar trade-off that utilises the attentional cueing benefits of visual field location and emotion results in the presence of auditory threat, therefore suggesting the potential adaptive response strategies anxious participants recruit based on the emotion-relevant contextual information attached to visual emotional stimuli. Finally, no trade-off is observed in cases where visual stimuli have undergone gaze direction manipulation and the emotions responded to both belong in the negative spectrum (i.e. fear and anger); in this case, it is the attentional cueing posed by the direction of gaze that inhibits the influence of anxiety.

6 CHAPTER 6: GENERAL DISCUSSION

6.1 CHAPTER OVERVIEW

The present thesis is concerned with the laterality of behavioural responses to facial expressions of primary affect. The empirical chapters in this thesis have introduced a novel behavioural methodology, utilising rapid, near-threshold stimulus display times (50-100ms) in a speeded target detection task, where the type of emotion (angry, happy, fearful) was irrelevant to participant responses. By keeping the underlying methodological parameters outlined in empirical chapter 2 constant, this paradigm was subsequently adapted across empirical chapters 3-5 to include specific factors that the affective behavioural and neuroscience literatures suggest as significantly manipulating stimulus valence and influencing emotional perception, so as to infer the extent to which preferential hemispheric engagement, as evidenced by response efficiency, depends on valence.

To briefly summarise, chapter 2 introduced a behavioural paradigm that effectively investigated behavioural lateralisation through measures of response efficiency. Chapter 3 suggested that subcortical lateralisation may be indirectly investigated through the same response efficiency measures, by examining visual field asymmetries in response to positive and negative affect via nasally and temporally viewed stimuli. Chapter 4 investigated the modulating properties of specific valence-enhancing factors and facial expression on responses to negative affect such as the presence of auditory threat, and manipulated gaze direction (rightward, leftward, gaze-ahead). Lastly, chapter 5 examined the behavioural manifestation of the modulating properties of individual variability in anxiety levels towards primary affect (angry, fearful, and happy). Findings from these chapters suggest an interpretation of laterality of response efficiency as being susceptible to modulation by both contextual and individual parameters. In the following sections, this chapter will first summarise the findings of the present thesis, will readdress the question of laterality based on the present results, and will then focus on the two key comparisons across paradigms of this thesis; namely, the happy vs angry comparison and the resulting happy face advantage, and the superiority of anger over fear which goes against

suggestions of a fear benefit repeatedly reported in the literature. Finally, this chapter will consider directions for future research based on implications from the findings of the present thesis.

6.2 SUMMARY OF EXPERIMENTAL CHAPTER FINDINGS

The first empirical chapter introduced a behavioural paradigm designed to investigate the hypothesis of differential hemispheric contribution in response to two distinct facial expressions of basic affect (anger and happiness) through measures of response efficiency. The decision to focus on developing a purely behavioural methodology was motivated by the lack of established response patterns in earlier behavioural studies of laterality as opposed to neuroimaging accounts suggesting distinctly lateralised activation depending on the type of emotion perceived. Although neuroimaging and neurophysiological studies on the suggested lateralised pattern of responses towards positive and negative affect have established distinctly lateralised subcortical activation routes that are known to increase vigilance and aid detection and response efficiency to basic emotional stimuli, reports from the behavioural literature have produced a variety of laterality patterns which seems to be dependent on the type of paradigm, type of stimuli, and stimulus and response time parameters. In experiment 2.1, participants were tasked with identifying the visual field location of the emotional face (left or right) – regardless of whether stimuli displayed a positive or negative emotion. Additionally, due to the usage of stimulus durations (i.e. within the 50-100ms range suggested by Posner et al) that are close to the detection threshold, responses collected may reflect spontaneous, reflexive reactions to the presence of emotional stimuli that might originate from individuals' inherent attentional bias towards valenced information.

A lateralised response pattern was observed for measures of response efficiency, showing an angry face advantage for response latency and a markedly less pronounced accuracy advantage when displayed on the left visual field (i.e. right hemisphere). Conversely, a happy face advantage was observed for both speed and accuracy when displayed on the right visual field (i.e. left hemisphere). In terms of response latency, this lateralised pattern was only significant for salience intensity 3 and diminished when stimuli became explicitly angry or happy (intensities 4 & 5). In terms of accuracy, happy faces showed specific advantageous processing for

accurate recognition when displayed on the right visual field while angry stimuli produced negligible differences. Across response efficiency measures, happy faces were quicker and more accurately responded to overall.

The significant response latency-specific laterality pattern evident only when stimuli were at salience intensity 3 may possibly be interpreted in terms of the ambiguity of self-relevance those particular stimuli pose on participants. Specifically, this particular intensity where the interaction between visual field location and type of emotion was observed was halfway between ambiguous and salient. The detection threshold analyses for both angry and happy stimuli showed that stimuli at this intensity were suprathreshold for correct recognisability. Combining stimulus near-threshold detectability with the rapid stimulus duration time used (50ms) may have resulted into not allowing higher-order cognitive perceptual processes that require overall cerebral engagement to take over, therefore restricting promoting reflex responses.

Findings from chapter 2 support hypotheses of lateralised responses to primary affect at a behavioural level as being dependent on valence (positive or negative) (Adolphs, 2002; Jansari et al., 2000; Killgore & Yurgelun-Todd, 2007; Reuter-Lorenz, & Davidson, 1981; Wedding & Stalans, 1985). Furthermore, this chapter demonstrated that this laterality occurs under very specific contextual, stimulus-driven parameters such as expression salience. It may be possible that behavioural lateralisation is not a sustained phenomenon, but instead its presence might depend on the contextual information attached to the stimulus (i.e. salience of expression, nature of the emotion observed). A possible overarching interpretation might highlight that emotional perception at this basic level is not a static process; it adapts, changes and translates into distinct patterns of behavioural manifestation depending on the presence or absence of additional relevant context. The contextual specificity that lateralised responses require as demonstrated in chapter 2 may be a possible explanation for contentious laterality patterns reported in the behavioural lateralisation domain.

Based on the prioritising nature of attentional mechanisms that are fine-tuned in filtering environmental information so that biologically significant stimuli such as facial expressions of emotion may be sped through and responded to efficiently, the neuroimaging and neurophysiological literatures have so far investigated in great detail the role of different subcortical structures in recognising, perceiving, and attending to emotions. The behavioural literature has in turn successfully used

asymmetries in visual attention and behaviour using nasal-temporal hemifield asymmetries as a behavioural index of subcortical activation. Given this background, Chapter 3 focused on an unexplored question in the literature: the use of nasal-temporal asymmetries as an indicator of subcortically driven, asymmetrically-distributed attention to positive and negative facial expressions.

Chapter 3 examined whether subcortically driven attentional asymmetries, previously reported in the literature as resulting from using subliminal or masked emotional stimuli would manifest as nasal-temporal hemifield preferences when using suprathreshold facial expressions of positive and negative affect. The methodology in chapter 3 utilised measures of response efficiency (participant manual reaction times and accuracy scores) as a response mode that might accurately reflect oculomotor behaviour. Contrary to predictions, data from experiment 3.1 did not find robust nasal-temporal asymmetries, apart from in the form of a marginally non-significant interaction between emotion and nasal/temporal hemifield for response latency. The hypothesis of nasal/temporal asymmetries resulting from the nature of the emotion observed was not confirmed, aside from temporally viewed happy faces producing marginally quicker response times.

Chapter 4 was concerned with the increased emotional importance stimulus contextual parameters such as auditory threat and direction of gaze in facial expressions might have on response efficiency. Across two experiments, the modulatory effects of auditory threat were examined first independently of, and secondly in conjunction to, gaze direction in relation to the reflexive responses these factors have been suggested to result in. To briefly reiterate main findings, receding sounds were shown to significantly influence response latency in the sound-only experiment, with happy faces resulting in quicker responses overall. A lateralised response accuracy pattern was found only for angry faces, which when on the left visual field were responded to more accurately than when on the right. The response speed benefit for receding sounds was also observed when the gaze-direction manipulation was introduced in the second experiment utilising only negative affect (angry vs fearful), with angry/receding stimuli producing the quickest overall reaction times. The response time advantage for receding stimuli was also observed within the fearful expressions, with fearful/receding achieving quicker responses than fearful/looming. Angry faces (regardless of sound) were always more accurately responded to regardless of directionality of gaze, as well as for both auditory stimuli.

Findings from this chapter provided new evidence for the modulation of behavioural responses to facial expressions of emotion that may relate more closely to startle-like reflexive responses instead of more higher-order, reflective responses.

Chapter 5 investigated the modulatory effects of individual perceived state anxiety levels on response efficiency in conjunction with the additional stimulus parameters of auditory threat and gaze direction, as well as by examining the effects of individual anxiety on the lateralisation of response efficiency based solely on the distinction between positive and negative affect. When considering the influence of anxiety on the lateralisation of response efficiency for positive and negative affect, the first experiment in chapter 5 revealed anxiety's significant influence in response efficiency to ambiguous – but still visible – facial expressions of affect. For response latency, the higher anxiety participants reported, the more speeded responses were to emotional expressions. The accuracy data reinforced the influence of stimulus ambiguity on response efficiency. Again it was the most ambiguous stimuli (intensity 1) that in this case elicited lower accuracy scores as a function of increasing state anxiety scores. Calculation of detection thresholds confirmed the speed-accuracy trade off for high ambiguity facial expressions. Although this was evident for both types of affect, angry faces in particular showed a larger magnitude of decreasing accuracy as state anxiety levels increased. The second experiment in chapter 5 provided evidence for the modulatory role of state anxiety in responses to facial expressions of affect when paired with additional auditory threat (looming and receding sounds). In this case, state anxiety interacted with target visual field location of stimuli, without valence influencing the direction or strength of these interactions. For response latency, significant relationships between visual field location (left vs right) and state anxiety showed left visual field stimuli eliciting decreased response latency as a function of increasing anxiety, whereas right visual field stimuli revealed the opposite pattern (increased response latency as anxiety scores increased). For detection accuracy, it was again visual field location that interacted with state anxiety, whereby left visual field stimuli showed increased accuracy as a function of increasing state anxiety and right visual field stimuli elicited decreased accuracy as state anxiety increased. Overall, findings from this experiment reversed the speed-accuracy trade off pattern observed in experiment 5.1. In the presence of additional, auditory threat acting as a localizer of the source of potential danger, it was response efficiency based on visual field location of target

stimuli that was the most affected when individual state anxiety is taken into account. Findings from the last experiment in chapter 5 did not reveal a modulatory role for individual state anxiety levels on response efficiency. This experiment employed gaze direction (ahead, leftward and rightward) on two negative types of affect (anger/fear) to test the assumption of a possible modulatory relationship between individual levels of state anxiety and response efficiency. Given the strong attentional cue gaze direction was shown to be in the absence of any additional contextual stimulus information, participant responses were predominantly guided by a combination of gaze direction and visual field location for both types of affect. Responses were quicker and more accurate for angry faces overall, with best accuracy achieved when a rightward gaze and right visual field visual target presentation were combined.

6.3 LATERALISATION

The behavioural literature reports inconsistent findings in terms of the unilateral vs bilateral hemispheric engagement specifically when perceiving and responding to primary emotions. For example, right-hemisphere engagement has been reported for the processing of both positive and negative, visual and auditory emotional stimuli (e.g. Borod & Caron, 1980; Borod et al., 1998; Borod, Koff, & White, 1983; Campbell et al., 1990; Hugdahl, Iversen, & Johnsen, 1993; Ladavas et al., 1980; Ley & Bryden, 1979; McLaren & Bryson, 1987; Safer, 1981). Conversely, right-biased lateralisation which is less prominent for positive (vs negative) affect has also been reported in studies using the same types of stimuli (i.e. audiovisual affect) (e.g. Dimond, Farrington, & Johnson, 1976; Ehrlichman & Halpern, 1988; Ley & Bryden, 1979; Sackeim, Gur, & Saucy, 1978; Sackeim & Gur, 1978). Other behavioural work reports negative emotion-specific laterality effects, with no converse lateralisation for positive emotions (e.g. Best, Womer, & Queen, 1994; Bryden, Free, Gagné, & Groff, 1991; Mandal et al., 1999), but at the same time, there has been a number of studies suggesting that it is positive affect that is preferentially processed by the left hemisphere, while negative affect is processed by the right hemisphere. This lateralisation pattern (positive/LH vs negative/RH) has been predominantly found in studies investigating visual field asymmetries during visual presentation of emotional stimuli such as faces and words (Lane et al., 1997; Moretti, Charlton, & Taylor, 1996;

Reuter-Lorenz et al., 1990; Reuter-Lorenz, & Davidson, 1981; Schwartz et al., 1979; Van Strien & Valstar, 2004; Van Strien & Van Beek, 2000).

Findings from the present thesis add some clarity to the discrepancy across laterality patterns in the literature. By developing a methodologically comparable experimental protocol across studies, the thesis has managed to show that lateralised processing of affect is indeed an observable effect, but this effect is highly dependent on the methodological context within which it is examined. Across studies comparing positive versus negative facial expressions, less salient stimuli (lowest intensities) were the ones that consistently produced lateralised responses according to the valence hypothesis (happy/LH and angry/RH). It became evident that the higher the expression salience, the more likely an overall left visual field bias (and therefore RH engagement) guided participant responses. It seems as though when the nature of the emotion conveyed by a stimulus is not particularly clear to the observer, participants are more sensitive to subtle emotional nuances within the stimulus and subsequently result in clear, emotion-dependent unilateral engagement. Analyses of detection thresholds across studies in the thesis add further support to the laterality hypothesis. For threshold measures across paradigms, a very clear lateralisation pattern in terms of accurate target detection was observed. Specifically because thresholds are not dependent on specific intensities or non-linearities of measurement scales that tend to compress performance at floor and ceiling, they offer a valid gauge on lateralisation. Essentially, the type of emotion results in differential hemispheric engagement at very early stages in the perception process; when stimuli are of ambiguous salience, and therefore require the engagement of rapid-onset, fast-route bottom-up attentional networks. The fact that lateralisation patterns are particularly difficult to replicate simply adds to this interpretation. Specifically, it would be near impossible to successfully replicate laterality patterns that result from behavioural observations, unless the temporal profile of the emotional attention process can be successfully and systematically captured. The present thesis has therefore laid the groundwork for a methodology that attempts to systematically investigate the onset-offset of emotion-specific lateralisation purely based on measures of response efficiency.

6.4 POSITIVITY BIAS

In the present thesis, all paradigms employing happy facial expressions found a robust and consistent response bias for happy faces (both in terms of response latency and accuracy), which did not falter even when the emotional load on the facial expression was manipulated by the addition of emotion-enhancing factors such as sound (i.e. Exp. 4.1 & 5.2). Unlike the weaker, and context-dependent laterality effect, a happy face bias was present at all expression salience intensities when compared to angry faces. In terms of detection thresholds, all paradigms in the present thesis apart from exp. 3.1, ch.3 (nasotemporal), showed a significant difference between the expression intensity required for happy vs angry faces to become accurately detectable by participants in a time-limited forced-choice response setting. This finding is in line with a proportion of the behavioural literature that posits a happy advantage often correlated to participant mood and emotional state, and particularly in studies using facial expression morphs (i.e. gradual progression from neutral to emotional within a dynamic display). For example, Joorman and Gotlib (2006) conducted an emotion-identification behavioural study whereby they examined differences in correctly identifying the target facial expression of emotion in groups of depressed, socially anxious, and control participants. The authors used dynamic facial expression morphs, where a neutral expression would gradually change into a happy, sad, or angry one. Joorman and Gotlib observed that out of all three participant groups, the depressed participants consistently produced more accurate responses in identifying happy expressions instead of sad or angry ones (Joormann & Gotlib, 2006). Additional support for this effect comes from more recent work by Becker et al, who showed that when using facial expression dynamic morphs of happy and angry expressions, happy faces are accurately identified more quickly than angry (Becker et al., 2012). In a similar vein, work by Jackson and Arlegui-Prieto that investigated individual normal (i.e. non-clinical) mood state of participants correlating to speed of accurate emotion detection and speed of change of expression overall reported that the higher participants' positive mood was, the less sensitive they were in identifying the appearance of negative (angry, sad) expressions (Jackson & Arlegui-Prieto, 2016). These examples from the literature have shown that in dynamic facial expression displays (i.e. morphs), an overall positive bias is present even when the emotion of the stimulus is

subtle and highly ambiguous. A similar happy face advantage has been observed in static emotion displays employed in visual search tasks where for example happy faces are more quickly and accurately identified as targets as opposed to angry and fearful faces (Juth et al., 2005), and has also been shown in studies using schematic faces (as opposed to photographs) of facial expressions (Leppänen & Hietanen, 2004). The experiments in this thesis that have utilised happy expressions verify this positivity bias, in the context of static facial expressions displayed for near detection threshold durations, and of varying expression salience. In light of the threshold calculations across these experiments, a consistent trend of earlier and more accurate target detection for ambiguous happy stimuli. Contrarily to the weaker and less reliably replicable laterality effect across paradigms, the positivity/happiness advantage appears to be a strong and consistent trend. This finding does go against the literature of an anger, or threat, advantage which has been observed particularly in studies utilising schematic representations of facial affect (e.g. Horstmann, 2007; Horstmann & Bauland, 2006). Discussions in the empirical chapters of this thesis have considered as a tentative interpretation the possibility of social ambiguity that happy, low salience faces may potentially convey. This interpretation seems logical particularly from an evolutionary perspective; the most successful and effective predators are those who are able to hide their negative intentions. As a defence mechanism therefore, it may be the case that we are fine-tuned in quickly responding (and allocating our attentional resources) to ambiguous happy stimuli, possibly as they may signal the presence of an underlying abstract threat. A slightly more concrete conclusion however may be that we are essentially drawn to (and subsequently respond to) positive emotions overall.

6.5 ANGER SUPERIORITY OVER FEAR

Another key finding from experiments in the present thesis was the lack of a response efficiency benefit for fearful faces when compared to angry. Particularly in the neuroimaging literature reviewed, a consistent and very robust effect for fearful faces in terms of lateralised responses has been reported (see ch. 1 for a discussion). The two experiments in the present thesis that directly compared fearful faces to angry did so in conjunction to additional emotion-enhancing factors such as gaze direction (direct vs. averted) and the presence of auditory threat (looming vs.

receding sounds). These two studies found no evidence of a laterality effect specific to fear, with angry faces (particularly when paired with receding sounds and direct gaze) seem to bias participant responses overall. In the literature, fear is reported as a useful social signal that alerts the observer to the presence of potential danger; especially if the fearful face is paired with gaze that is averted from the observer and could therefore be interpreted as gazing towards the location of the threat. For example, Adams and Kleck (2003a) examined the influence of gaze on responses over two behavioural paradigms, where participants were shown angry, happy, fearful and sad stimuli that were either blended or pure expressions. The authors manipulated gaze direction to either averted (left vs. right hemifield), or directed to the observer. Response latency findings from the two studies confirmed that correct categorisation of emotion resulted from an interaction between direction of gaze and emotion displayed, whereby both angry and happy faces with a direct gaze were responded to more quickly, and fearful and sad faces with averted gaze were responded to more quickly (Adams & Kleck, 2003a). Interestingly however, a subsequent attempt to replicate Adams and Kleck's gaze direction and emotion interactions by Bindermann et al however failed to reproduce the same patterns of behavioural responses (Bindemann et al., 2008), which was also the case in the two paradigms in the present thesis utilising fearful faces with manipulated gaze. Specifically, two experiments reported by Bindermann et al, which were designed to replicate Adams and Kleck's emotion and gaze direction interactions resulting from pure emotional facial expressions did not find significant differences between angry and fearful, or happy and sad faces as dependent on gaze direction. Bindermann and colleagues suggested that the lack of replication of the gaze-direction and emotion interactions reported by Adams and Kleck (2003a) might be a result of potential stimulus confounds (i.e. artificial vs naturalistic eye gaze manipulation). This is a plausible interpretation, as the highly sensitive nature of laterality and emotion-specific effects (aside from that for happy faces) is evident across results in the present thesis. Aside from the possibility of a stimulus artefact of the facial expression photographs and the type of gaze manipulation employed, another possibility is the strength of the receding sound effect which was replicated across the two studies utilising fear (as well as the studies that used sound and examined the difference of responses for happy vs angry faces). It could be the case that the receding sound translated into a form of positive emotion for participants; as the

receding sound implies danger moving away from the observer, it may have been interpreted through initial attentional filters as 'safe', i.e. positive. If this is the case, then the robust happy face advantage observed in the remaining paradigms is in this case observed through usage of receding sounds regardless of type of facial affect, and ambiguity of the facial expression. Another final possibility for the lack of a fear effect may be that it is not as strong a stimulus as happy or angry faces in terms of producing robust, lateralised behavioural responses. Essentially, fear-specific lateralisation may only be observable in terms of asymmetrical subcortical activation (e.g. Vuilleumier & Driver, 2007), and not in terms of visual-field asymmetries and behavioural response.

6.6 IMPLICATIONS AND DIRECTIONS FOR FUTURE RESEARCH

Results from chapter 2 lead to new, testable hypotheses. Given the contextual specificity needed for a distinctly lateralised pattern to translate into response efficiency, new research avenues could explore how laterality correlates to levels of physiological arousal. Although the present thesis is concerned with effects on observable behaviour, replication of the behavioural effects and the establishing of the contextual specificity required for laterality may be provided via additional physiological measures such as skin conductance and changes in heart rate. Further support for a context-specific interpretation may also come from future work involving primary affective stimuli of higher ecological and biological validity to the ones used in this thesis. For example, neuroimaging studies on emotional attention and perception often use masked phobic stimuli (i.e. spiders, snakes, mutilation scenes) (e.g. Canli, Desmond, Zhao, Glover, & Gabrieli, 1998; Carlsson et al., 2004; Lang, Bradley, & Cuthbert, 1997; Lang, Greenwald, Bradley, & Hamm, 1993; Miltner, Krieschel, Hecht, Trippe, & Weiss, 2004). The paradigm developed in chapter 2 may be adapted to utilise equally short presentations of masks (50ms) following subthreshold presentations of phobic stimuli (<50ms).

Findings from this chapter also raise questions as to the effect positive affect has on laterality. In terms of the interpretation offered in other work reporting strong happy facial expression response biases specific to gaze direction manipulated faces (e.g. Bindemann, Burton, Hooge, Jenkins, & de Haan, 2005; Bindemann, Burton, & Langton, 2008), it could be that a similar perceptual bias occurs; the near-detection

threshold stimulus display time of 50ms, paired with the simultaneously competing bilateral presentation of both neutral and happy stimulus could be falsely perceived as carrying a similar propensity for ambiguity of social intent to that of a happy face with averted gaze as Bindermann and colleagues report (2005; 2008). One alternative possibility may be that positive and negative affect draws from different, emotion-specific identification and recognition attentional systems, which result in emotion-specific response patterns, possibly occurring at differing latencies. Although investigated solely for negative affect in humans and animals (e.g. Adams, Gordon, Baird, Ambady, & Kleck, 2003; Adolphs, Russell, & Tranel, 1999; Bishop, Duncan, & Lawrence, 2004; Hoffman, Gothard, Schmid, & Logothetis, 2007; Kuraoka & Nakamura, 2007; Liddell et al., 2005; Straube, Langohr, Schmidt, Mentzel, & Miltner, 2010), this may be extended to include investigations of positive affect. Behaviourally, what might appear as a happy face advantage may be a product of a different activation network with distinct timing and cognitive processing demands, that results in sequence of processing and response events separate to that for anger. Findings from chapter 3 were discussed in relation to methodological and theoretical suggestions to interpret the lack of nasal/temporal asymmetries that was hypothesised to result from different types of emotional facial expressions. In terms of methodology, the decision of utilising response efficiency measures instead of the typically used choice saccades in this field of research (e.g. Mulckhuysen & Theeuwes, 2010; Simion, Valenza, Umiltà, & Dalla Barba, 1998; Sylvester, Shulman, Jack, & Corbetta, 2007) was addressed. A possible limitation specific to the paradigm utilised in Exp. 3.1 might be that although manual and saccadic responses have shown some overall differences in reference to different types of stimuli, these differences have not been successfully established in identifying nasal-temporal asymmetries. For example, in a target visual field location identification task, Bompas and Sumner found response latency differences only for both choice saccades and manual responses, with saccadic responses showing a more pronounced bias than manual responses (Bompas & Sumner, 2008). Although both response types displayed asymmetries towards the two competing stimuli, these differences were of different magnitudes. Another methodological limitation might relate to the type of paradigm used. Specifically, there are some suggestions in the literature that deviation from attentional cueing paradigms or distractor effect tasks might significantly impact the resulting presence or absence of behavioural nasal-temporal asymmetries. For

example, Bompas and colleagues, comment on the lack of replicable nasal-temporal asymmetry findings when different paradigms to the ones commonly reported have been used (Bompas et al., 2008). The authors suggested that as they observed differences in response latencies between the two types of responses collected, this might have been attributable to differences in the time taken from processing stimuli to making a decision to respond.

Although predictions on the existence of nasal-temporal asymmetries find a functional basis due to the existence of structural asymmetries in retinal projections to the midbrain, as well as on the existence of attentional asymmetries across the hemifields, findings from this field of research have not proven conclusive. For example, when attempting to identify the presence of asymmetries across a number of saccadic tasks by looking at landing point accuracy and saccadic latency, Jóhannesson and colleagues reported that while the saccadic latency measure identified no asymmetries, the landing point accuracy showed very moderate asymmetric activation (Jóhannesson et al., 2012). Jóhannesson et al highlight that superior colliculus mediated responses (in this example in the form of choice saccades) might be a more subtle effect than originally hypothesised (Jóhannesson et al., 2012). On the whole, this chapter attempted to implement a novel methodology to investigating nasal/temporal asymmetries through manual behaviour. The evidence suggests that such asymmetries are of a particularly subtle nature, and might not be robustly identifiable through manual response modes. A possible future consideration therefore could be the application of this paradigm using early onset involuntary saccadic responses (pre-saccades) as a more sensitive behavioural index for the behavioural manifestation of subcortically driven attentional asymmetries.

Chapter 4 produced novel evidence for the way in which facial expressions of affect combined with emotion enhancing contextual parameters interact in terms of observable behaviour. So far, investigations on the role that auditory threat and gaze direction have on perception have been limited either in terms of task demands (i.e. reflective versus reflex/startle responses), or in terms of how threat naturally occurs in the environment (audiovisual stimuli versus solely audio or solely visual). One main implication of findings from chapter 4 may be that audiovisual threat might be perceived as a unified percept, which specifically benefits anger (instead of fear). This benefit adapts from reflexive reactions (sound-only), to highly accurate responses in

the case of added contextual information in the form of eye gaze. Although evidence from the literature has suggested an advantage for looming sounds due to their threat localising benefits (e.g. Bach et al., 2015; Romei et al., 2009) that should in turn facilitate a looming bias in participant behavioural responses (e.g. Neuhoff, 2001), findings from chapter 4 showed the opposite trend. This may have been due to a stimulus artefact for receding sounds, although as addressed in chapter 4, including the suggested 10ms onset delay of sound stimuli reported in the literature (e.g. Leo et al., 2011) might have proven counterintuitive for the paradigm used.

The main implication of findings from chapter 4 is the highlighting of evidence for anger-specific lateralised responses of differing patterns. For example, in the sound-only study (exp4.1) increased accuracy was observed for left visual field angry faces while happy face accuracy was equivocal across visual field locations. In the gaze-direction and sound study (exp4.2), angry faces on the left visual field were responded to quicker, while fearful face response times were equivocal across visual field locations, regardless of face-gaze. Although evidence from the neuroimaging literature suggests the processing of fearful stimuli near the awareness threshold, in the case of behavioural responses anger biases reflexive responses. These findings add support to the suggestion of lateralised processing of primary affect being the product of a highly adaptive sequence of events, heavily-tied not only to the context within which it is being investigated (i.e. paradigm type), but also to the stimulus type itself (changes within facial expressions of affect such as directionality of gaze, ecological validity of natural vs. schematic/chimeric faces).

Although the final chapter in this thesis (ch 5) was concerned with individual variability outside of any participant groupings, there are some population elements that might provide further insight as to how basic emotional perception differs across individuals. Although primary emotions are universal across populations and therefore do not fall prone to any societal or cultural biases, factors such as gender differences might add further explanatory dimensions to basic emotional perception. Establishing the specific, individual nature of basic emotional perception might also find future clinical applications by establishing unique, individual emotion-related symptomatology outside of general patient groupings that might allow for the tailoring of subsequent treatments at an individual level. On the whole, this chapter demonstrated the importance of specific individual variability in basic emotional

perception, based on individual's background anxiety state. This might aid our understanding of the interaction between the theoretically separate primary and background emotional categories.

6.7 CONCLUSION OF THE THESIS

In summary, the present thesis investigated the lateralisation of response efficiency to valenced expressions of primary affect in relation to the modulatory role of specific affect-manipulating factors. By using methodologically comparable paradigms, experiments in this thesis introduced novel evidence for the laterality of response efficiency as being subject to modulation by both contextual and subject-specific parameters. The empirical chapters in this thesis have introduced a novel behavioural methodology, utilising rapid, near-detection threshold stimulus display times in a speeded target detection task, where the type of emotion (angry, happy, fearful) was irrelevant to participant responses. Upon establishing laterality patterns in accordance to the valence hypothesis in the original paradigm proposed in chapter 2 (negative emotions lateralise to the right hemisphere whereas positive emotions lateralise to the left hemisphere), subsequent chapters explored how the directionality of lateralisation changed depending on nasal vs. temporal hemifield presentation of stimuli under monocular viewing conditions, the presence of looming and receding sounds concurrent to visual facial expression stimuli, changes in gaze direction (direct gaze vs. averted), and finally in terms of individual participant anxiety.

Findings from this thesis lead to new research hypotheses concerned with the temporal profile of affect-specific behavioural lateralisation either combined with, or separate from additional emotion-enhancing factors (i.e. sound and gaze), the utility of behavioural measures as indirect indices of subcortical asymmetrical emotional attention networks, and the importance of individual variability in behavioural responses to basic emotional stimuli. A final, overarching conclusion is that behavioural lateralisation of primary affect is not a sustained phenomenon, but instead is a dynamic process, modulated by the contextual information attached to the stimulus.

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APPENDIX A

State Trait Anxiety Inventory

Read each statement and select the appropriate response to indicate how you feel right now, that is, at this very moment. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe your present feelings best.

| | 1 | 2 | 3 | 4 | | |
|---|------------|----------|----------|--------------|---|---|
| | Not at all | A little | Somewhat | Very Much So | | |
| 1. I feel calm | | | 1 | 2 | 3 | 4 |
| 2. I feel secure | | | 1 | 2 | 3 | 4 |
| 3. I feel tense | | | 1 | 2 | 3 | 4 |
| 4. I feel strained | | | 1 | 2 | 3 | 4 |
| 5. I feel at ease | | | 1 | 2 | 3 | 4 |
| 6. I feel upset | | | 1 | 2 | 3 | 4 |
| 7. I am presently worrying over possible misfortunes | | | 1 | 2 | 3 | 4 |
| 8. I feel satisfied | | | 1 | 2 | 3 | 4 |
| 9. I feel frightened | | | 1 | 2 | 3 | 4 |
| 10. I feel uncomfortable | | | 1 | 2 | 3 | 4 |
| 11. I feel self confident | | | 1 | 2 | 3 | 4 |
| 12. I feel nervous | | | 1 | 2 | 3 | 4 |
| 13. I feel jittery | | | 1 | 2 | 3 | 4 |
| 14. I feel indecisive | | | 1 | 2 | 3 | 4 |
| 15. I am relaxed | | | 1 | 2 | 3 | 4 |
| 16. I feel content | | | 1 | 2 | 3 | 4 |
| 17. I am worried | | | 1 | 2 | 3 | 4 |
| 18. I feel confused | | | 1 | 2 | 3 | 4 |
| 19. I feel steady | | | 1 | 2 | 3 | 4 |
| 20. I feel pleasant | | | 1 | 2 | 3 | 4 |

