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Assessing the impact of emotion in dual pathway models of sensory processing.

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Abstract

In our daily environment, we are constantly encountering an endless stream of information which we must be able to sort and prioritize. Some of the features that influence this are the emotional nature of stimuli and the emotional context of events. Emotional information is often given preferential access to neurocognitive resources, including within sensory processing systems. Interestingly, both auditory and visual systems are divided into dual processing streams; a ventral object identity/perception stream and a dorsal object location/action stream. While effects of emotion on the ventral streams are relatively well defined, its effect on dorsal stream processes remains unclear.

The present thesis aimed to investigate the impact of emotion on sensory systems within a dual pathway framework of sensory processing. Study I investigated the role of emotion during auditory localization. While undergoing fMRI, participants indicated the location of an emotional or non-emotional sound within an auditory virtual environment. This revealed that the neurocognitive structures displaying activation modulated by emotion were not the same as those modulated by sound location. Emotion was represented in regions associated with the putative auditory 'what' but not 'where' stream. Study II examined the impact of emotion on ostensibly similar localization behaviours mediated differentially by the dorsal versus ventral visual processing stream. Ventrally-mediated behaviours were demonstrated to be impacted by the emotional context of a trial, while dorsally-mediated behaviours were not. For Study III, a motion-aftereffect paradigm was used to investigate the impact of emotion on visual area V5/MT+. This area, traditionally believed to be involved in dorsal stream processing, has a number of characteristics similar to a ventral stream structure. It was discovered that V5/MT+ activity was modulated both by presence of perceptual motion and emotional content of an image. In addition, this region displayed patterns of functional connectivity with the amygdala that were significantly modulated by emotion.

Together, these results suggest that emotional information modulates neural processing within ventral sensory processing streams, *but not* dorsal processing streams. These findings are discussed with respect to current models of emotional and sensory

processing, including amygdala connections to sensory cortices and emotional effects on cognition and behaviour.

Keywords: Emotion; emotional processing; sensory processing; localization; visual streams; auditory streams; vision; audition; functional magnetic resonance imaging; multi-voxel pattern analysis

Co-Authorship Statement

Chapter 1 and 5, the introduction and general discussion respectively, were written by James Kryklywy with input from Derek Mitchell. Chapter 2, entitled “Emotion modulates activity in the ‘what’ but not ‘where’ auditory processing stream,” was written by James Kryklywy with input from all co-authors. Ewan Macpherson was involved in stimulus design, Steven Greening was involved in data collection and Derek Mitchell was involved in both experimental design and data collection. Chapter 3, entitled “Emotion modulates allocentric but not egocentric stimulus localization: Implications for dual visual systems perspectives,” was written by James Kryklywy with input from Derek Mitchell, who also assisted in experimental design. Chapter 4, entitled “Imaging Emotional Motion: interactions between emotional content visual and motion perception,” was written by James Kryklywy with input from Derek Mitchell and Joana Vieira.

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CHAPTER 1

1. Introduction

Imagine walking down a city street. You can hear cars rumbling past and people deep in conversation. You can see the faces of countless individuals each with their own perspectives and experiences. You can feel the shoulders of other passersby as you move through the crowds. Suddenly, you hear a single scream and everything seems more vivid than before. Your senses heighten; you are now a little more aware of your surroundings, noticing the world in new detail. These instinctive responses focus your senses onto specific objects in your environment, conveniently allowing you to process things more efficiently than before, while inconveniently holding your attention to specific objects, not allowing you to disengage. This situation, while possibly uncommon for many, is an example of the type of stress our sensory processing systems encounter on a daily basis. Within our environment, we experience a constant incoming stream of sensory information which must be sorted and prioritized to avoid becoming overwhelming. The emotional nature of an object and the emotional context surrounding an event are two factors that can greatly influence this prioritization.

1.1 Emotional Processing

Emotion can be portrayed as internal states elicited by reward or punishment, (Rolls, 2005), involving exposure to reinforcing stimuli or events, (i.e., emotional stimuli). These internal states are thought to originate as an evolutionary mechanism to represent a desire for, or an aversion to, an object/situation; they are a *common currency* which allows us to compare of the value of objects, and guide our behaviour towards approaching beneficial object/situations while avoiding detrimental ones (Rolls, 2000). Emotion is a multidimensional construct with two unique elements contributing to its representation: valence and intensity (Anderson et al., 2003; Anderson & Sobel, 2003; Bradley, Greenwald, Petry, & Lang, 1992; Kensinger & Corkin, 2004; Russell, 1980). Emotional valence is considered to be the nature of the response that a stimulus elicits along a positive-negative axis, while emotional intensity refers to the level of arousal it elicits (Bradley et al., 1992; Russell, 1980). To ensure the reliability of response elicited by a stimulus in any given experiment, emotional stimuli datasets commonly are validated and normalized with subjective rating acquired from a large sample population, with measurements of both valence and arousal (Bradley & Lang, 1999; Lang, Bradley,

& Cuthbert, 2005). Furthermore, emotions are considered transient states rather than lasting patterns of behaviour or states of mind. They are produced reflexively upon exposure to a particular stimulus or thought and decay quickly post stimulus, without encompassing multiple events and objects (Beedie, Terry, & Lane, 2005; Gross & Thompson, 2007; Rolls, 2000).

Casual observation of the world around us would suggest that people pay more attention to emotional rather than neutral stimuli. Empirical study supports this assumption. Considerable evidence suggests that emotional information has the ability to gain rapid, preferential access to brain resources, with emotional objects generally processed faster (Eimer, Kiss, Press, & Sauter, 2009; Kawasaki et al., 2001; Schupp et al., 2000), more likely to reach conscious awareness (Oliver, Mao, & Mitchell, 2015), and more captivating of spatial awareness (Calvo & Nummenmaa, 2008; Fox et al., 2000; Frischen, Eastwood, & Smilek, 2008; Lamy, Amunts, & Bar-Haim, 2008; Ohman, Flykt, & Esteves, 2001) than neutral ones. The effects of emotion are often reflexive and involuntary (L. F. Barrett, K.N., & Gross, 2007; Dolan & Vuilleumier, 2003; Ohman, 2002; Tracy & Robins, 2008), yet also heterogeneous in nature; the impact of emotion can have great variability between paradigm and participant (Vuilleumier & Huang, 2009). To understand what may underlie this variability, it is important to consider the neurocognitive systems that control emotional processing.

Emotions are processed in a distributed manner within the brain; diverse neural networks contribute to the representation of different positive and negative environmental cues (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Numerous overlapping emotional processing networks have been uncovered, including those implicated in the representation and identification of facial expressions (Vuilleumier & Pourtois, 2007), processing of emotional speech prosody (Fruhholz, Ceravolo, & Grandjean, 2012; Nicholson, Takahashi, & Nakatsu, 2000), and assessment of environmental threat (Frewen, Dozois, Joanisse, & Neufeld, 2008; Ohman, 2005; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006). Interestingly, the amygdala appears to act as a central hub within many of these networks.

1.1.1 The Amygdala

The amygdala is an almond-shaped structure comprised of a number of individual nuclei, located deep in the anterior medial temporal lobe. It exhibits extensive anatomical and functional connections to numerous regions across the brain (Amaral & Price, 1984; Bickart, Dickerson, & Barrett, 2014; Kim et al., 2011; Roy et al., 2009). In fact, a review by Young and collaborators (1994) indicated that the amygdala possesses some degree of structural connection to more than 80% of neocortical regions investigated in non-human primates (64 of 72 investigated regions; Young, 1993), including, but not limited to, ventral occipital lobe, prefrontal cortex, and inferior temporal lobe. In addition, it has been demonstrated that regions of both the auditory (Reser, Burman, Richardson, Spitzer, & Rosa, 2009) and visual cortex (Amaral, Behniea, & Kelly, 2003; Freese & Amaral, 2005) receive direct feed-forward projections from amygdaloid nuclei. Of note, however, anatomical connections with the amygdala *were not* found with some areas associated with the dorsal visual stream (see 1.3.1 for review of this pathway), including the frontal eye-fields and supplementary motor area, or the auditory 'where' pathway (see 1.2.1 for review of this pathway), including the most caudal regions of the superior temporal gyrus (STG; Young, 1993). Furthermore, in addition to extensive anatomical projections to neocortex, the amygdala also receives rich sensory inputs across modalities (LeDoux, 2007; Pessoa, 2008; Price, 2003). This extensive connectivity is believed to partially underlie emotion-related changes in perceptual experience.

While acting as a central hub in numerous emotion-related anatomical and functional networks, the amygdala is particularly involved in the processing of arousal and valence during the perception of both auditory (Fecteau, Belin, Joanette, & Armony, 2007; Scott et al., 1997) and visual (Breiter et al., 1996; Kapp, Whalen, Supple, & Pascoe, 1992; Kryklywy, Nantes, & Mitchell, 2013; Lane, Chua, & Dolan, 1999; D. Sander, Grafman, & Zalla, 2003) emotional stimuli. This provides further evidence of the amygdala's role as a central player in numerous large-scale emotion-related networks. Specifically, the amygdala appears to be involved in the representation of fear-learning and fear-related stimuli (Barad, Gean, & Lutz, 2006; Johansen et al., 2010; LeDoux, 2003; Ohman & Mineka, 2001). Its role in emotional processing is not limited to this, however, as evidence has implicated amygdala activity in the coding of positive

associations (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Hoffman, & Kilts, 2002; Paton, Belova, Morrison, & Salzman, 2006), the disambiguation of emotional expressions (Adolphs, 2002; Whalen, 1998), the representation of emotional voices (Fecteau et al., 2007; Scott et al., 1997), and reflexive emotional reactivity (Hare et al., 2008; Machado, Kazama, & Bachevalier, 2009). Moreover, functional brain imaging in humans has demonstrated that amygdala activity modulates the representation of objects in sensory processing areas (Lundy & Norgren, 2001; Morris et al., 1998; Ruden, 2005), potentially influencing perceptual experience.

1.2 Auditory System

Audition is the predominant way in which we are able to identify, localize and perceive objects that are outside of our current visual field. Studies investigating the structure and organization of the auditory cortex have revealed dual pathways of processing for sound localization and sound identification: the 'where' and 'what' pathways, respectively (Bushara et al., 1999; Maeder et al., 2001; Recanzone & Cohen, 2010). This architecture is reminiscent of, and likely inspired by, the 'vision for action' and 'vision for perception' streams identified for visual processing (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982) described below (see 1.3). Human auditory pathways appear to diverge from Heschl's gyrus (HG; Ahveninen et al., 2006) adjacent to primary auditory cortex (A1; Rauschecker & Romanski, 2011). Medial regions of this structure display activity that is not characteristic of property-specific auditory processing, while eccentric regions display activity associated with increased specialization (D. J. Barrett & Hall, 2006; Warren & Griffiths, 2003).

Additional evidence for the dissociation of auditory cortex into discrete 'where' and 'what' processing streams comes from a number of convergent methodologies. For example, a double dissociation of sound location and identity processing has been observed in cats between the posterior and anterior auditory field, respectively (Lomber & Malhotra, 2008). Furthermore, numerous neuroimaging studies conducted in humans have identified distinct cortical regions underlying processing of sound identity and sound-source location, generally dividing these functions along a posterior medial-

anterior lateral axis (e.g., Ahveninen et al., 2013; Alain, Arnott, Hevenor, Graham, & Grady, 2001; Hart, Palmer, & Hall, 2004; Maeder et al., 2001).

1.2.1 Posterior-Medial 'Where' Stream

While historically, there has been much difficulty performing neuroimaging studies on auditory localization, as the presentation of spatialized sounds is not trivial within an MRI scanner, substantial evidence suggests that sound location is processed in the posterior and medial portion the temporal lobe. Specifically, spatial cues used for localization are processed in regions posterior to A1 (Arnott, Binns, Grady, & Alain, 2004; Harrington, Stecker, Macpherson, & Middlebrooks, 2008; Rama et al., 2004; Rinne, Ala-Salomaki, Stecker, Patynen, & Lokki, 2014; Stecker, Harrington, Macpherson, & Middlebrooks, 2005), including the posterior STG, posterior superior temporal sulcus (STS) and the inferior parietal lobule (IPL). These areas appear to be functionally connected with regions of lateral prefrontal cortex (PFC), and the superior frontal sulcus (SFS). Together, these regions comprise a distributed network for spatial auditory processing (Ahveninen et al., 2006; Bizley & Cohen, 2013; Krumbholz, Eickhoff, & Fink, 2007; see Figure 1.1a).

The auditory 'where' pathway does not appear to display any topographical representation of sound, but rather exhibits generalized increased activity during tasks involving sound localization (Arnott et al., 2004; D. J. Barrett & Hall, 2006; Sestieri et al., 2006). Auditory localization tasks typically involve presenting sounds in dichotic listening paradigms, or within standardized virtual auditory environments. The general increase in activity, and lack of topographical representation, suggest a population rate code to represent sound location in human auditory cortex (Mizrahi, Shalev, & Nelken, 2014; Salminen, May, Alku, & Tiitinen, 2009). This method would allow sound locations to be represented by contrast between the rate of firing amongst separate populations of neurons (Miller & Recanzone, 2009). Indeed, it has been suggested that the representation of auditory spatial cues relies on two populations of neurons, each with widely tuned spatial sensitivity that encompasses the majority of an auditory hemifield (Salminen et al., 2009; Salminen, Tiitinen, & May, 2012). The level of activation contrasted between these two opponent populations is believed to reflect the location of

the auditory object (Stecker, Harrington, & Middlebrooks, 2005; Stecker & Middlebrooks, 2003). Additionally, there appear to be individual cortical regions that respond particularly well to sounds arising from broad locations within these broad receptive fields. For example, BA40 and BA37, show increased activation for sounds originating around the midline relative to eccentric positions (Zimmer, Lewald, Erb, & Karnath, 2006), suggesting increased processing of these environmental regions. Regions of frontal cortex, including SFS and inferior frontal cortex (IFC), also display neural activity modulated by sound location (Alain et al., 2001; Arnott et al., 2004). These regions appear to be functionally connected with both IPL and posterior STG, respond preferentially to task relevant stimuli (Ahveninen et al., 2006), and are implicated in the direction of attention to relevant information.

1.2.2 Anterior-Lateral 'What' Stream

While auditory spatial information appears to be processed along a posterior-medial-temporal to parietal to superior-frontal pathway, non-spatial auditory information is processed along an anterior-lateral-temporal to inferior-frontal axis. In humans, pitch, phoneme, and pattern recognition are initially performed alongside spatial localization within A1 (Obleser et al., 2006; Wessinger et al., 2001) and the planum temporale (PT; Arnott et al., 2004). While the spatial information is subject to further processing in the posterior-medial temporal lobes and subsequent areas (see 1.3.1), processing of identity related cues involves anterior regions of the temporal lobe, including STS, STG, and the anterior temporal pole, as well as regions of the inferior frontal gyrus (IFG; Alain et al., 2001; Arnott et al., 2004; see Figure 1.1b). Sound identification and classification processes performed within the auditory 'what' stream are exceptionally diverse in nature, including, but not limited to, focal and ambient environmental sounds (Doehrmann, Naumer, Volz, Kaiser, & Altmann, 2008; Engelien et al., 1995; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Lewis et al., 2004), pure auditory tones (Muller, Kleinhans, & Courchesne, 2001), speech (Binder et al., 2000), and non-linguistic vocalizations (Belin, Zatorre, & Ahad, 2002).

Evidence for and refinement of this theoretical pathway is supplied by multiple convergent results and methodologies. Neuroimaging studies have provided consistent

support for identity specific processing areas within auditory cortex (Ahveninen et al., 2006; Alain et al., 2001; Arnott et al., 2004; Bushara et al., 1999; Rama et al., 2004; Sestieri et al., 2006). Furthermore, additional evidence for a functional dissociation of auditory identity processing has come from studies using transcranial magnetic stimulation (TMS) as disruption of activity within the anterior auditory cortex produces significant impairments in sound identification processes (Ahveninen et al., 2013). Similar deficits in auditory identification are observed after lesions to anterior STS and middle temporal gyrus (MTG; Bidet-Caulet et al., 2009; Clarke et al., 2002; Nicholson et al., 2000; Trumpp, Kliese, Hoenig, Haarmeier, & Kiefer, 2013; Zundorf, Lewald, & Karnath, 2016). Additional evidence supporting this dissociation stems from reversible lesioning of auditory cortex performed in cats (Lomber & Malhotra, 2008) and electrophysiological recordings in macaques (Rauschecker & Scott, 2009; Rauschecker & Tian, 2000).

Interestingly, some auditory regions thought to be utilized primarily for early stages of sound location processing have also been found to display patterns of neural activity sensitive to auditory object identification. Specifically, human neuroimaging studies have found that identity-related processing occurs in both the posterior PT and posterior STS in regions immediately surrounding A1 (Benedict et al., 2002; Buchanan et al., 2000; Burton, Diamond, & McDermott, 2003). Indeed, nearly half of all sound-identity studies conducted have found activity within these regions (Arnott et al., 2004), suggesting a mixture of spatial and identity-related processing in early auditory areas.

1.2.3 Emotion in Audition

While much of the work investigating the impact of emotion on the senses has focused on the visual domain (see 1.3.4), emotional cues have some pronounced effects within audition as well. Emotional content can be recognized from auditory information across numerous different types of stimuli, including, but not limited to, language (Paulmann, Ott, & Kotz, 2011; Shanahan, 2008), verbal intonation (Wildgruber, Pihan, Ackermann, Erb, & Grodd, 2002; Wildgruber et al., 2005), music (Blood & Zatorre, 2001; Koelsch, Fritz, DY, Muller, & Friederici, 2006), and non-linguistic vocalizations (Aeschlimann, Knebel, Murray, & Clarke, 2008; Bachorowski & Owren, 2003; Laukka et al., 2013). Interestingly, while some of these cues are inherently culture-dependent (i.e.,

language), others appear to be more fundamentally characteristic of human auditory processing (Bachorowski & Owren, 2003). For example, non-linguistic affective vocalizations, particularly those representing primary negative emotional states, exhibit consistent and reliable emotional prosody (Aeschlimann et al., 2008) and can be distinguished uniformly across numerous cultures, akin to facial expression recognition (Laukka et al., 2013).

Emotional differentiation of sounds is performed very quickly during auditory processing with differences in neural activity identified between emotional and non-emotional sounds as early as 150ms post stimulus onset (Sauter & Eimer, 2010). Furthermore, emotional sounds appear to maintain an elevated status of processing prioritization, eliciting increased activation across large areas of auditory cortex within the temporal lobe (Buchanan et al., 2000; Ethofer et al., 2006; Ethofer et al., 2012; Fecteau et al., 2007; Wildgruber et al., 2002; Wildgruber et al., 2005). In addition to augmented activation of auditory cortices, emotional sounds also appear to cause significant changes in neural processing outside of the temporal lobe. Notably, both positive and negative vocalizations have been demonstrated to elicit increased amygdalar activation compared to neutral sounds (Fecteau et al., 2007; K. Sander, Brechmann, & Scheich, 2003).

There have been a number of studies which attempt to identify the ‘what’ of auditory emotion, (i.e., auditory features that carry emotional information). These studies have implicated specific auditory features in the experience of emotion from sounds, including fundamental frequencies (Arias, Busso, & Yoma, 2014; Kramer, 1963; Lieberman & Michaels, 1962; Protopapas & Lieberman, 1997), tempo (Kamenetsky, Hill, & Trehub, 1997; G. D. Webster & Weir, 2005), and amplitude (Scherer & Oshinsky, 1977). These features, however, are not necessary to evoke emotional responding and associated neural activation, as controlling for all of these characteristics does not always eliminate auditory affect recognition (Ethofer et al., 2006). In contrast to the extensive investigation of auditory features related to emotion, very little work has investigated the role of emotion on auditory spatial processing. While dichotic listening tasks suggest that crude spatial cues may impact the processing resources dedicated to

emotional sounds (Erhan, Borod, Tenke, & Bruder, 1998; Jancke, Buchanan, Lutz, & Shah, 2001), the exact impact of emotion on the representation of sound location remains unknown.

1.3 Visual System

To act with volition on an object in the immediate environment, generally one must first view and represent that object within the brain. For the majority of humans, this process is done predominantly by our visual systems. The human visual system is tasked with representing, identifying, and directing interactions between both stationary and moving objects in our environment. While some basic processing is completed by subcortical structures, such as the lateral geniculate nucleus of the thalamus (De Valois, 1960; Roska et al., 1993), superior colliculus, and amygdala (Pasley, Mayes, & Schultz, 2004), the majority of the higher order processing is performed at a cortical level.

Cortical visual processing is thought to be performed by two distinct pathways or streams (Ungerleider & Mishkin, 1982). Akin to the auditory processing streams previously discussed, the visual processing streams appear to be both anatomically segregated and functionally specialized (Goodale & Milner, 1992; Milner & Goodale, 1993). Much of the information processed in visual cortices enters the visual system at primary and secondary cortices, including V1 and V2 in the posterior occipital lobe. Beyond this, two visual streams quickly emerge (Baizer, Ungerleider, & Desimone, 1991; Ungerleider & Mishkin, 1982). A dorsal processing pathway, running between the occipital-temporal cortex and the posterior IPL (Goodale & Milner, 1992; Milner & Goodale, 1993), mediates visually-guided action and goal directed behavior (Goodale, 2011), though the exact nature of dorsal-visual functioning and its contribution to perception and visual awareness remains debated (Hebart & Hesselmann, 2012; Kravitz, Saleem, Baker, & Mishkin, 2011; Schenk, 2012; Schenk & McIntosh, 2010). In contrast, a ventral processing pathway, running between the occipital-temporal cortex and the inferior temporal cortex (Goodale & Milner, 1992; Milner & Goodale, 1993), mediates our perception of the world; that is, our conscious experience of ‘seeing’ (Kravitz et al., 2011; Milner & Goodale, 2006). It should be noted that complex behaviour relies on input from both systems. Thus, while segregation and separation of visual pathways does

exist, dynamic interaction between them must also occur (Cloutman, 2013; Goodale & Westwood, 2004; Himmelbach & Karnath, 2005; Lee & van Donkelaar, 2002).

1.3.1 Dorsal 'Vision for Action' Stream

The dorsal visual stream involves a series of neurocognitive structures, including dorsal portions of the occipital and temporal cortex, parietal cortex, and the superior frontal sulcus (see Figure 1.1c). Originating from visual area 5, and the extended middle temporal area (V5/MT+; Goodale & Milner, 1992; Rizzolatti & Matelli, 2003), there are numerous projections that comprise this pathway, including projections to visual area 3A, medial superior temporal areas, the fundus of the superior temporal area, and the ventral and lateral IPL (Ungerleider & Mishkin, 1982). This pathway has likely further extensions into the dorsolateral PFC (Foxe & Simpson, 2002), an area implicated in both spatial working memory (Iba & Sawaguchi, 2003; Kikuchi-Yorioka & Sawaguchi, 2000; Levy & Goldman-Rakic, 2000; Rypma & D'Esposito, 2003) and saccadic eye-movements (Funahashi, Bruce, & Goldman-Rakic, 1991). Output from the dorsal visual pathway is believed to influence cortical regions involved in motor control, as well as relay information to evolutionarily older visuomotor regions in the brainstem and midbrain. These include re-entrant connections to the visual thalamus and pulvinar (Kaas & Lyon, 2007), and a cortico-pontine-cerebellar pathway implicated in the refinement of visually guided movement (Glickstein, 2000). Notably, some of the cortical regions associated with more tertiary stages of this stream, such as IPL, are not exclusive to the dorsal visual pathway, but are also involved in the posterior-medial auditory pathway (Arnott et al., 2004) and may be involved in controlling spatial attention across domains (Behrmann, Geng, & Shomstein, 2004).

The primary function of the dorsal stream is related to the online direction of goal directed movements (Goodale, 2011). It specifies parameters of a movement to allow visual information to guide an interaction in real-time (Milner & Goodale, 2008) utilizing egocentric coordinates, or effector-specific frame of reference (Committeri et al., 2004; Zaehle et al., 2007). Structures within the dorsal stream receive bottom-up information relating to both visual target location and body positioning or direction (e.g., arm position) thus allowing processing in this stream to be diagnostic of the positioning of

these objects relative to each other (Thaler & Goodale, 2010). It, in turn, utilizes this information to modulate skilled action, rather than generating any noticeable visual percepts (Goodale, 2011). A frequently cited example of skilled action is that of reaching and grasping; the motion of the arm towards an object and the grip aperture scaling prior to grasping the object are both dorsal-mediated behaviours (Culham et al., 2003; Goodale & Milner, 1992; Milner & Goodale, 2008; Tanne, Boussaoud, Boyer-Zeller, & Rouiller, 1995). This mediation is particularly evident in visual stream lesion studies, in which patients with severe damage to the ventral visual stream retain their ability to grasp objects they are presented, while reporting no visual awareness of the item (Goodale, Milner, Jakobson, & Carey, 1991; Whitwell, Milner, Cavina-Pratesi, Barat, & Goodale, 2015). Of note, the dorsal visual stream is relatively insensitive to countermanding instruction (Pisella et al., 2000) and visual illusion (Haffenden & Goodale, 1998). When presented with two objects that are visually different in length yet, in reality, equal, grip aperture was scaled correctly while reaching directly to both objects (e.g., Müller-Lyer illusion; Bruno & Franz, 2009; Dewar & Carey, 2006). This demonstrates a resistance to task irrelevant information by the dorsal visual stream, an important characteristic to consider when investigating the effect of emotional distraction on visual processes.

1.3.2 Ventral 'Vision for Perception' Stream

Originally outlined in the primate cerebral cortex by Ungerleider and Mishkin (1982), the ventral visual stream originates at visual area V4, and proceeds along several routes to the anterior and inferior temporal lobe and ventrolateral PFC (Distler, Boussaoud, Desimone, & Ungerleider, 1993; Kaas & Lyon, 2007; M. J. Webster, Bachevalier, & Ungerleider, 1994; see Figure 1.1d). This pathway displays connections with a number of subcortical structures, including the striatum (Cheng, Saleem, & Tanaka, 1997; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Saint-Cyr, Ungerleider, & Desimone, 1990), nucleus accumbens (Kravitz et al., 2013) and amygdala (Amaral et al., 2003). The ventral visual stream is traditionally believed to act as a serial-staged hierarchical system; information enters the system from early visual areas at V4, and continues through anterior temporal and inferior frontal cortex (Macko et al., 1982; Ungerleider & Mishkin, 1982), undergoing a series of processing stages with increasingly complex cognitive representations of visual information (Serre, Oliva, & Poggio, 2007).

Recent anatomical and functional developments, however, suggests that a number of feed-forward and feed-back connection are involved in ventral visual processing (Rousselet, Thorpe, & Fabre-Thorpe, 2004), allowing for direct communication between different processing stages and the associated subcortical regions (Kravitz et al., 2013). Of particular interest here, the amygdala has extensive anatomical connection to a number of ventral visual areas (Amaral et al., 2003; Freese & Amaral, 2005).

While the exact nature of the dorsal visual stream remains debated (Hebart & Hesselmann, 2012; Kravitz et al., 2011; Schenk, 2012; Schenk & McIntosh, 2010), the theoretical characterization of the ventral visual stream has remained relatively stable. Processing in the ventral visual stream is understood to be involved primarily with tasks of object perception and identification (Goodale & Milner, 1992; Milner & Goodale, 2008) and utilizes a predominantly allocentric, or scene-based, frame of reference (Committeri et al., 2004; Schenk, 2006; Zaehle et al., 2007). Processing in this stream is related to the representation of enduring characteristics of objects and their spatial relation to one another (Milner & Goodale, 2008). For example, activity in the ventral stream has been related to short- and long-term visual memory (Bergmann, Rijpkema, Fernandez, & Kessels, 2012; Christophel, Hebart, & Haynes, 2012) and facial recognition (Davidenko, Remus, & Grill-Spector, 2012; Jeffreys, 1989; Nagy, Greenlee, & Kovacs, 2012; Rossion, Hanseeuw, & Dricot, 2012), and is modulated by such stimulus characteristics as reward value (Jakobsdottir, de Ruitter, Deijen, Veltman, & Drent, 2012). Much of the processing of specific stimuli categories is functionally clustered to particular regions of the ventral visual stream, with sub-regions of this stream displaying characteristic patterns of responding to specific classes of stimuli (e.g., faces; Rossion et al., 2012, scenes; Epstein & Kanwisher, 1998, tools; Beauchamp & Martin, 2007, etc.). Representational specificity of the ventral visual stream is thought to be developed by a combination of experience and properties of the underlying neural architecture (Kanwisher & Dilks, 2012; Kravitz et al., 2013). Unlike the dorsal stream, many processes in the ventral stream are susceptible to visual illusion. For instance in both the Titchener and Müller-Lyer illusions, identical objects are presented, yet are perceived to be of varying sizes. This underscores an ability of the ventral visual stream to be mediated by visual context and task irrelevant information.

Interestingly, some visually guided action appears to be heavily mediated by the ventral stream processes in addition to the expected dorsal stream processes. For example, pantomimed tool use relies on the recruitment of the ventral visual system to maintain a sustained mental representation of the tool to perform the action rather than direct interaction with the visual environment (Westwood, Chapman, & Roy, 2000). Similarly, delaying the performance of a visually guided action can cause additional recruitment of the ventral visual stream (Singhal, Monaco, Kaufman, & Culham, 2013), and disruption of these areas during delay has the ability to influence the trajectory, but not the end point, of a visually guided action (Cohen, Cross, Tunik, Grafton, & Culham, 2009). These examples highlight the complex interaction between the visual processing streams, and illustrate how minute changes in behaviour can greatly alter the neurocognitive systems required for their execution.

1.3.3 Motion Processing

Unique among visual processing areas are those whose primary function is to represent and decode motion. Movement and motion processing has typically been ascribed to regions of visual cortex known as V5/MT+ (Ahlfors et al., 1999; Riecansky, 2004; Thakral & Slotnick, 2011). These regions were originally identified in the macaque monkey along the middle temporal and medial superior temporal gyrus as a population of neurons with greater sensitivity to moving compared to stationary visual stimuli (Maunsell & van Essen, 1983a; Nowlan & Sejnowski, 1995; O'Keefe & Movshon, 1998; Wang, 1997). In addition to input from early visual areas V1, V2 and V3 (Maunsell & Van Essen, 1983b), V5/MT+ also receives direct input from multiple subcortical regions, including the pulvinar, thalamus, and superior colliculus (Lanyon et al., 2009; Schoenfeld, Heinze, & Woldorff, 2002). In humans, neuroimaging studies have found that area V5/MT+ responds to global motion (Giaschi, Zwicker, Young, & Bjornson, 2007), implied motion (Fawcett, Hillebrand, & Singh, 2007), and biological motion, including dynamic facial expression (Schultz, Brockhaus, Bulthoff, & Pilz, 2013; Schultz & Pilz, 2009; Trautmann, Fehr, & Herrmann, 2009), with the degree of activation related to salience-based characteristics such as motion velocity (Chawla, Phillips, Buechel, Edwards, & Friston, 1998; DeAngelis & Uka, 2003) and coherence (Aspell, Tanskanen, & Hurlbert, 2005). Interestingly, V5/MT+ also responds to stationary visual stimuli

during the perception of illusory motion (He, Cohen, & Hu, 1998; Tootell et al., 1995). Disruption of V5/MT+ processing with TMS can result in deficits in object speed processing (McKeefry, Burton, Vakrou, Barrett, & Morland, 2008) and motion recognition (Laycock, Crewther, Fitzgerald, & Crewther, 2007), behaviours necessary for direct visually-guided action with our immediate environment.

While traditionally thought to be subsumed by the dorsal visual stream (Born & Bradley, 2005), categorization of V5/MT+ within the two visual system hypothesis remains inconsistent. While the prevailing view remains that this region is primarily a dorsal stream structure (Born & Bradley, 2005; Goodale & Milner, 1992; Rizzolatti & Matelli, 2003), others advocate for an increased role as a contributor to ventral visual processing (Kravitz et al., 2013). V5/MT+ does indeed function as a relay for information entering the dorsal stream (Goodale & Milner, 1992; Maunsell & van Essen, 1983a; Rizzolatti & Matelli, 2003), exhibiting projections to tertiary regions of the dorsal processing stream (Maunsell & Newsome, 1987; Ungerleider & Desimone, 1986) while disruption of its activity can lead to impairments in reaching behaviours (Whitney et al., 2007). Bi-directional projections and functional connectivity, however, have also been established to subcortical structures more related to ventral stream processing, including the amygdala (Amaral et al., 2003; Young et al., 1994), and disturbances of V5/MT+ processes can lead to impaired word recognition (Laycock, Crewther, Fitzgerald, & Crewther, 2009). Furthermore, some critical function-related characteristics exhibited by V5/MT+ are more consistent with ventral-based processing than dorsal-based processing. For example, activation of V5/MT+ during the processing of static images has been linked with the presence of the motion aftereffect, a unique form of visual illusion (Antal et al., 2004; Culham et al., 1999; Fawcett et al., 2007; Hogendoorn & Verstraten, 2013; Tootell et al., 1995). This susceptibility to illusion is more consistent with ventral rather than dorsal stream processing. As such, it is an intriguing question of how these regions, which feed into the dorsal visual stream yet also display connections (e.g., to the amygdala) and functional limitations (i.e., susceptibility to illusion) consistent with the ventral stream, will respond to perceptual distraction typically associated with the ventral visual stream.

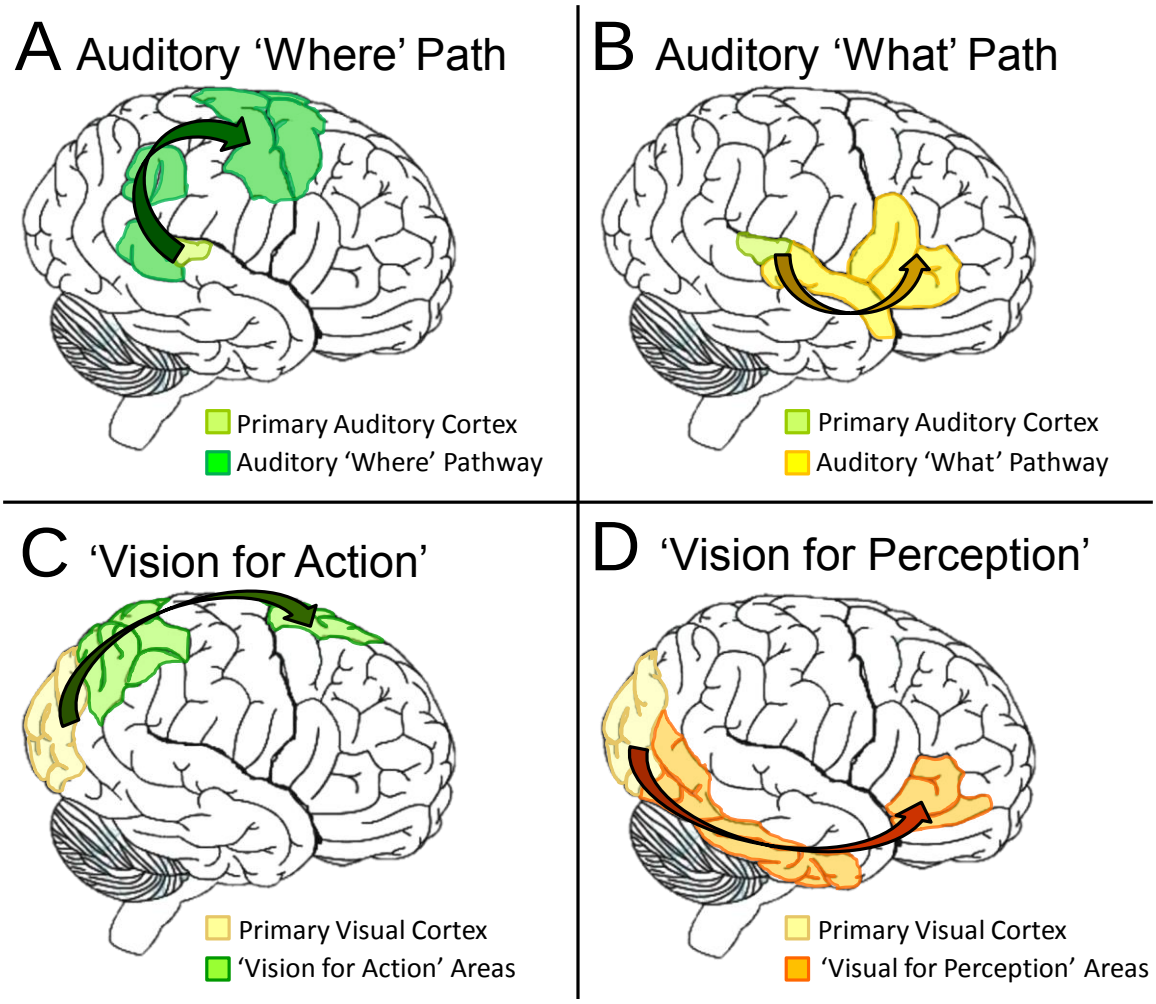

Figure 1.1 Dual pathway models of sensory processing.
A) Auditory 'Where' Pathway. Spatial processing for auditory information begins in A1, and projects along a posterior medial axis into secondary auditory cortex on the STG. From here addition projections carry information into the IPL and SFS. B) Auditory 'What' Pathway. Processing of non-spatial auditory information also begins in A1. Information is projected into anterior lateral STG and further into IFC. C) 'Vision-for-Action' Pathway. Visual information enter cortex primarily through areas V1 and V2. Projections from these areas through dorsal occipital lobe, IPL and SFS are thought to underlie our control of visually guided movements. D) 'Vision-for-Perception' Pathway. Visual information is carried from V1/V2 through ventral occipital lobe and into ITC and IFC. Processing in this pathway underlies our perceptual knowledge of visual object information.

Note: Arrows indicate the primary flow of information transfer in each stream. This is not strictly serial. There are feedback connections betweenvisual and auditory areas in each stream as well contributing to processing.

1.3.4 Emotion in Visual Processing

Attention to emotional stimuli has been heavily studied in the visual system, as emotion is known to have diverse and robust effects on a number of visual processes. Neurally, the emotional nature of an image is known to modulate activity within visual processing areas (Lang et al., 1998; Morris et al., 1998; Vuilleumier & Driver, 2007). Behaviourally, people tend to display a bias towards attending to emotionally-charged rather than neutral stimuli, particularly those with a negative valence. Increased emotionality can facilitate stimulus identification of a target image (Graves, Landis, & Goodglass, 1981), or potentiate the effects of distractors (Blair & Mitchell, 2009; Vuilleumier & Driver, 2007). Many of these effects are believed to be mediated by feedback connections originating in the amygdala (Furl, Henson, Friston, & Calder, 2013; Morris et al., 1998), a region previously noted for its extensive role in emotional processing (see 1.1.1). Evidence suggests that functional connectivity between the amygdala and early visual processing areas is modulated by the emotional content of an image (Amting, Greening, & Mitchell, 2010; Foley, Rippon, Thai, Longe, & Senior, 2012; Furl et al., 2013; Morris et al., 1998). Furthermore, extensive anatomical pathways have been described directly connecting these regions both in diffusion tensor imaging studies of human populations (Catani, Jones, Donato, & Ffytche, 2003) and in non-human primates (Amaral et al., 2003; Amaral & Price, 1984; Catani et al., 2003).

When investigating the impact of emotion on visual processing, most research relies on predominantly ventral-based visual processing, including expression recognition (Adolphs, 2002; Anderson & Phelps, 2000; Han, Alders, Greening, Neufeld, & Mitchell, 2012), assessment of emotional scenes (Ferrari, Codispoti, Cardinale, & Bradley, 2008; Lane et al., 1999; Sabatinelli et al., 2011), and stimulus detection (Lamy et al., 2008; Ohman et al., 2001; Pessoa, Japee, & Ungerleider, 2005; Vuilleumier, 2005). Neuroimaging studies have demonstrated augmented neural processing in the ventral visual stream for emotional compared to neutral stimuli during the presentation of emotional faces (Morris et al., 1998), aversive pictures (Lang et al., 1998), and fear-conditioned stimuli (Krolak-Salmon, Henaff, Vighetto, Bertrand, & Mauguiere, 2004). The consistent and robust effect of emotion in these areas suggests a widespread role for

emotion in modulating activity and allocating processing resources within the ventral visual stream.

Little research has directly addressed the role of emotion in the dorsal visual stream. In non-human primates, emotion does not appear to impact the activation of parietal neurons during visually guided action (Rolls et al., 1979), while in humans, the presence of fearful stimuli has been shown to affect planned, but not automatic control of, visually guided action (Ta, Liu, Brennan, & Enns, 2010). Furthermore, while bilateral lesions of the amygdala, a structure an extensive role in emotional processing (LeDoux, 2003, 2007; Phelps, 2006), leads to reduced grey matter along the ventral visual stream, it does not cause any morphometric abnormalities in dorsal visual stream structures (Boes et al., 2012).

There does exist some evidence to suggest that dorsal stream regions, including occipital and parietal lobe, display augmented activation while processing emotional compared to neutral movie scenes (Goldberg, Preminger, & Malach, 2014). It should be noted, however, that the emotional scenes used in this study may include more motion or otherwise be characterized by greater visual complexity than neutral ones, as the stimuli were not controlled for degree of visual motion or other confounds. Furthermore, dorsal visual activations observed in these tasks are unrelated to behaviours traditionally associated with the dorsal visual stream (i.e., visually-guided action); participants were required only to observe and assess the content of these videos (Goldberg et al., 2014). As such, subsequent activation during this task may be related to indirect motion processing effects, rather than a direct impact of emotion of on vision-for-action. As such, the effects of emotional information on dorsal stream processing, as conceptualized by the two visual systems hypothesis, remain unclear.

Motion-processing regions have been demonstrated to show context dependent reactivity to emotional information. Specifically, V5/MT+ displays augmented activation for emotional compared to neutral videos, but no activation differences between emotional and neutral static facial expressions (Furl et al., 2013). Interestingly, the stimuli used in this study did not change in their relative distance from the observer, a cue

thought to be critical in determine the emotional significance of an object (Panksepp, 1998). Recent studies that address threat distance have utilized either abrupt changes in visual angle (Coker-Appiah et al., 2013) or third person threat proximity (i.e., the distance of a threatening object to an onscreen avatar; Mobbs et al., 2007) to approximate threat distance rather than varying the distance to the actual observer. Moreover, neuroimaging investigations during these experiments have focused primarily on responsivity in the frontal cortex, or the periauqeductal gray (Coker-Appiah et al., 2013; Mobbs et al., 2007; Mobbs et al., 2010), often neglecting the role of visual motion processing regions. As described above (see 1.3.1), V5/MT+ serves as an entry point for information into the dorsal visual stream, and augmentation of this region may be reflected in activity of more tertiary areas of the processing pathway. In addition, connectivity models suggest that dynamic facial emotion modulates backward connections from the amygdala to V5/MT+ (Furl et al., 2013). This notion is supported by studies in both amygdala-lesioned non-human primates (Hadj-Bouziane et al., 2012) and human epilepsy patients with amygdala sclerosis (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Reactivity of motion-sensitive regions to complex emotional scenes, however, remains unknown.

1.4 Thesis Objectives and Hypotheses

The overall objective of this thesis was to determine the impact of emotion on sensory processing. In particular, the role of emotion was investigated with respect to its impact in dual pathway models of sensory processing. While emotional information has been demonstrated to impact stimulus representation in both the anterior-lateral auditory 'what' pathway and the ventral visual 'perception' pathway (hereby referred to as ventral sensory pathways), its impact on processing in the posterior-medial auditory 'where' pathway and dorsal visual 'action' pathway (hereby referred to as dorsal sensory pathways) remained to present relatively unknown. Three independent studies were conducted to address unique aspects of this overall objective.

1.4.1 Study I

The objective of Study I was to identify the neural processes involved in localization of emotional sounds and how they affect one's ability to localize and

discriminate these stimuli. Previous work has identified improved visual detection during emotional 'pop-out' of visual stimuli (Lamy et al., 2008), as well as increased auditory cortex activity during the presentation of emotional compared to neutral stimuli (Fecteau et al., 2007; Viinikainen, Katsyri, & Sams, 2012). Our *primary hypothesis* was that the prioritization of emotional stimuli conferred by the visual system during object processing would also apply to the auditory system. This hypothesis was founded on previous studies in vision, auditory behavioural studies demonstrating increased attentional resource allocation to emotional words and noises (Goydke, Altenmuller, Moller, & Munte, 2004; Sauter & Eimer, 2010), as well as neuroimaging studies of dichotic listening tasks (Ethofer et al., 2012; Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003). This study utilized virtual auditory environments to mimic the presentation of naturalistic spatialized auditory information in an fMRI scanner.

Study I attempted to address two *specific aims*:

1. **Determine influence of emotional valence on localization speed and accuracy for auditory stimuli presented in virtual space.**
   Based on evidence presented in behavioural studies utilizing dichotic listening tasks and EEG, we hypothesized that subjects would display a 'negativity bias' wherein they would be faster to target and locate a sound that has a negative valence (fear or distress).

2. **Identify neural responses associated with localizing emotional sounds in virtual space.**
   Auditory emotional content may act to directly augment stimulus representation in space, wherein we expected enhanced activation will be observed in regions of the auditory 'where' stream, including PSTG and STS. Alternatively, auditory processing pathways may show differential responding to emotional information, similar to visual stream reactivity to cognitive demand and illusion. In this scenario, we expected to see augmented activity to emotional content in the auditory 'what' stream, including ASTG and IFG, but not necessarily in the 'where' stream.

1.4.2 Study II

Whereas Study I focused on the impact of emotion within the dual pathway architecture of the auditory system, Study II shifted that focus into the visual domain. Specifically, Study II investigated whether there is a differential effect of emotion on behaviours mediated to different extents by the dorsal and ventral visual stream. Extensive previous work investigating the impact of emotion on ventral-based visual tasks identified a consistent effect of emotional content on both behavior and neuronal activity in the ventral visual stream (Amting, Miller, Chow, & Mitchell, 2009; Graves et al., 1981; Lang et al., 1998; Morris et al., 1998; Vuilleumier & Driver, 2007). To date, little to no studies directly investigated the effects of emotion on primarily dorsal stream-mediated behaviours. Our *primary hypothesis* was that the augmentation of emotional stimuli in the ventral visual stream would not be mirrored by the dorsal stream. Specifically, significant emotional modulation of localization accuracy would be identified during behaviours recruiting the ventral visual stream (i.e., allocentric localization), while no emotional modulation would be observed for primarily dorsal stream-mediated behavior (i.e., egocentric localization). This hypothesis was based on connectivity patterns displayed by emotion-related structures to visual processing areas, including robust connections between the amygdala and ventral but not dorsal visual regions (Amaral et al., 2003; Amaral & Price, 1984), as well a general insusceptibility of the dorsal visual stream to illusion and task irrelevant information (Bruno & Franz, 2009; Dewar & Carey, 2006; Haffenden & Goodale, 1998). Egocentric and allocentric localization behaviours were used to target the dorsal and ventral visual streams respectively.

Study II attempted to address one *specific aim:*

1. **Determine the effect of emotion independently on primarily dorsal versus ventral-mediated behaviours.**
   Based on evidence presented in tasks of visual emotion and illusion, we hypothesized that subjects would display significant changes in localization accuracy during tasks of allocentric localization in accordance with the

emotional nature of the trial; however, we did not expect to observe similar effect during dorsally-mediated egocentric localization.

1.4.3 Study III

The objective of Study III was to delineate the impact of emotion on motion processing during the presentation of complex visual scenes. Recent work demonstrated that through backwards connections with the amygdala, activation of V5/MT+ is modulated by the emotional nature of dynamic facial expression (Furl et al., 2013). Our *primary hypothesis* for Study III was that the augmentation of representation in visual motion processing areas observed for dynamic emotional expressions would also be apparent during the perception of moving emotional scenes. Specifically, we predicted that activation in V5/MT+ would be significantly enhanced during the perception of emotional compared to neutral images, and that this will be related to functional connectivity between this region and the amygdala. To control stimuli for low-level visual features across motion categories, illusory motion aftereffects were used to induce the perception of movement in complex emotional scenes. This was performed by presenting a one of three patterns of consistent motion followed by static pictures of varying emotional content, creating visually identical pictures which appear to be moving in opposite directions. The presence of motion aftereffects is mediated by continued activation of V5/MT+ following the presentation of a pattern of constant visual movement (Hogendoorn & Verstraten, 2013; Tootell et al., 1995).

Study III attempted to address three *specific aims*:

1. **Determine the influence of emotional valence on motion perception and activity in visual motion-related areas during illusory motion.**
   Previous work has demonstrated that V5/MT+ activity corresponds to the duration and intensity of the motion aftereffect. Furthermore, activity in this region is modulated by emotion content while viewing dynamic facial expression. We hypothesized that illusory motion in emotional scenes would have similar effects on the neural activation of motion sensitive regions and the subjective perception of illusory motion. Specifically, we expected that approaching or receding emotional cues would lead to significantly greater

activation in V5/MT+, due to the self-relevance of the illusory motion direction.

2. **Determine the impact of emotional valence on the functional connectivity of visual motion areas during motion perception.**
   Following previous work outlining connectivity patterns between V5/MT+ and the amygdala, we predicted that context-dependent functional connectivity between these regions would be modulated by the emotional nature of a moving visual scene.

3. **Determine the impact of motion direction on the representation of emotional intensity.**
   Founded on studies investigating threat proximity, we predicted that direction of perceived motion would impact the subjective intensity of emotional scenes. Furthermore, we expected that this effect will be mediated by activity in the amygdala and prefrontal cortex.

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CHAPTER 2

2. Emotion modulates activity in the 'what' but not 'where' auditory processing stream[1].

Abstract:

Auditory cortices can be separated into dissociable processing pathways similar to those observed in the visual domain. Emotional stimuli elicit enhanced neural activation within sensory cortices when compared to neutral stimuli. This effect is particularly notable in ventral sensory streams. Little is known, however, about how emotion interacts with dorsal sensory streams, and essentially nothing is known about the impact of emotion on auditory stimulus localization. In the current study, we used fMRI in concert with individualized auditory virtual environments to investigate the effect of emotion during an auditory localization task. Surprisingly, participants were significantly slower to localize emotional relative to neutral sounds. A separate localizer scan was performed to isolate neural regions sensitive to stimulus location independent of emotion. When applied to the main experimental task, a significant main effect of location, but not emotion, was found in this ROI. A whole-brain analysis of the data revealed that posterior-medial regions of auditory cortex were modulated by sound location; however, additional anterior-lateral areas of auditory cortex demonstrated enhanced neural activity to emotional compared to neutral stimuli. The latter region resembled areas described in dual pathway models of auditory processing as the 'what' processing stream, prompting a follow-up task to generate an identity-sensitive ROI (the 'what' pathway) independent of location and emotion. Within this region, significant main effects of location and emotion were identified, as well as a significant interaction. These results suggest that emotion modulates activity in the 'what,' but not the 'where,' auditory processing pathway.

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2.1 Introduction

The ability to interact effectively in an environment requires the accurate recognition and localization of surrounding objects and the capacity to prioritize these objects for behaviour. One characteristic known to modulate this is the emotional nature of the stimuli (Pessoa and Ungerleider, 2004, Vuilleumier, 2005, Lang and Davis, 2006, Adolphs, 2008). Considerable evidence suggests that emotional visual stimuli gain rapid and often preferential access to the brain's processing resources. At the behavioural level, emotional visual stimuli are detected faster than neutral stimuli (Graves, Landis, & Goodglass, 1981), are more likely to enter into awareness (Amting, Greening, & Mitchell, 2010; Mitchell & Greening, 2011) and can cause significantly greater influence on task-relevant behaviours (Mitchell et al., 2008; Vuilleumier & Driver, 2007). These effects are thought to be conferred by enhanced sensory processing; thus, in the visual domain, emotional stimuli elicit greater activity than similar neutral stimuli within areas of visual cortex (Morris et al., 1998; Vuilleumier & Driver, 2007). Similarly, studies of auditory processing have demonstrated that the analysis of emotional auditory stimuli occurs rapidly (Goydke, Altenmuller, Moller, & Munte, 2004; Sauter & Eimer, 2009) and is associated with enhanced activity in sensory (i.e., auditory) cortices (Fecteau, Belin, Joanette, & Armony, 2007; Viinikainen, Katsyri, & Sams, 2011). Despite some emerging work concerning the influence of emotion on the representation of auditory objects, essentially nothing is known about how emotion influences auditory stimulus localization.

There is accumulating evidence that auditory processing occurs within two separate cortical streams (Ahveninen et al., 2006; Alain, Arnott, Hevenor, Graham, & Grady, 2001; Barrett & Hall, 2006; Clarke et al., 2002; Lomber & Malhotra, 2008; Mathiak et al., 2007; Rauschecker, 2012; Rauschecker & Tian, 2000) that may share some similarities with the well-established dorsal and ventral processing streams of the visual system (Haxby et al., 1991; Milner & Goodale, 1993). Spatial cues used for localization are processed primarily in posterior-medial regions of auditory cortex (Arnott, Binns, Grady, & Alain, 2004; Bushara et al., 1999; Lomber, Malhotra, & Hall, 2007) including the posterior superior temporal gyrus (STG) and the transverse temporal

gyrus. In contrast, sound identity cues, including pitch and language features are processed in anterior-lateral regions of auditory cortex along the anterior STG (Altmann, Henning, Doring, & Kaiser, 2008; Warren & Griffiths, 2003). It should be noted, however, that there are regions of temporal lobe, including primary auditory cortex and adjacent areas, in which neural activation has been demonstrated to code both location and identity-related cues (Arnott et al., 2004).

Despite continuous advances toward understanding the neural mechanisms underlying both enhanced representation of emotion within sensory cortices and our representations of auditory space, the impact of emotion during auditory localization remains unknown. Specifically, it remains unclear whether evidence of enhanced activity observed in prior studies to emotional relative to neutral, non-spatialized auditory stimuli (Fecteau et al., 2007; Viinikainen et al., 2011) would also translate into enhanced auditory stimulus localization and augmented activity in areas of auditory cortex sensitive to object location.

The potential of auditory virtual environments (AVEs) as a method to examine neural pathways associated with auditory stimulus localization has been described in previous studies (Bohil, Alicea, & Biocca, 2011; Fujiki, Riederer, Jousmaki, Makela, & Hari, 2002; Langendijk & Bronkhorst, 2000; Wightman & Kistler, 1989a, 1989b). Previous neuroimaging studies investigating auditory localization have created AVEs using generic head-related transfer functions (HRTFs) generated from measurements of mannequins or a prototypical head shape (Ahveninen et al., 2006; Bushara et al., 1999; Krumbholz, Nobis, Weatheritt, & Fink, 2009). These, however, fail to accommodate for individual differences in head size and pinnae structure that alter a sound as it enters the ear canals, resulting in imperfect perception of spatialized sounds (Middlebrooks, Macpherson, & Onsan, 2000; Wenzel, Arruda, Kistler, & F.L., 1993). Such variables have been shown to influence reactions to and ratings of emotional auditory stimuli (Vastfjall, 2003). Despite its potential importance, we are not aware of any neuroimaging studies utilizing unique AVEs created from individualized HRTFs.

In the present study, we investigated whether the emotion-related enhancements observed in the visual domain at the behavioural (Amting et al., 2010; Graves et al., 1981) and neural levels (Morris et al., 1998; Vuilleumier & Driver, 2007) would also be found during auditory stimulus localization. We hypothesized that positive and negative auditory cues would receive prioritized processing relative to neutral stimuli. We predicted that this prioritization would be reflected by increased accuracy, decreased reaction time, and increased neural activity within the posterior-medial 'where' pathways of auditory processing during the localization of emotional compared to neutral sounds. Additionally, consistent with previous studies involving non-spatialized emotional auditory cues (Fecteau et al., 2007), we predicted that anterior-lateral areas of auditory cortex (i.e., the putative 'what' processing pathway) would also show enhanced activity for emotional compared to neutral sounds.

To test these predictions, we created AVEs by generating sounds based on each individual's unique HRTFs. While undergoing fMRI, participants located or identified a series of auditory stimuli presented in these virtual environments. The current study consisted of three related tasks. Task 1 was designed as a functional localizer, aimed at independently identifying ROIs specifically related to sound localization while controlling for object identity. Task 2 was conducted in the same scanning session as Task 1. In this task, participants were required to identify the source locations of positive, negative and neutral sounds presented within an individualized AVE. This task served two purposes. First, the 'where' ROI derived from the Task 1 localizer was applied to the data in Task 2 and interrogated to determine potential effects of emotion on auditory stimulus location-sensitive areas. Second, Task 2 allowed us to perform an exploratory whole-brain analysis examining the effects of, and interactions between, emotion and location during auditory stimulus localization.

Contrary to expectations, the results showed that emotion did not modulate regions of auditory cortex sensitive to location. However, a distinct region of anterior lateral temporal cortex identified in this exploratory study was modulated by emotion. This area strongly resembled regions associated with sound-identity processing in previous studies (i.e. the putative 'what' pathway; Barrett & Hall, 2006; Warren &

Griffiths, 2003). Furthermore, this effect parallels patterns of activity elicited by emotion in the ventral visual stream. To help determine the degree to which this area could be characterized as part of the 'what' auditory pathway, a follow-up localizer was conducted in a subset of participants in a subsequent session. This functional 'what' pathway localizer identified ROIs that were modulated by sound identity while location and emotion were held constant. The resulting ROI was extracted and applied to the data generated from Task 2, allowing us to independently test the effects of emotion on the resulting 'what' pathway. Following all initial analyses, multivoxel pattern analysis (MVPA) utilizing whole brain spherical searchlights was performed. This allowed for the identification of neural regions wherein patterns of activity are predictive of either emotion or location information. This method has recently been demonstrated to be highly sensitive for decoding how neural patterns code mental representations, beyond traditional univariate approaches (Mahmoudi, Takerkart, Regragui, Boussaoud, & Brovelli, 2012; Norman, Polyn, Detre, & Haxby, 2006) and can be particularly beneficial for delineating population-based neural encoding, like that found in auditory processing.

2.2 Methods

2.2.1 Subjects

Eighteen healthy human subjects, (9 male, 9 female) with a mean age of 23.56 (range 19-35, *SD* 4.51), completed Tasks 1 and 2. All subjects granted informed consent and were in good mental health, as assessed by a Structured Clinical Interview for DSM-IV (*Diagnostic and Statistical Manual of Mental Disorders*, 4th Edition). All subjects had normal hearing, normal or corrected-to-normal vision and were fluent English speakers. Ten of these subjects (5 male, 5 female), with a mean age of 24.3 (range 19-35, SD 5.42), returned to complete Task 3. All participants were reimbursed for their time at the end of each study session. All experiments were approved by the Health Science Research Ethics Board at the University of Western Ontario.

2.2.2 Stimuli and Apparatus

Stimuli

Twelve sounds were chosen from the *International Affective Digitized Sound* (IADS) stimulus set that were of a neutral, negative or positive affective nature as defined

by standardized ratings (Bradley & Lang, 1999). Each stimulus category contained two single-source non-verbal human vocalizations, one multi-source non-verbal human vocalization, and one non-human sound. All sounds were cropped to a variable duration of 2000-3000ms (balanced across stimuli; variable durations were used to facilitate deconvolution of the BOLD signal). Importantly, all stimuli were matched for their onset amplitude and root mean-square amplitude, which ensures that the power and energy were consistent. Positive and negative stimuli were balanced for arousal ratings (mean positive = 6.58, mean negative = 6.92) and valence levels (positive = 7.56, negative = 2.36, absolute neutral = 5). In additional, to create a novel unrecognizable noise for Task 1, the 12 task sounds of Task 2 were merged into a single audio file, segmented into <3ms fragments, and subsequently scrambled, reconstituted and cropped to a duration of 15000ms. This sound maintains the average long-term power spectrum of the stimulus set of Task 2, while remaining unidentifiable.

In order to localize neural regions that were sensitive to stimulus identity, a novel set of nine neutral sounds were chosen from the IADS (mean valence 5.28, SD 0.98) for use in Task 3. These nine sounds were human, animal, or machine in origin (3 of each). An additional three segments of scrambled noise (identical to that used in Task 1) comprised a fourth sound class. All sounds in this set were 5000ms in duration, and were matched for onset amplitude and root-square mean amplitude.

Auditory Virtual Environment

Throughout the experiment, all sounds were presented within an auditory virtual environment through Sensimetric MRI-Compatible Insert Earphones. Volume was controlled by a Dayton Audio Class T Digital Amplifier. Initial volume was set to 88-90dBs and adjusted slightly to the comfort level of each individual participant. To induce the perceptual experience of spatialized sounds using insert-style headphones, HRTFs were measured individually for each subject.

To obtain the HRTF measurements, miniature electret microphones (Knowles FG3629) were mounted facing outwards in foam earplugs inserted flush with the ear canal entrances. The participant stood on an adjustable platform which positioned his or

her head at the height of a 1.5-m radius array of 16 loudspeakers (Tannoy i5 AW) spaced in 22.5-degree intervals around the listener. The array was located in a large hemi-anechoic chamber, and the floor area within the array was covered with acoustical foam to attenuate reflections. The impulse response from each loudspeaker to each ear microphone was measured using the averaged response to 32 periods of a 2047-point maximum-length sequence signal (Rife & Vanderkooy, 1989) presented at a sampling rate of 48828 Hz via a Tucker Davis Technologies RX6 real time processor and QSC CX168 power amplifiers. During the measurement procedure, head motion was minimized by monitoring head position with an electromagnetic tracker (Polhemus FASTRAK) while participants were asked to aim the light from a head-mounted LED accurately at a frontal target position. To correct for individual loudspeaker characteristics, each HRTF measurement was equalized in the frequency domain by dividing by the appropriate loudspeaker transfer function measured with a reference microphone (Bruel & Kjaer 4189) placed at the centre of the array in the absence of the listener's head. The impulse responses were windowed in post-processing to remove any residual reflections. The resulting HRTF measurements were resampled to 44.1 kHz and combined with the equalization filters for the headphones supplied by the manufacturer to create a new set of auditory filters limited to the 10-kHz bandwidth of the headphones. These individualized filters were then applied to each sound by time-domain convolution to create the experience of a virtual 3-dimensional auditory space; sounds presented with headphones were perceived to originate from controlled physical locations external to the participants.

Sounds for Tasks 1 and 2 were spatialized to four locations along the horizontal plane (-90°, -22.5°, 22.5° and 90° from the sagittal midline; negative = left). Sounds for Task 3, along with an additional 500-ms artificially generated white noise were spatialized to a location directly along the sagittal midline, in front of the listener. The entire set of stimuli (across locations, sound sources, and listeners) was normalized such that each stimulus had the same root-mean-square level computed on the concatenated left- and right-ear signals.

2.2.3 Procedure

Pre-Scan Training

Prior to entering the scanner, participants were acclimatized to the auditory virtual environment by completing two modified version of the task. Nine sounds of varying emotional quality were chosen from the IADS (3 from each emotion category: positive, negative, and neutral) for presentation during the training task. All sounds were spatialized to the 4 locations of our virtual auditory environment (-90°, -22.5°, 22.5° and 90° from the sagittal midline; negative = left) and cropped to a duration of 3000ms. The first training task involved discriminating between two of the potential four locations in a series of trials. These two locations were randomly selected but were always adjacent. For each location pairing, the sounds were initially presented along with a visual cue indicating where the sound originated from in virtual space. Following this, the participant completed a series of trials wherein their task was to indicate the virtual location of the sound with a button press. Presented sounds were chosen from the IADS and were distinct from those used during the experimental task. A single trial consisted of a fixation cross (2000-3000ms) followed by a white noise burst (500ms) located directly along the midline that served as an auditory fixation cross, and a target sound. Target sounds were presented at one of two possible positions during this stage of training. Feedback was given after each trial indicating whether the participant correctly identified the sound location. Once participants demonstrated accuracy of greater than 75%, they were presented with a subsequent pair. Possible location pairings were as follows: -90°/-22.5°, -22.5°/22.5°, and 22.5°/90°. Once criterion was met for each pairing, the task was repeated using the full array of locations. Following completion, a second training task was performed. This was similar in structure to the final section of the first training task (discriminating between four possible locations); however, only a target white noise burst was presented (3 seconds). A criterion of 75% was needed to complete this task. All location familiarization tasks were completed again once the participant was in the scanner to ensure participant accuracy was not affected by ambient scanner noise. During this session, dummy EPI volumes were collected to ensure that ambient noise produced by the MRI machine would not interfere with the auditory virtual environment, or compromise localization accuracy.

Task 1: Isolating Location-Sensitive Regions of Auditory Cortex (the 'where' pathway)

In Task 1, 18 participants (9 female, 9 male) performed a pure auditory localization task (using neutral stimuli only) to help identify neural regions involved in representing auditory space. This task was designed as a functional localizer allowing us to generate an ROI corresponding to the 'where' pathway of auditory processing. Participants were instructed to close their eyes and listen to a series of 15000-ms scrambled sounds. Each sound was presented in one of the four virtual locations (8 times per location for a total of 32 events broken into 2 runs). Participants were instructed to actively fixate on the sound location for the duration of its presentation, and to indicate with a button press the location of the perceived source during the sound presentation. Between each sound presentation, there was a 15000-ms period of silence. Order of presented sound location was randomized for each run.

Task 2: Locating Emotional Sounds within Auditory Space

In Task 2, the same 18 participants (9 female, 9 male) completed an emotional auditory localization task. Participants were asked to close their eyes for the duration of each scan to reduce possible confounds of visual feedback. Each trial began with a white noise burst (500ms) spatialized to a location along the sagittal midline, in front of the participant. This acted as an 'auditory fixation cross' to reorient the subject's attention to a standard central point and was immediately followed by a spatialized target sound (2000-3000ms) and a period of silence (2000-3000ms). The target was randomly presented in one of the four possible locations. The participant was required to locate the target sound with a button press indicating the perceived location as quickly and accurately as possible. Over the course of a single run, participants heard each of the 12 sounds in every location a single time for a total of 48 trials (16 trials per emotion condition). Additionally, there were 16 silent 'jitter' trials incorporated into each run, for a total of 64 trials per run. All trials were selected in random order within each run. The task run was repeated six times for a total of 384 trials.

Task 3: Isolating Identity-Sensitive Regions of Auditory Cortex (the 'what' pathway)

Task 3 was conducted during a follow-up scanning session in a subset of the original sample to identify auditory areas associated with auditory object identification.

This additional functional localizer scan was initiated in response to the results of Task 1 and 2, outlined below, in order to better explore the potential dissociable effects of emotion on the auditory 'what' and 'where' processing pathways. Specifically, it was designed to independently derive functional ROIs corresponding to the 'what' pathway of auditory processing. This type of cross-validation, using separate sources for region identification and signal estimation, avoids problems of circularity in interpreting neuroimaging results (Vul & Pashler, 2012), thus allowing the interrogation of ROIs over the time course of Task 2 without fear of statistical bias (Esterman, Tamber-Rosenau, Chiu, & Yantis, 2010; Vul & Kanwisher, 2010). In the scanner, 10 participants (5 female, 5 male) performed a block design auditory identification task similar to that used in Task 1. During this task, each 15000-ms sound presentation consisted of a triad of stimuli belonging to a single object class presented directly in front of the listener along the mid-sagittal plane within the AVE. There were four possible object classes: human, animal, machine and scrambled sounds. Over the course of two runs, each object class was presented 8 times, for a total of 32 events. Participants were instructed to actively attend to the identity of the sound objects for the duration of their presentation, and to indicate the identity of the presented sounds (human, animal, machine or scrambled) via button press. Between the presentation of each triad, there was a 15000-ms period of silence. Presentation order was randomized.

2.2.4 Behavioural Data Analysis

To investigate the possible effect of emotional content on sound localization, we recorded reaction times and accuracy level for the duration of Task 2. A 4 (location) X 3 (emotion) repeated-measures ANOVA was conducted for each of the behavioural measures. Follow-up pair-wise t-tests were performed to delineate the nature of any significant effects.

2.2.5 Imaging Acquisition and Analysis

MRI Data Acquisition

Subjects were scanned during all task performances using a 3T Siemens Scanner with a 32-channel head coil. fMRI images were taken with a T2*-gradient echo-planar imaging sequence (repetition time [TR] = 2500ms, echo time [TE] = 36ms; field of view [FOV] = 18.8cm, 78 x 78 matrix). Tasks 1 and 2 took place over a single scan session.

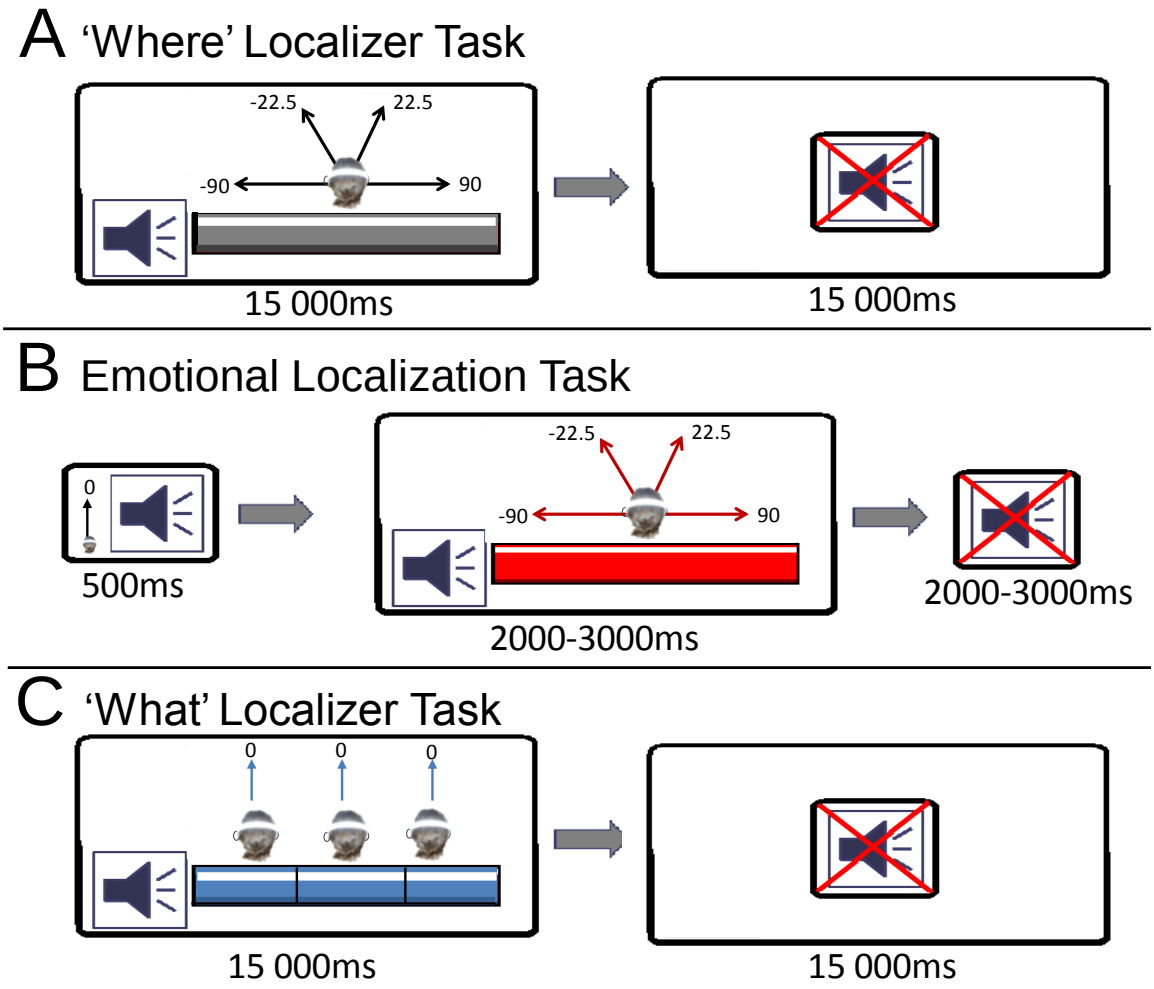

Figure 2.1 Trial schematic for Emotional Auditory Localization and Auditory Pathway Functional Localizers.

A) *'Where' Localizer.* To localize areas of auditory cortex involve in processing spatial information, Task 1 presented 15 s of white noise alternating with 15 s of silence. The white noise was presented from 1of 4 potential locations. Participants were required to identify the sound location. B) *Emotional Auditory Localization Task.* Each trial of Task 2 began with a 500 ms auditory fixation cross. Following this, an auditory cue of varying emotional content was presented at 1 of 4 potential locations. Participants were required to locate this sound using a button pres as quickly and as accurately as possible during this time. A 2 s period of silence was presented between each trial. C) *'What' Localizer.* To localize areas of auditory cortex involved in processing non-spatial information, 15 s of sound was presented from a position directly in front of the listener and alternated with 15 s of silence. Each 15 s ms of sound was comprised of three 5s sound clips with a similar source of origin (i.e., human, animal, machine or white noise). Participants were required to indicate the category of sound source for each trial.

Task 3 took place in a separate session. For all functional runs, complete brain coverage was obtained with 38 interleaved slices of 2.4 x 2.4mm in plane with slice thickness of 2.4mm, forming 2.4mm isovoxels. A series of 148 functional images were collected for each run of Task 2 and a series of 202 functional images were collected for each run during Tasks 1 and 3. A high resolution T1 weighted anatomical scan was obtained covering the whole brain (TR = 2300ms, TE = 4.25ms; FOV = 25.6cm, 192 axial slices; voxel size = 1mm isovoxels; 256 x 256 matrix) in both scan sessions.

Univariate fMRI Analysis

Analysis of the fMRI data was conducted using Analysis of Functional NeuroImages (AFNI) software (Cox, 1996) at both the individual and group levels. Motion correction was performed by registering all volumes to the relevant functional volume acquired temporally adjacent to the anatomical scan. The dataset for each participant was spatially smoothed (using an isotropic 4mm Gaussian kernel) to reduce the influence of individual differences. The time series data were normalized by dividing the signal intensity of a voxel at each time point by the mean signal intensity of that voxel for each run and multiplying the result by 100. Thus, resultant regression coefficients represent the percent signal change from the mean activity. Regressor files modeling the presentation time course of relevant stimuli were created for each of the 12 conditions of Task 2 (4 locations X 3 emotions) during correct trials only, and for each of the four conditions of Task 1 (4 locations) and Task 3 (4 classes of objects). The relevant hemodynamic response function was fit to each regressor to perform linear regression modeling. To account for voxel-wise correlated drifting, a baseline plus linear drift and quadratic trend were modeled for each time series. This resulted in a β coefficient and t value for each voxel and regressor. To facilitate group analysis, each individual's data were transformed into the standard space of Talairach and Tournoux. Following this, a 4 (location) X 3 (emotion) repeated-measures ANOVA was performed on the imaging data from Task 2, while two separate one-way ANOVAs were performed on the imaging data from Tasks 1 and 3 to examine the effects of location and sound-identity respectively (4 levels of each). ANOVAs at this level were conducted using the AFNI function GroupAna, yielding an F value for each main effect and interaction at each voxel. Percent signal change from the mean activity was extracted from significant clusters of activation

for each relevant regressor using the AFNI function 3Dmaskave. To correct for multiple comparisons, a spatial clustering operation was performed using AlphaSim with 10000 Monte Carlo iterations on the whole brain EPI matrix.

Multivariate fMRI Analysis

A multi-voxel pattern analysis (MVPA) was conducted on the data from Experiment 2. All MVPA analyses were implemented in the Princeton MVPA Toolbox for Matlab. Analyses were conducted using a data-driven searchlight MVPA approach using 10mm searchlight radii. 3dDeconvolve was used to determine a β coefficient for each voxel on each individual trial over all six function runs of Task 2. In addition, the AFNI function 3dSkullStrip was used to generate a mask from each participant's anatomical scan containing only grey matter voxels in native space. To ensure that no grey matter voxels were inadvertently removed, this mask was dilated two levels using the AFNI function 3dmask_tool. All functional data used in subsequent MVPA analyses were filtered by these anatomical masks.

Classification procedures were perform twice for each searchlight; first using functional data modelling the location of the auditory stimuli, and second using EPI data modelling the emotional content. Spherical searchlights were generated for centred on each voxel containing β coefficient for all voxels in a 10mm radius from this centre point. Classification was performed within each searchlight using a back-propagation classification procedure. Predictive accuracy for each searchlight was assigned to the centre voxel. This resulted in six separate maps of predictive accuracy for each participant, one representing each repetition of the n-1 classification procedure. Outputs were averaged across runs using the AFNI functions 3dcalc and transformed into the standard space of Talarach and Tournoux. Group analyses were then performed to determine where predictive accuracy of our classifier was significantly greater than chance (i.e., >33.3% for emotion data and > 25% for location data).

2.3 Results

2.3.1 Behavioural Results

To delineate the effects of emotion on auditory localization, participants were presented a series of positive, negative and neutral sounds within a virtual auditory

environment while undergoing fMRI. Participants were instructed to localize these sounds as quickly and accurately as possible (Task 2).

A 4 (location) X 3 (emotion) ANOVA was conducted on the reaction time and error data (Table 2.1) to determine the impact of stimulus emotion on auditory localization at a behavioural level. This yielded a significant main effect of emotion ($F_{(2, 34)} = 12.617$, $p < 0.005$) on the reaction times. We had originally predicted that emotion would enhance the localization of auditory stimuli. However, contrary to these predictions, follow-up t-tests revealed that this effect was driven by significantly *slower* localization of emotional sounds (both positive and negative) when compared to neutral sounds ($p < 0.001$ and $p < 0.05$ respectively). There was no significant effect of sound location ($F_{(3, 51)} = .616$, $p > 0.05$) nor a location X emotion interaction ($F_{(6, 102)} = 1.891$, $p > 0.05$) identified in the reaction time data. The same analysis applied to the localization error data yielded no significant effects for either sound location ($F_{(3, 51)} = 0.158$, $p > 0.05$) or emotion ($F_{(2, 34)} = 1.783$, $p > 0.05$), nor did it yield a significant location X emotion interaction ($F_{(6, 102)} = 1.320$, $p > 0.05$).

2.3.2 Imaging Results: Univariate

Interrogating Location-Sensitive Regions of Auditory Cortex (the 'where' pathway)

In order to determine the impact of sound location independent of sound identity, location-related activity was assessed during the localization of unrecognizable scrambled sounds (Task 1). A one-way ANOVA (four locations) conducted on the whole brain EPI data obtained during Task 1 identified a significant effect of sound location ($p < 0.005$; corrected at $p < 0.05$) within regions of temporal cortex (Table 2.2). This activation included primary auditory cortex (BA 41/42) and extended medially along the transverse temporal gyrus (BA 13; Figure 2.2a). This region showed greatest activity to stimuli positioned far in the contralateral hemifield, decreasing activity to midline sounds, and significantly less activity to ipsilaterally positioned sounds ($p < 0.005$; Figure 2.2b). This area was then used as an auditory 'where' pathway ROI, and applied to the BOLD data collected in Task 2. The percent signal change to all locations and emotional categories within this ROI was extracted using 3Dmaskave, and subjected to a 4 (location) X 3 (emotion) ANOVA.

Table 2.1 Behavioural Results of Task 2

Emotion[a]	**Location**	**Time to Localization in ms; correct trials only**	**Localization Accuracy (%)**
Positive	-90°	775.1 (242.2)	83.8 (19.1)
	-22.5°	756.2 (199.2)	85.9 (16.6)
	22.5°	804.5 (199.4)	88.2 (14.1)
	90°	808.5 (251.9)	82.2 (20.0)
Negative	-90°	736.6 (210.0)	87.0 (15.3)
	-22.5°	776.2 (218.2)	84.3 (15.4)
	22.5°	779.9 (201.0)	83.1 (18.1)
	90°	733.6 (209.1)	84.7 (17.8)
Neutral	-90°	686.5 (153.3)	89.4 (12.0)
	-22.5°	736.5 (194.7)	85.6 (20.9)
	22.5°	751.7 (218.4)	88.2 (17.5)
	90°	727.5 (224.6)	85.9 (18.5)

[a] Significant effects of emotion were identified in the reaction time data. These effects of emotion were driven by significantly slower localization of positive and negative stimuli when compared to neutral stimuli ($p < 0.001$ and $p < 0.05$ respectively).

Standard deviations in parentheses.

. As expected, activity within the 'where' pathway ROI was significantly modulated by sound location ($F_{(3, 51)} = 38.435$, $p < 0.001$), wherein there was increased activity for sounds presented in the contralateral hemifield relative to the ispilateral hemifield (Figure 2.2c). Contrary to our original predictions, however, there was no significant main effect of emotion ($F_{(34,2)} = 0.776$, $p > 0.05$), nor was there a significant location X emotion interaction ($F_{(6, 102)} = 1.164$, $p > 0.05$). Thus, emotion did not modulate activity in location-sensitive areas of auditory cortex

Whole Brain Analysis: Locating Emotional Sounds in Auditory Space

An exploratory whole brain analysis by way of a 4 (location) X 3 (emotion) ANOVA was conducted on the data from Task 2 to identify neural regions that varied as a function of location and emotion. A significant main effect of location ($p < 0.005$; corrected at $p < 0.05$) was identified in regions of temporal and parietal cortex (Table 2.2). This activation extended from the primary auditory cortices (BA41/42) posteriorly and medially along the transverse temporal gyrus and into the inferior parietal lobule (Figure 2.3a). Percent signal change from the mean activity for each significantly activated voxel was extracted from all regions displaying significant main effects or interactions using 3Dmaskave. Contributing to this effect, activity in posterior superior temporal gyrus (posterior areas of BA 13) varied as a function of location; activity was greatest to stimuli presented in the far contralateral hemifield of auditory virtual space, and decreased progressively with distance from that location (Figure 2.3b). This general pattern of activation emerged bilaterally, with each hemisphere showing an inverse pattern of activation to the other. This result is consistent with studies that describe auditory stimulus location encoding as involving differential activation of units across the two hemispheres, as opposed to local encoding within specific nuclei or regions (Grothe, Pecka, & McAlpine, 2010; Stecker, Harrington, & Middlebrooks, 2005). Similar patterns of activity were identified in areas of precuneus, inferior parietal lobule, pre/post-central gyrus and medial occipital gyrus that exhibited main effects of sound location.

A significant main effect of emotion was identified in bilateral temporal cortex ($p < 0.005$; corrected at $p < 0.05$; Table 2.2). Activation extended from the primary auditory cortices (BA 41/42) anterior and inferior along the superior temporal gyrus (to BA 22; Figure 2.3c). This region showed significantly greater activation bilaterally during the

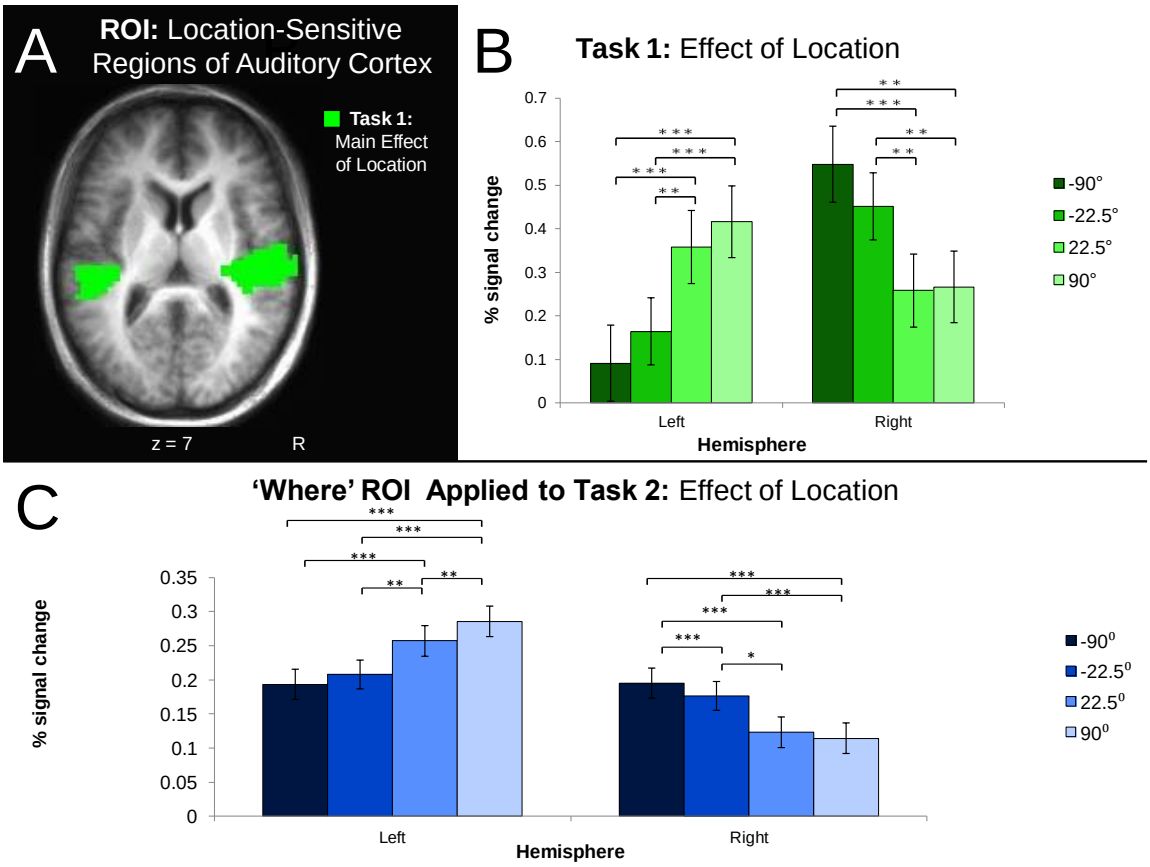

Figure 2.2 Neural regions significantly modulated by sound location (Task 1).
A) Activity in posterior aspects of bilateral superior temporal gyrus is significantly modulated by sound location. B) These effects of location were parametric, wherein cortical activation increases as a sound is presented more eccentrically in the contralateral hemifield. C) A location-sensitive 'where' ROI generated from Task 1 was applied to the EPI data acquired during Task 2. As expected, a significant main effect of location was identified in this region. The nature of this effect was consistent with the parametric location effects reported above.
[* $p < 0.01$; ** $p < 0.005$ *** $p < 0.001$]

presentation of emotional sounds (positive and negative), when compared to neutral sounds ($p < 0.001$ and $p < 0.005$ respectively; Figure 2d).

A significant interaction was identified within regions of right auditory cortex (BA 41/42/22; Figure 2.4a), bilateral precuneus (BA 31/7; Figure 2.4c), and bilateral occipital lobe (BA 17/18/19; Figure 3e; $p < 0.005$, corrected at $p < 0.05$; Table 2.2; Figure 2.4a-f). To identify the nature of these effects, a series of one-way ANOVAs were performed, and where significant ($p < 0.05$), these were followed-up with paired t-tests. First, the impact of location within each emotion was examined. Right auditory cortex showed greater activity to positive stimuli presented in the contralateral relative to ipsilateral hemifield ($p < 0.01$); however, no such effect was observed for neutral or negative stimuli ($p > 0.05$). The impact of emotion within each location was also examined. Sounds coming from the contralateral hemifield (i.e. 90° and 22.5° left of the sagittal midline) elicited greater activity in right auditory cortex for emotional relative to neutral sounds (positive > neutral, $p < 0.001$; negative > neutral, $p < 0.01$; positive > negative $p < 0.05$). These results are illustrated in Figure 2.4b. Bilateral precuneus and occipital lobe displayed strikingly similar patterns of activation. Within both regions, the impact of location within emotion was significant during the presentation of negative ($p < 0.005$) but not neutral ($p > 0.05$) sounds. Within bilateral precuneus, the impact of location during the presentation of positive stimuli was significant ($p < 0.05$), while in the occipital lobe, it was not ($p > 0.05$). These results are illustrated in Figure 2.4d/f. The impact of emotion within each location for both regions was also examined, yielding similar patterns of activation. Sounds coming from the medial right location (i.e. 22.5° right of the sagittal midline) significantly modulated activity in both precuneus and occipital regions across emotional categories (positive > neutral, $p < 0.05$; positive > negative, $p < 0.005$; neutral > negative $p < 0.005$). Significant changes in activity as a function of emotion were not found in any of the other locations ($p < 0.05$). These results are illustrated in Figure 2.4d/f. The effects in visual cortex were unexpected as subjects had their eyes closed during the task; however, it is noteworthy that occipital lobe activity has been associated with mental imagery in the absence of visual input (Borst & Kosslyn, 2008; Kosslyn, Thompson, Kim, & Alpert, 1995). The effects may therefore be due to the relative propensity of the different classes of sounds to induce mental imagery.

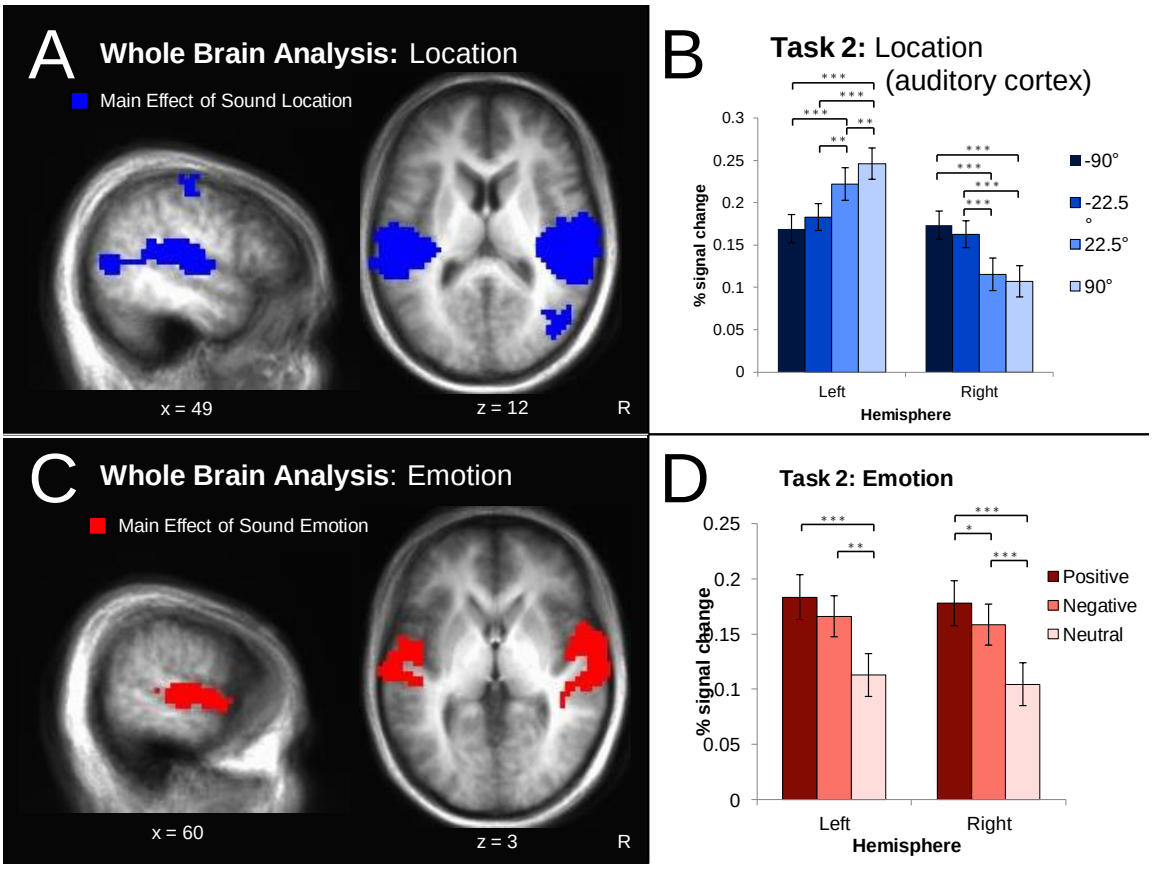

Figure 2.3 Neural regions demonstrating significant main effects of sound location and emotion in a whole brain analysis (Task 2).

A) Posterior superior temporal gyrus activity was significantly modulated bilaterally as a function of sound location. B) These effects of location are parametric, wherein cortical activation increases as a sound is presented more eccentrically in the contralateral hemifield. C) Anterior superior temporal gyrus activity bilaterally was significantly modulated by sound emotion. D) These effects of emotion are driven by significantly greater activation during the presentation of positive and negative relative to neutral sounds.

[* $p < 0.01$; ** $p < 0.005$ *** $p < 0.001$]

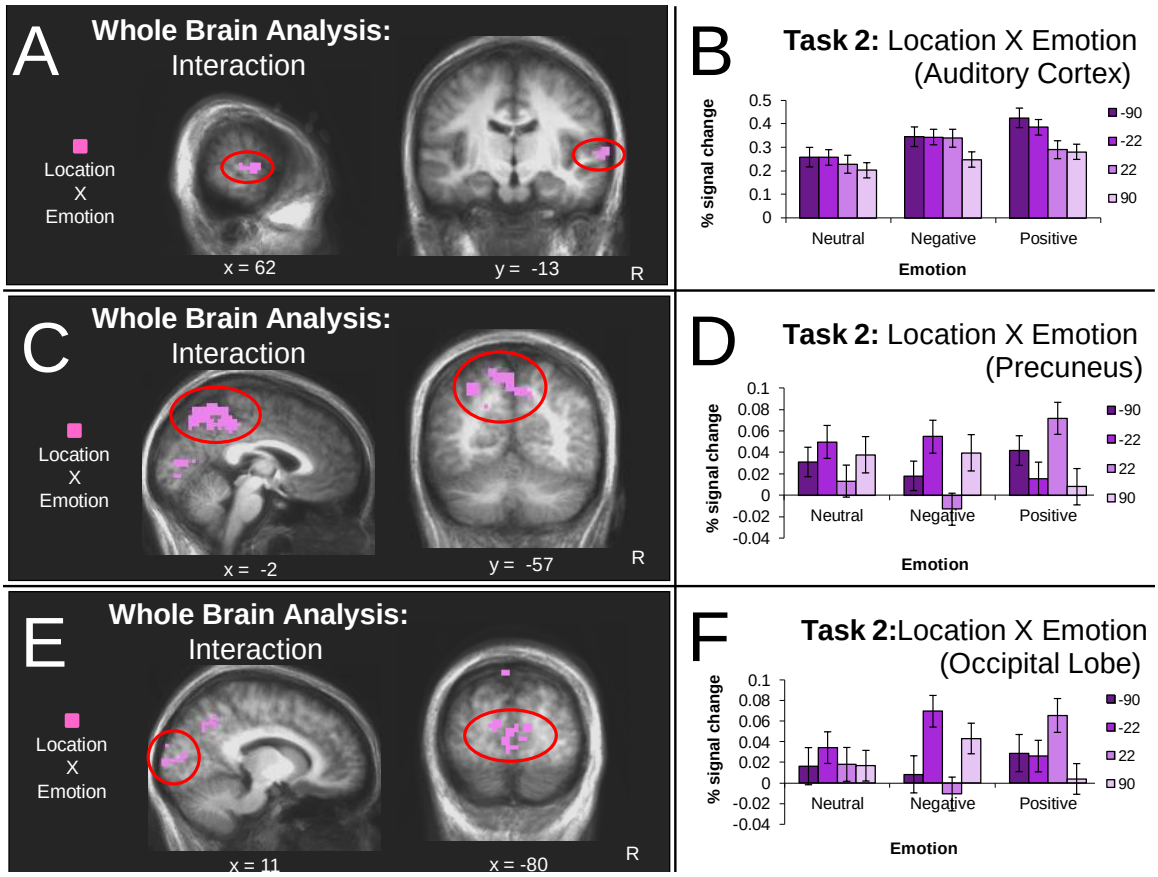

Figure 2.4 Neural regions demonstrating a significant location X emotion interaction in a whole brain analysis (Task 2).

A) Right superior temporal gyrus was significantly modulated as a function of a location X emotion interaction. B) These effects are driven by an increased response to emotional (both positive and negative) relative to neutral sounds when presented in the contralateral hemifield ($p < 0.001$ and $p < 0.01$ respectively). C/E) A significant location X emotion interaction emerged in bilateral precuneus and occipital lobe. D/F) Within both the precuneus and occipital cortex, the impact of location within each emotion was significant during the presentation of negative and positive but not neutral sounds.

[* $p < 0.01$; ** $p < 0.005$ *** $p < 0.001$]

Interrogating Identity-Sensitive Regions of Auditory Cortex (the 'what' pathway)

The whole-brain analysis (Task 2) identified a separate anterior-lateral area of auditory cortex that was modulated by emotion. This region resembled areas implicated in the putative 'what' auditory processing stream (Altmann et al., 2008; Warren & Griffiths, 2003), raising the question of whether emotion has dissociable effects on the 'what' versus 'where' auditory processing streams. To test this hypothesis, a follow-up localizer scan (Task 3) was performed to extract a sound identity sensitive 'what' pathway ROI (independent of location and emotion) that could then be applied to the Task 2 data. A one-way ANOVA (with four sound categories) was conducted on the EPI data revealing object-identity sensitive areas within temporal cortex ($p < 0.005$; corrected at $p < 0.05$; Table 2.3). This activation included regions of cortex anterior and lateral to primary auditory cortex along the superior temporal gyrus (BA 22; $p < 0.005$; corrected at $p < 0.05$; Figure 2.5a). Further exploration of this effect revealed that significantly greater activity was elicited in this area for sounds in the human, animal and machine categories compared to scrambled sounds ($p < 0.001$; Figure 2.5b). In addition, this region showed significantly greater activity to biologically generated sounds (human and animal) relative to machine-generated sounds ($p < 0.005$, $p < 0.001$ respectively).

The identity-related (what-pathway) ROI was then applied to the BOLD data collected in Task 2, and the percent signal change was extracted from each mask for all locations and emotional categories using 3Dmaskave, and subjected to a 4 (location) X 3 (emotion) ANOVA. Within the 'what' pathway ROI, activity was found to be significantly modulated by both sound location ($F_{(3, 51)} = 26.223$, $p < 0.001$) and emotion ($F_{(2, 34)} = 8.914$, $p < 0.005$; Figure 2.5c). Activity in this region was significantly increased for sounds presented in the contralateral hemifield when compared with sounds presented in the ispilateral hemifield ($p < 0.001$). Additionally, this region showed enhanced activation for positive and negative versus neutral stimuli ($p < 0.005$ and $p < 0.05$ respectively). Lastly, a significant location X emotion interaction was observed in this region ($F_{(6, 102)} = 2.450$, $p < 0.05$).

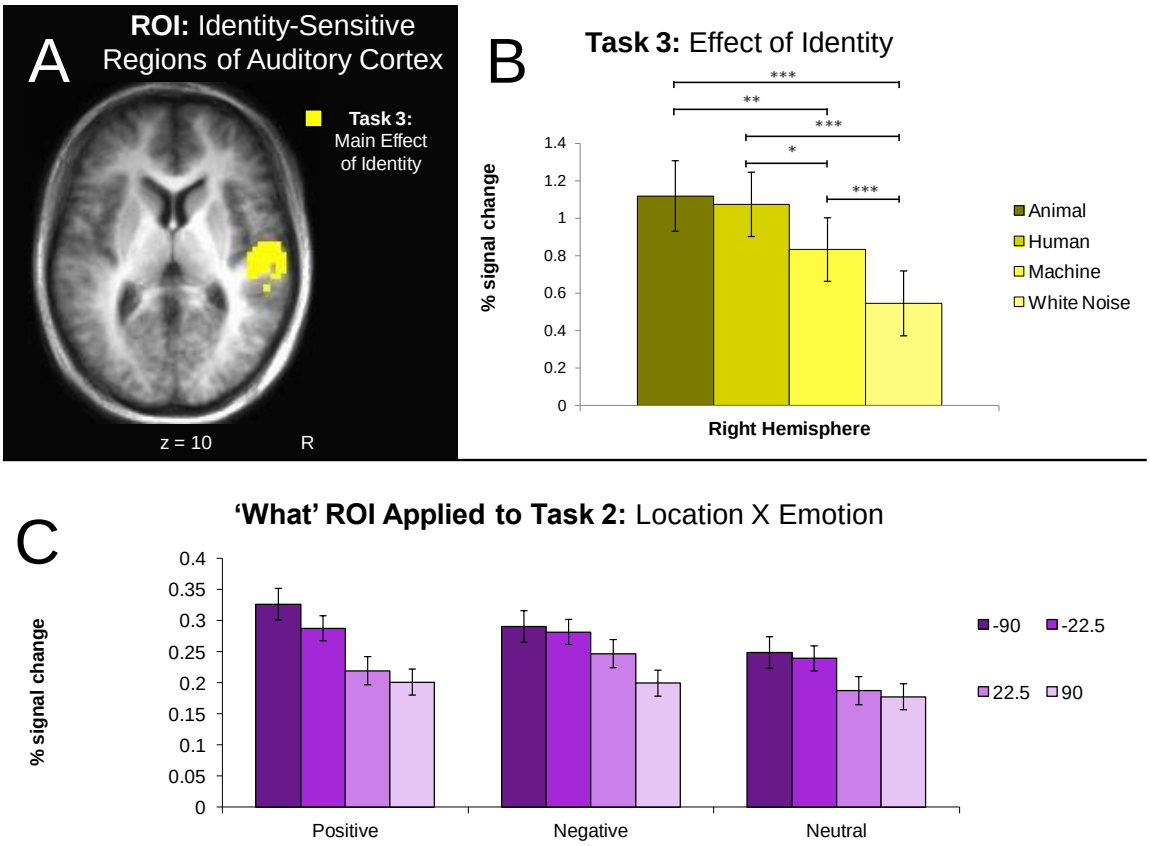

Figure 2.5 Neural regions significantly modulated by sound identity (Task 3). A/B) Activity in bilateral superior temporal gyrus was significantly modulated by sound identity, driven by increased in activation during ecologically relevant sounds relative to scrambled sounds and biological relative to non-biological sounds. C) Within the sound identity-sensitive ('what') ROI, a significant main effect of location was identified in this region) in the Task 2 data. Positive and negative stimuli elicited significantly greater activation in this ROI relative to neutral stimuli Additionally, the 'what' ROI displayed a significant location X emotion interaction effect wherein there was greater activity for both positive and negative stimuli presented in the contralateral relative to ipsilateral hemifield

[* $p < 0.01$; ** $p < 0.005$ *** $p < 0.001$]

Table 2.2 Results of Task 1, 2 & 3

Areas modulated by sound location and sound emotion during auditory localization.

Effect	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
'Where' ROI[a]	R	STG, TTG	41/22/13	44	-22	12	9342
	L	STG, TTG	41/22/13	-44	-25	10	3807
Whole Brain Analysis: Location	R	STG, TTG, MTG	42/41/39/37	48	-27	12	22113
	L	STG, TTG	42/41	-48	-23	10	10908
	R	IPL, Precuneus	7	17	-68	41	5319
	R	Precuneus	7	10	-46	47	3186
	R	Pre-central Gyrus	6	29	-7	52	945
	R	Post-central Gyrus	4/3	48	-16	52	729
	R	IPL	40	43	-47	50	567
	R	Post-central Gyrus	3	23	-32	59	513
	R	MOG	19	32	-76	24	459
Whole Brain Analysis: Emotion	R	STG	22/21	55	-8	2	8668
	L	STG	22/21	-54	-11	2	4995
Whole Brain Analysis: Interaction	R/L	Precuneus, SPL, CC	31/7	-6	-54	45	4728
	R/L	Cuneus, MOG	19/18/17	3	-83	9	1617
	R	STG	42/41/22	60	-16	6	387
'What' ROI	R	STG, TTG	42/41/22	54	-20	8	4266

Significant clusters are thresholded at $p < 0.005$ (corrected to $p < 0.05$).

STG = superior temporal gyrus; TTG = transverse temporal gyrus; MTG = middle temporal gyrus; IPL = inferior parietal lobule; MOG = middle occipital gyrus; CC = cingulate cortex.

Note: XYZ are Talairach coordinates and refer to centre of mass.

To identify the nature of the interaction effects in the 'what' pathway, a series of one-way ANOVAs were performed. First, the impact of location within each emotion was examined. Within this ROI, there was greater activity for both positive and negative stimuli presented in the contralateral relative to ipsilateral hemifield ($p < 0.001$ and $p < 0.05$ respectively); however, no such effect was observed for neutral stimuli ($p > 0.05$). The interaction was further examined by comparing the impact of emotion within each location; however, no significant effects were identified for this contrast ($p > 0.05$). This effect contrasts with that found in the 'where' pathway ROI, which featured a significant effect of location, but no significant effect of emotion or location X emotion interaction. Furthermore, the coordinates of the interaction identified during Task 2 are more closely related to the coordinates of the 'what' ROI compared to the 'where' ROIs, so this effect is not unexpected. It should be noted that Task 3 involved a subset of the original sample used in Tasks 1 and 2, and therefore had less power to define the ROI. Nevertheless, the fact that this independently derived ROI shows the same functional properties exhibited in the emotion-sensitive regions uncovered in Task 2 (despite reduced power) lends further support to the conclusion that the auditory 'what' pathway is modified by both emotion and location characteristics.

Univariate Conjunction Analysis

To identify the degree of overlap between auditory processing streams and emotion-related activity within auditory cortex, a series of conjunction analyses were performed using AFNI's 3dcalc function. This was performed for all combinations of significant activity from the 'where' ROI generated from Task 1, the whole brain analysis of Task 2 (effect of emotion and effect of location) and the 'what' ROI generated from Task 3 (Table 2.3). The resulting maps indicate areas of overlap and exclusion for all clusters that showed significant effects. Of particular interest, location-related activity in Task 2 overlapped to a greater extent with the 'where' ROI than with the 'what' ROI (Figure 2.6a/b). Contrastingly, emotion- related activity in Task 2 overlapped to a greater extent with the 'what' ROI than with the 'where' ROI (Figure 2.6c/d).

Table 2.3 Conjunction of Task 1, Task 2 and Task 3

Conjunction	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
Task 2: Location + Task 1: 'Where' ROI	R	STG, TTG	41/13	46	-22	12	8856
	L	STG, TTG	41/13	-44	-25	10	3672
Task 2: Location + Task 3: 'What' ROI	R	STG, TTG	41	54	-20	9	3510
	L	STG. TTG	22	-56	-18	6	162
Task 2: Emotion + Task 3: 'What' ROI	R	STG	22	58	-13	4	1377
	L	STG	22	-56	-18	6	162
Task 2: Emotion + Task 1 'Where' ROI	R	STG	41	45	-9	4	243
	L	STG	41	-44	-12	4	216
	R	STG	22	58	-12	7	189
Task 2: Location + Task 2: Emotion	R	STG	41/22	56	-12	6	1890
	L	STG	41/22	-54	-14	5	1512
Task 1: 'Where ROI + Task 3: 'What' ROI	R	STG, TTG	41	52	-20	9	2376

STG = superior temporal gyrus; TTG = transverse temporal cortex.

Note: XYZ are Talairach coordinates and refer to centre of mass for each overlap.

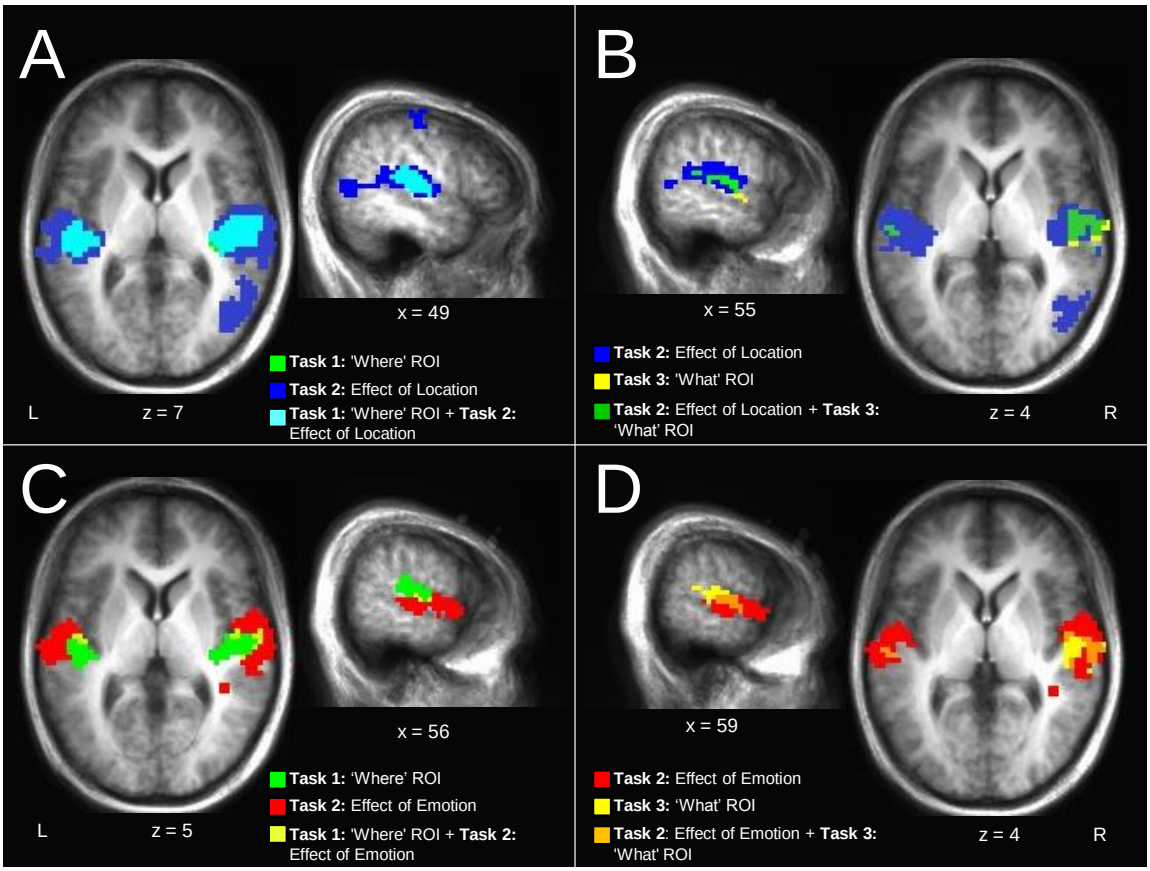

Figure 2.6 Distinct areas of superior temporal gyrus are responsive to emotion and location.

A) Conjunction of areas responsive to changes in location in Task 2 (blue) and the 'where' ROI (green) identified considerable overlap (light blue) encompassing all significant activity from Task 1. B) Conjunction of areas activated based on changes in location in Task 2 (blue) and the 'what' ROI (yellow). The overlap (green) predominantly covers areas of primary auditory cortex. C) Conjunction of areas activated based on changes in emotion in Task 2 (red) and the 'where' ROI (green) identified only a small area of overlap limited to an area corresponding to primary auditory cortex. D) Conjunction of areas activated based on changes in emotion in Task 2 (red) and the 'what' ROI (yellow). The overlap (orange) covers areas of primary auditory cortex and extends anterior along the superior temporal gyrus.

2.3.3 Imaging Results: Multivariate

Multi-Voxel Pattern Analysis (MVPA): Searchlight Results

Multi-voxel pattern analysis using 10mm spherical searchlights identified patterns of activity predictive of location and emotion similar to those identified in the univariate analyses (Table 2.4; Figure 2.7). Particularly, voxel activity pattern in bilateral STS predicted both the location and emotion of the sound at a level significantly above chance, with anterior region of this structure only predictive of only the emotional information. In addition, middle frontal gyrus, posterior cingulate cortex and extensive regions of bilateral post- and pre-central gyrus, and were predictive of sound location.

Multi Voxel Pattern Analysis (MVPA): Conjunction Analysis

A second series of conjunction analyses examined the degree of overlap between univariate analyses and MVPA conducted on data from Task 2 (Table 2.5). Large areas of overlap along bilateral STG were identified between regions identified as location-sensitive by univariate analyses, and location predictive by MVPA (Figure 2.8a). In addition, univariate emotion-sensitive regions were highly overlapping with regions identified by MVPA as emotion-predictive (Figure 2.8b).

While minimal overlap was identified between univariate main effects of location and emotion (Figure 2.8c), this division was not as notable in MVPA. Notably, regions of posterior STG identified in univariate analyses as location but not emotion sensitive displayed pattern of activation that were in fact predictive of both emotion and location (Figure 2.8d). This suggests a greater impact of emotion in early auditory processing regions than previously identified.

Table 2.4 MVPA Searchlight Results

Predictive	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
Location	L	STS, TTG, Pre/PostCG,	2/4/13/41/42	-46	-25	20	18784
	R	STS, TTG, Pre/PostCG	2/4/13/41/42	48	-22	15	16312
	L	MFG	8	-28	17	36	1288
	L	pCC	31	-14	-61	20	832
	R	CG	24	6	-14	43	568
	R	MOG	19	25	-84	22	376
	L	PhG	35	-31	-20	-15	248
Valence	R	STS, Ins	13/22/41/42	54	-14	6	9264
	L	STS, Ins	13/22/41/42	-50	-14	6	7464

$p < 0.001$, corrected to $p < 0.05$

Ins = Insula, IPL = Inferior Parietal Lobule, LG = Lingual Gyrus, MTG = Middle Temporal Gyrus, PostCG = Poscentral Gyrus, STG = Superior Temporal Gyrus, THAL = Thalamus, TTG = Transverse Temporal Gyrus

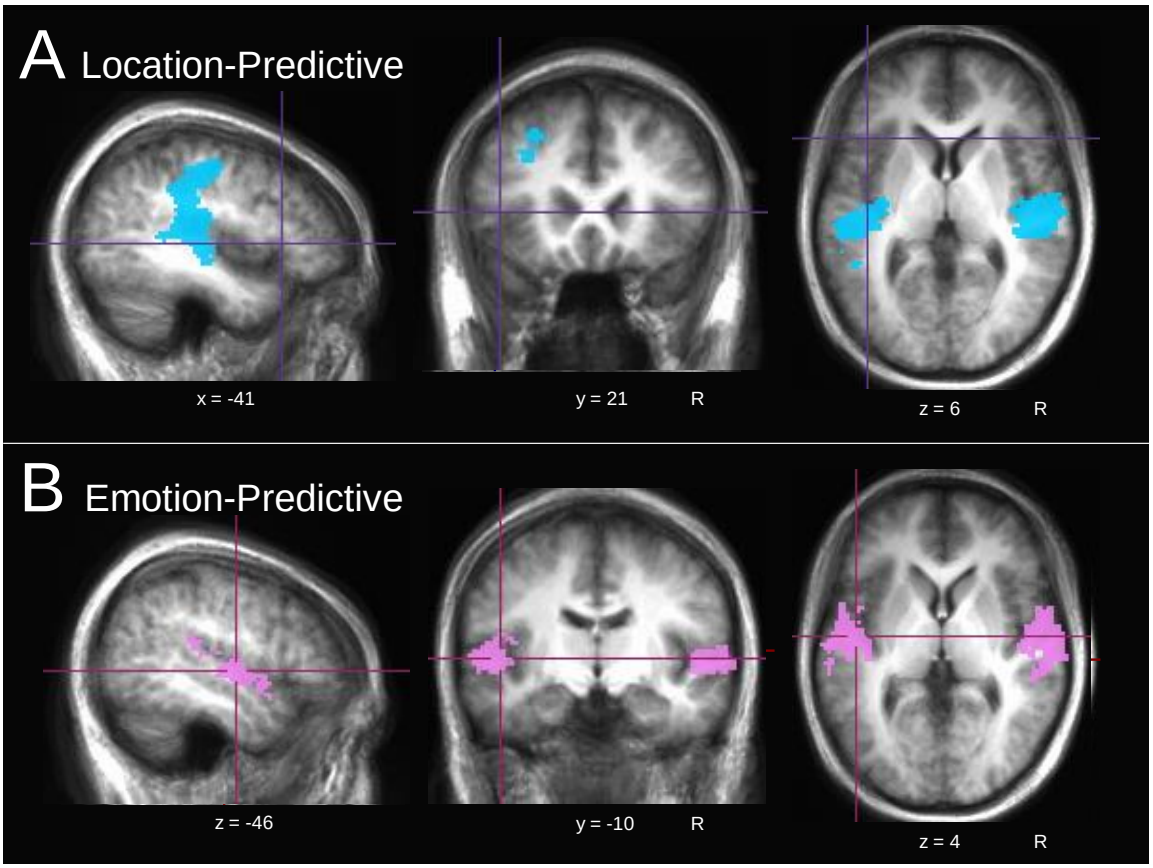

Figure 2.7 Neural regions displaying activity pattern predictive of location and emotion: 10mm searchlight MVPA.

A) Sound location was predicted by patterns of activation within large regions of bilateral STG extending into the pre- and post- central gyrus. In addition, activity in regions of middle frontal and cingulated cortex were also predictive of sound location. Highlighted regions display portions the theorized auditory 'where' processing stream displaying location-predictive activity not identified as location sensitive in univariate analyses. B) The emotional nature of a sound was predicted by patterns of activity in bilateral STG.

Table 2.5 Conjunction of Multivariate and Univariate Results.

Conjunction	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
Univariate: ME Location + MVPA: Location Predictive	R	STG, TTG	13/41/42	48	-23	13	10416
	L	STG, TTG	13/41/42	-47	-27	11	5440
Univariate: ME Emotion + MVPA: Emotion Predictive	R	STG	22	56	-7	1	3144
	L	STG	22	-50	-2	-1	1104
	L	STG	22	-61	-21	5	312
MVPA: Location Predictive + Emotion Predictive	R	STG, TTG, Ins	13/22/41/42	52	-21	10	3744
	L	STG, TTG, Ins	13/41/42	-45	-25	11	1960

STG = Superior Temporal Gyrus, TTG = Transverse Temporal Gyrus, Ins = Insula,

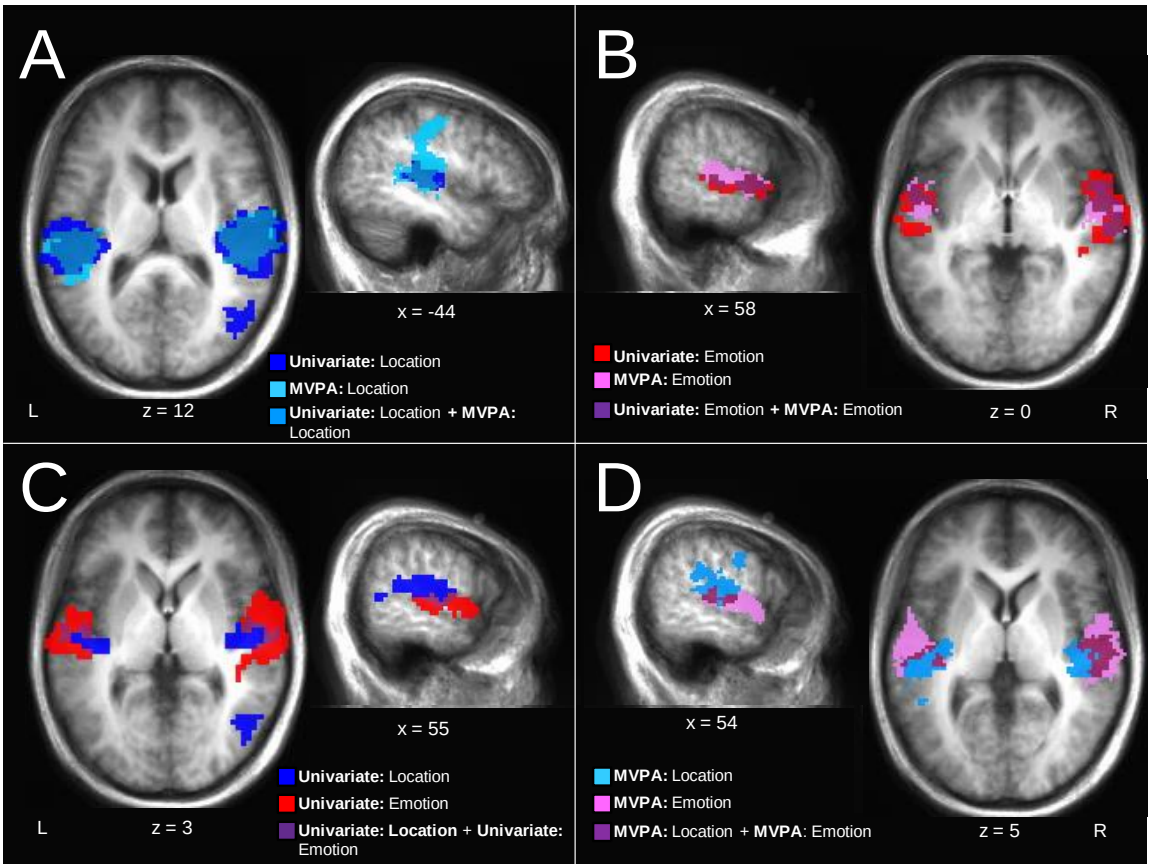

Figure 2.8 Distinct areas of superior temporal gyrus are responsive to emotion and location.

A/B) Conjunction of univariate and MVPA results for both sound location (blues) and emotion (red/pink) in Task 2. MVPA results were found to overlap with the analogous univariate results within secondary auditory areas, while also extending independently into both primary and tertiary auditory processing regions. C/D) Independent conjunctions of univariate vs. MVPA results. While distinct neural regions were identified as sensitive to individual auditory features in both analyses, most extensive overlap was identified in the MVPA conjunction analysis. This overlap lay predominantly over regions involved in the early stages of auditory processing (BA 13/41).

2.4 Discussion

Considerable evidence from visual studies suggests that emotional stimuli gain rapid and often preferential access to the brain's processing resources. Although less work has been conducted in the auditory domain, enhanced effects of emotion on auditory cortex have also been observed across multiple investigative techniques, including fMRI (Wiethoff et al., 2008) and NIRS (Plichta et al., 2011). However, essentially nothing is known about how emotion influences auditory stimulus localization. In the current study, we used fMRI in concert with individualized auditory virtual environments to investigate the effect of emotion on sound localization. Surprisingly, participants were significantly slower to localize positive and negative sounds relative to neutral ones. Moreover, activity in an independently identified location-sensitive region of auditory cortex was not modulated by emotion. Subsequent whole-brain analyses were conducted on a task involving the localization of emotional and neutral stimuli. This analysis revealed that enhanced activity to positive and negative stimuli was observed in anterior-lateral areas of auditory cortex irrespective of location. In contrast, posterior-medial regions of auditory cortex, as well as the inferior parietal lobule and precuneus, were modulated by location, irrespective of emotion. Both the response of anterior-lateral regions of auditory cortex to sound location and the lack of response of posterior-medial region of auditory cortex to emotion ran contrary to original predictions. These unexpected results raised the possibility that emotional sounds augment activity in the anterior-lateral 'what' pathway, but not the posterior-medial 'where' pathway during auditory localization. To more clearly delineate the functional significance of the divisions identified, we conducted an additional functional localizer scan to independently identify regions of auditory cortex that responded to changes in sound identity (i.e., areas associated with encoding 'what' in dual pathway models of auditory processing; Alain et al., 2001; Altmann et al., 2008; Rauschecker & Tian, 2000; Warren & Griffiths, 2003). This functionally-derived ROI was then applied to the original study.

Additional multivariate analyses were performed to investigate this effect with greater sensitivity to neural pattern representations and population-coding. This identified

regions of cortex predictive of both location and emotional auditory cues. Activity in posterior superior temporal gyrus, pre- and post-central gyrus and middle frontal gyrus was found to be predictive of sound location, while activity in anterior superior temporal gyrus, inferior frontal gyrus, insula and thalamus was found predictive of auditory emotion. These regions are consistent with the theorized correlates of the auditory 'where' and "what" processing stream. Collectively, these results support the conclusion that whereas sound location modulates activity within the 'what' and 'where' functionally-derived pathways, emotion modulates neural activity in the 'what' *but not* the 'where' pathway.

2.4.1 Regions associated with processing auditory object location

A main effect of location was observed in bilateral temporal cortex (Tasks 1 and 2), precuneus, and inferior parietal cortex (Task 2). Of note, the location-related effects were characterized in posterior-medial auditory cortex by greatest activity to stimuli positioned furthest in the contralateral hemifield, decreasing activity to midline sounds, and significantly less activity to ipsilaterally positioned sounds. This general pattern of activation emerged bilaterally, with each hemisphere showing the inverse pattern of activation. ROIs generated from Task 1 confirmed that independently defined location-sensitive regions in STG were not modulated by emotion.

2.4.2 Regions associated with processing auditory object identity

In the current study, areas within STG were implicated in processing both the emotional and object identity features of auditory stimuli (Tasks 2 and 3). The identity-related effect identified in Task 3 was characterized in anterior-lateral auditory cortex by greater activity to biological relative to non-biological sounds, but did not distinguish between human and non-human sounds. This result appears to contradict previous work that implicates superior temporal sulcus (STS) specifically in human voice processing (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Ethofer et al., 2012). One critical difference between these studies and the current study is the treatment of non-vocal human sounds (i.e., sounds that do not involve vocal fold vibration). Previous work found that contrasting vocal human sounds with non-vocal sounds yielded voice selective activity of the STS (Belin et al, 2000). Other studies yielding similar effects in STS contrasted human vocal sounds (human non-vocal sounds were excluded) with both

animal and environmental sounds (Ethofer et al., 2012). The current study, however, classed all sound originating from a human source into the 'human' category (e.g., clapping and crying were both 'human'). This regressor was designed to be an easily distinguishable auditory class, and not to represent neural changes associated with vocal processes. As such, it included one vocal and two non-vocal stimuli to eliminate any bias toward the identification of regions displaying voice-specific activation. The neural region observed in the present study may be located in an area slightly superior to that implicated in prior studies of human vocalizations. Interestingly, the use of linguistic utterances may also impact the location of emotion-sensitive regions. For example, Ethofer et al. (2012) demonstrate that an area of STG identified as selective for human voices is also sensitive to the emotional inflection of pseudo-linguistic stimuli. This region, while overlapping with the emotion-sensitive areas in the present study, extends into more posterior-lateral areas of temporal cortex. In future work, it will be interesting to determine whether verbal and non-verbal emotional sounds augment activity in dissociable areas of temporal cortex.

2.4.3 Regions associated with processing both auditory object identity and location

In addition to showing an effect of object identity, areas of right anterior-lateral STG also showed a significant effect of location, and a significant location X emotion interaction. Activity in this region was modulated by location for positive and negative stimuli, but not neutral stimuli. Furthermore, these regions showed increased activity to positive and negative relative to neutral stimuli, but only for those stimuli presented in the contralateral hemifield. Thus, these areas show some evidence of location-related encoding for emotional, but not neutral stimuli. These findings raise the intriguing possibility that anterior-lateral regions of right auditory cortex may be involved in integrating information about object identity and location for emotionally salient stimuli. It also calls into question strict boundaries between spatial and object identity encoding in human STG. Further work will be required to delineate the underlying neuroanatomy and the stimulus parameters associated with these different processes in humans.

2.4.4 Representation of emotion in a dual pathway model of audition

Considerable evidence exists supporting the suggestion that the visual system is comprised of separable ventral and dorsal pathways responsible for processing objects for

identity and action respectively (Milner & Goodale, 1998). It has also recently been proposed that auditory cortices can be separated into similar *'*what*'* and *'*where*'* pathways (Alain et al., 2001; Lomber & Malhotra, 2008; Rauschecker, 2012). In the present study, a functional dissociation between anterior-lateral and posterior-medial divisions of auditory cortices was observed that resembled the boundaries described in some dual pathway models of auditory processing (Bushara et al., 1999; Lomber & Malhotra, 2008; Warren & Griffiths, 2003). To further explore this possibility, results from Tasks 1 and 3 were used to independently generate functionally defined ROIs corresponding to these pathways. This analysis revealed that whereas sound location modulates neural activation within both the 'what' and 'where' auditory processing pathways, emotion modulates activity in the 'what' *but not* the 'where' processing pathway. Importantly, the location X emotion interaction observed in the anterior-lateral 'what' pathway (but not the posterior-medial 'where' pathway) showed that spatial processing in the 'what' pathway was present specifically for emotional stimuli. Subsequent MVPA performed on the data suggests that this functional division is not a strict one at early stages of auditory processing, but rather emerges as information is passed farther along the auditory processing streams. This result, while inconsistent with the initial univariate analysis presented in this study, is not contradictory to theories of dual stream auditory processing. Indeed, nearly 50% of studies investigating representations of sound identity have identified 'what' related processing in these regions (Arnott et al., 2004). It is suggested that processing performed in these regions may be related to multiple auditory characteristics, with increasing specialization as information moves to more tertiary auditory regions (Ahveninen et al., 2013; Ahveninen et al., 2006; Alain et al., 2001). This notion was supported by the MVPA results, which identified distinct location and emotion processing regions in the parietal cortex and anterior temporal lobe respectively.

2.4.5 Effects of emotion on localization behaviour

It would seem advantageous for organisms to rapidly and accurately localize the source of emotional auditory stimuli in the environment. Contrary to expectations, participants in the present study were slower to localize positive and negative sounds relative to neutral ones; so why might emotional stimuli be associated with slower localization performance in the present study? One possibility is that important

differences exist between the dual pathways of the visual and auditory systems. Our finding that participants were significantly slower to localize emotional relative to neutral sounds conflicts with evidence from the visual domain suggesting that dorsal stream guided behaviours are less susceptible to processing limitations (Fecteau et al., 2007; Pisella et al., 2000) and emotional interference (Ngan Ta, Liu, Brennan, & Enns, 2010). Another possibility is that, unlike in the visual system, both object perception and localization in the auditory domain may be sensitive to processing load. In the current study, emotion may have augmented the representation of object features at the expense of spatial-cues, thereby slowing localization performance. Consistent with this interpretation, we observed evidence that both spatial and emotional characteristics were integrated in anterior-lateral areas of auditory cortex, making this a potential site of competition between stimulus features. This integration of object and spatial features within the putative 'what' auditory area raises questions about the extent to which the 'what' and 'where' streams of the auditory system are functionally segregated.

It is important to note that the precise relationship between emotion and the putative 'what/where' pathways of the auditory system was only preliminarily addressed in the current study. First, the nature and anatomical mapping of the putative dual processing stream in the auditory system remains unclear, as is the degree to which its function resembles that of the visual system. In addition, the dissociable effects of emotional versus neutral stimuli within regions of auditory cortex observed were unexpected, and the interpretation is based in part on ROIs generated from follow-up scans involving a smaller sample. Although generated from activity in a sample smaller than the initial population, this ROI displayed similar functional properties to the regions identified in the original task, providing cross-validation for our original interpretation. Nevertheless, in future work it would be beneficial to precisely map the boundaries of the 'what/where' auditory processing streams, and establish the impact of emotion on each.

2.5 Conclusions

Although the emotional content of a sound has been demonstrated to influence processing in auditory cortex, the neural and behavioural effects of emotion on stimulus localization was previously unknown. Our results indicate that during sound localization,

the emotional content of a sound modulates activity in anterior-lateral regions of STG (areas corresponding to the putative 'what' pathway of auditory processing). In contrast, and contrary to predictions, emotion elicited no significant changes in neural activity to posterior-medial areas of STG (regions corresponding to the putative 'where' pathway). An unexpected interaction between emotion and location was also observed in anterior-lateral areas of STG suggesting that the boundaries between object identity and location decoding may be blurred; emotional sounds were associated with enhanced spatial processing in the 'what' pathway despite having no effect on the 'where' pathway. It is important to note that at the behavioural level, a significant delay in localization of emotional compared to neutral sounds was also observed. The idea was raised that this effect may have been driven by competition between spatial and emotional features for representation and control over behaviour. Interestingly, anterior-lateral auditory cortex activity was modulated by both spatial location and emotion in the univariate analyses, while MVPA identified pattern of activity in primary auditory cortex and immediately adjacent regions that were predictive of both auditory emotion and location. These results suggest these areas may be a potential site for such competitive interactions mentioned above. Finally, this work demonstrates, for the first time, the feasibility of utilizing individualized auditory virtual environments as a stimulus presentation tool during fMRI. This technique, which involves presenting auditory stimuli through headphones while maintaining spatial integrity and perceptual realism, holds promise for future neuroimaging studies investigating the spatial component of sound.

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CHAPTER 3

3. Emotion modulates allocentric but not egocentric stimulus localization: Implications for dual visual systems perspectives

Abstract:

Considerable evidence suggests that emotional cues influence processing prioritization and neural representations of stimuli. Specifically, within the visual domain, emotion is known to impact ventral stream processes and ventral stream-mediated behaviours; it remains unclear, however, the extent to which emotion impacts dorsal stream processes. In the present study, participants localized a visual target stimulus embedded within a background array utilizing allocentric localization (requiring an object-centred representation of visual space to perform an action) and egocentric localization (requiring purely target-directed actions), which are thought to rely on the ventral versus dorsal visual stream, respectively. Simultaneously, a task-irrelevant negative, positive, or neutral sound was presented to produce an emotional context for each trial. Consistent with our predictions, we found that during allocentric localization, response accuracy was enhanced in the context of negative compared to either neutral or positive sounds. In contrast, no significant effects of emotion were identified during egocentric localization. These results raise the possibility that negative emotional auditory contexts enhance ventral stream processing, but not dorsal stream processing, in the visual domain. Furthermore, this study highlights the complexity of emotion-cognition interactions, indicating how emotion can have a differential impact on almost identical overt behaviours that may be governed by distinct neurocognitive systems.

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3.1 Introduction

Emotion has far-reaching effects on multiple neurocognitive systems, often influencing the prioritization and processing of environmental stimuli in unexpected ways. It can bias the contents of awareness (Amting et al. 2010; Mitchell and Greening 2012), disrupt or facilitate visual discrimination (Krusemark and Li 2011), or influence behaviour during stimulus localization (Kryklywy et al. 2013). One factor that may contribute to the range of findings is the impact of emotion within dissociable processing streams in sensory cortices. Within the visual domain there are separable dorsal and ventral pathways, traditionally thought to be responsible for providing vision-for-action and vision-for-perception, respectively (Goodale and Milner 1993). Recently, however, this division has been suggested to be one of object-based spatial metrics (allocentric) and observer-based spatial metrics (egocentric; Schenk 2006), wherein both pathways conduct processing related to action and perception, but the coordinate reference frame for each is varied.

The ventral visual stream is strongly influenced by emotional stimuli (Vuilleumier 2005) and displays both functional and anatomical connectivity with the amygdala (Morris et al. 1998; Amaral et al. 2003). In contrast, the potential effects of emotion on dorsal visual stream processes remain comparatively unexplored. This is a particularly intriguing consideration given evidence that dorsal stream-mediated behaviours (i.e., target-oriented, egocentric behaviours) are relatively insensitive to countermanding instructions (Pisella et al. 2000) and optical illusions (Haffenden and Goodale 1998). In addition, there are some suggestions that the effect of emotion on the dorsal stream may be less than its effect on the ventral stream. For example, while fearful stimuli modulate conscious processes in phobic individuals, unconscious control of egocentric visually-guided action is unaffected (Ta et al. 2010). Furthermore, emotion does not appear to influence parietal cortex neurons during visually-guided action in macaques (Rolls et al. 1979). Finally, we have recently shown that whereas activity in the putative "what" area of auditory cortex is augmented by emotional stimuli, activity in the putative "where" pathway is not (Kryklywy et al. 2013). Nevertheless, at least one study has reported modulation of parietal areas to dynamic emotional stimuli (video clips; Goldberg et al.

2014), raising the possibility that emotion may enhance dorsal stream-mediated behaviours.

Interestingly, localization behaviours traditionally thought to rely on dorsal-stream processes have been demonstrated to utilize ventral-stream structures after subtle manipulations of the experimental task. Specifically, this effect is evident for manipulations that necessitate the mental maintenance of the visual scene, and subsequent allocentric representation of visual space. For example, reactivation of lateral occipital cortex (LOC; a ventral-stream structure), was necessary to perform delayed grasping (Singhal et al. 2006) but not immediate grasping tasks (Culham et al. 2003; Cavina-Pratesi et al. 2007). In addition, it has been demonstrated that transcranial magnetic stimulation (TMS) of LOC can influence grasping behaviour in delayed, but not immediate reach conditions (Cohen et al. 2009). Furthermore, it has been suggested that pantomimed actions are driven by stored perceptual representations of object, independent of those mediating on-line visuomotor control (Goodale et al. 1994). Additional neuroimaging data has supported this notion, demonstrating that pantomimed tool use, performed adjacent to the actual tool, activates regions of the middle temporal gyrus not commonly associated with the dorsal stream (Kroliczak et al. 2007). Each of these tasks, while requiring specific behavioural outputs, rely at least in part on an allocentric representation of the visual space. This type of object-centred behaviour has been demonstrated to utilize inferior occipitotemporal cortices in addition to superior occipital and parietal cortices normally seen during visually guided movement (Honda et al. 1998; Zaehle et al. 2007; Thaler and Goodale 2011). Taken together, these findings suggest that actions utilizing a mental representation of a visual scene rely on the integration of both the dorsal and ventral streams. As a consequence, such actions may display some of the ventral stream susceptibility to manipulation not associated with dorsal processes.

In the current work, we determined the relative impact of emotion on indirect and direct target localization. We chose to examine allocentric and egocentric localization behaviours by utilizing indirect and direct response outputs (Liu et al. 2003) because they are thought to differentially engage the ventral versus dorsal visual stream (Schenk 2006; Milner and Goodale 2008). We reasoned that because allocentric localization, requiring

indirect actions that utilize a conscious mental translation of space similar to pantomimed action, is thought to rely in part on ventral stream processes, it would be more susceptible to emotional manipulation. In contrast, egocentric localization, which requires a direct visually-guided interaction with the environment and no mental translation of space, is thought to depend predominantly on dorsal stream processes. To manipulate emotional context, we used standardized positive, negative, and neutral auditory cues during a target localization task. In addition, participant confidence was assessed using standardized self-report, allowing us to filter out trials where the participant was unaware of the presented target. We predicted that whereas the emotional context would significantly modulate response accuracy during indirect localization, it would have no effect on direct localization performance.

3.2 Methods

3.2.1 Subjects

Thirty healthy human subjects participated in the experiment. Data from one subject was not useable due to computer error, leaving twenty-nine subjects (11 male, 18 female; 27 right-handed) with a mean age of 22.0 (Range: 18-36**,** *SD*: 4.71). Participants had normal hearing, normal or corrected-to-normal vision, were fluent English speakers, and were without history of neurological or psychiatric illness. The study was approved by the Health Science Research Ethics Board at the University of Western Ontario.

3.2.2 Stimuli and Apparatus

The display consisted of 400 individual elements (short lines against a white background) arranged as a 20 x 20 array presented on a 32 inch LCD touch screen (MassMultimedia INC; refresh rate 60 Hz). This array was subdivided into 16 unique potential target regions, each containing 25 elements. With the exception of the target region, all individual elements in an array were aligned in a uniform orientation. Target regions were created by tilting the central nine (of 25) elements within a potential target region with respect to the rest of this field. Initial angles for the non-target sections of the array were 0° (vertical), 45°, 90° and 135°. The target area was tilted either 10°, -10° or 0° from this. This resulted in 192 display arrays, including 64 target-absent trials (target

tilt of 0°). The entire array was presented within a visual angle of ~27°, with individual elements subtending over ~1.15°.

Twelve auditory stimuli were chosen from the *International Affective Digitized Sounds* (IADS) stimulus set. These were of a neutral, negative or positive affective nature as defined by standardized ratings (Bradley and Lang 1999) and were used to set the emotional context for individual trials. All sounds were cropped to a total duration of 3500ms and were matched for their onset amplitude and root mean-square amplitude, which ensures that the power and energy were matched across all emotional conditions. Furthermore, positive and negative stimuli were balanced for arousal ratings (mean positive = 6.58, mean negative = 6.92) and valence levels (positive = 7.56, negative = 2.36, absolute neutral = 5). All sounds were presented with ALPHA Electronics Stereo Headphones, Model SDH-7.

3.2.3 Procedure

Participants completed a task designed to differentially tap into dorsal versus ventral stream processes that was adapted from prior work conducted in another laboratory (Liu et al. 2003). Specifically, participants were tasked with localizing target stimuli on a touchscreen display using allocentric (indirect action) versus egocentric (direct action) localization behaviours. While performing this task, participants were presented, via headphones, with task-irrelevant auditory stimuli that varied in their emotional content, as described above. Participants rested their forehead and chin on a secured head/chin support, ~50cm away from the display monitor (adjusted for arm length). The experiment consisted of a single testing session lasting ~1h, comprised of 4 blocks presented in random order (two indirect and two direct localization blocks), each containing 144 trials.

In the experiment, participants detected and localized target stimuli presented in an array (see Figure 2.1 for task details). To begin each trial, participants pressed and held the ‘k’ button on a standard QWERTY keyboard. Subsequently, a stimulus array would appear on one half (left or right side) of the display, paired with an auditory distractor cue. During the presentation of the stimulus array, participants maintained fixation on a centre fixation cross while they identified the target region. To ensure

fixation, eye gaze was monitored during this time period using a fast video-based eye-tracker at 1000 Hz (EyeLink 1000, SR Research). Once the participant had ascertained whether a target was present (i.e. whether an angular deviation > 0° existed), the participant was instructed to release the 'k' button, and the stimulus array disappeared. Following this, either a visual cue would appear prompting the participant to continue to the next trial (during target-absent trials), or the array would be replaced by an empty square of identical size (during target-present trials). Allocentric and egocentric localization blocks were manipulated to ensure that the overt behaviours were as similar as possible, whilst relying differentially on the degree of spatial representation required, and therefore the two visual streams. During the allocentric localization blocks, the empty response square was transposed to the opposite side of the screen from where the initial array and target had appeared. Upon release of the 'k' button, participants were to touch the area within the transposed square that corresponded spatially to where the target would have been presented. Alternatively, during the egocentric localization blocks, participants were instructed upon release to immediately press the touchscreen on the precise location in which the target had appeared. Each block was preceded with the instruction to either indirectly or directly localize the target. Following each target-present trial, participants indicated their confidence in the accuracy of their response on a scale of 0-100%. During each trial, an auditory cue was presented to set the emotional context. The sound began when the 'k' button was pressed, and would terminate either at the release of the 'k' button (for target-absent trials) or once the participant made a localization response (for target-present trials). For both blocks, all button presses and localization responses were made with the right hand. The presentation of auditory cues was randomized within a block.

The primary outcome measure of interest for this task was response accuracy, as assessed by measuring the distance of the response from the centre of the target area in millimeters. Response time (RT) was also assessed. This was defined as the length of time beginning at the initial button press to start each trial and ending at the touch response indicating target location. For the analysis, trials were segregated based on three factors; the post-trial confidence rating, the localization type of the block, and the

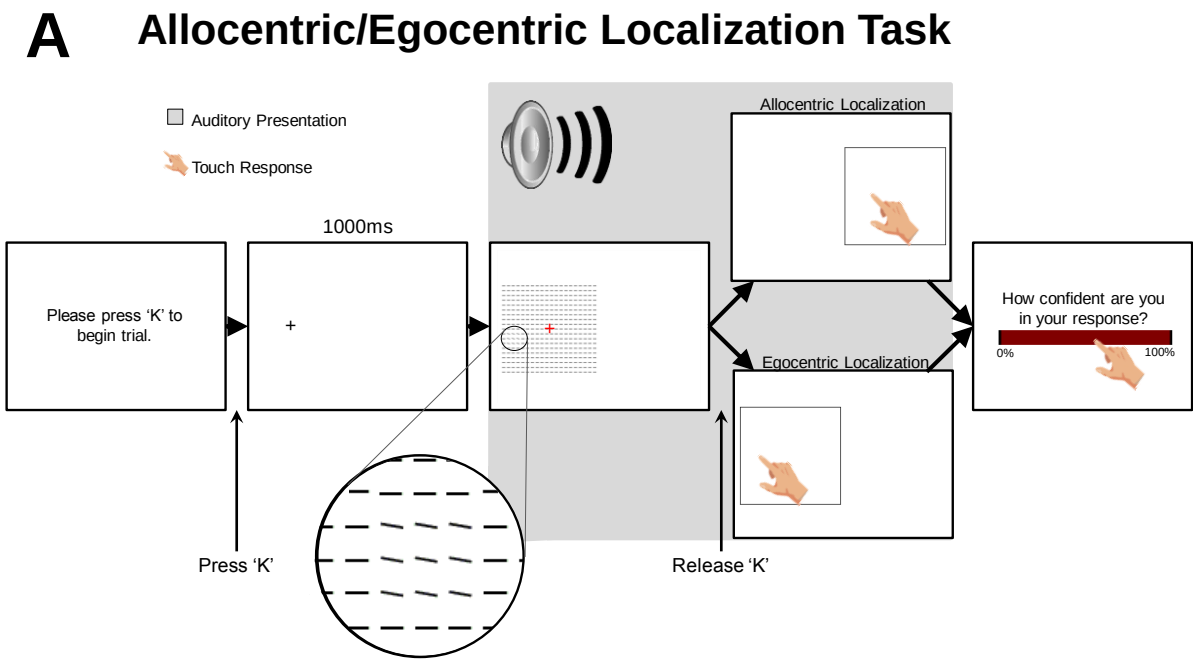

Figure 3.1 A trial schematic displaying the time-course for a single, non-null trial. To begin a trial, participants pressed and held the 'k' button on the keyboard. This button would remain depressed until the participant was ready to make a localization response (i.e., they identified the target location; see magnified region for target example). Examples of the allocentric and egocentric action blocks can be noted in the response area on the fourth screen (from left). Each trial ended with participants indicating a confidence level for their localization response.

emotional quality of the auditory cue. Confidence ratings were included because during pilot testing, it was noted that, on a minority of trials, participants would be unable to detect the target stimulus. In order to identify these trials, we separated the data into bins as a function of confidence. Thus, trials were divided into 5 bins, each representing a 20% range of confidence (e.g. confidence bin 1 = trials with confidence levels from 0-20%).

3.3 Results

3.3.1 Confidence Analysis

A 2 (Localization type: allocentric, egocentric) X 3 (Emotion: negative, neutral, positive) repeated-measures ANOVA was performed on the confidence ratings to determine the impact of localization type and emotion on the self-reported perception of accuracy. While this revealed no significant main effects of Localization Type ($F_{(1,28)} = 0.833$, $p > 0.10$), a marginal main effect of Emotion was identified ($F_{(2,56)} = 2.588$, $p = 0.084$). There was no significant Localization Type X Emotion interaction ($F_{(2,56)} = 0.750$, $p > 0.10$).

Confidence ratings across all trials within a confidence bin were subsequently used to filter responses made by participants which did not significantly differ from chance. A series of one-way t-tests (one-tailed, $\alpha = 0.05$) were used to compare the average distance to target within each confidence bin to the expected chance value (chance = 112mm). It was found that while responses in Confidence Bin 1 (0-20%) were not significantly better than chance ($p > 0.10$), responses at all other confidence bins were significantly more accurate ($p < 0.05$ for each comparison; see Figure 3.2a). For this reason, responses within Confidence Bin 1 were excluded from further analyses.

3.3.2 Localization Behaviours

Localization X Emotion

Additional 2 (Localization type: allocentric, egocentric) X 3 (Emotion: negative, neutral, positive) repeated-measures ANOVAs were performed on both the RT and response accuracy (distance-to-target) data to determine the impact localization type, and emotion on localization behaviour (see Table 3.1). No significant effects of Localization

Type ($F_{(1,28)} = 0.200$, $p > 0.10$), Emotion ($F_{(2,56)} = 0.671$, $p > 0.10$), or Localization Type X Emotion ($F_{(2,56)} = 1.427$, $p > 0.10$) were identified within the RT data.

Within the response accuracy data, a significant main effect of Localization Type was identified ($F_{(1,28)} = 4.756$, $p < 0.05$; Allocentric > Egocentric) as well as a marginal main effect of Emotion ($F_{(2,56)} = 3.102$, $p = 0.053$). The marginal effect was characterized by significantly greater response accuracy for trials paired with a negative auditory cue compared to trials paired with a positive auditory cue ($p < 0.05$). Of particular interest, this analysis also identified a significant Localization Type X Emotion interaction ($F_{(2,56)} = 5.596$, $p < 0.01$; see Figure 3.2b).

To delineate the Localization Type X Emotion interaction, two independent one-factor repeated measure ANOVAs were conducted, identifying the effect of emotion on response accuracy during the allocentric and egocentric localization tasks individually. These revealed a significant main effect of emotion during allocentric localization ($F_{(2,56)} = 7.336$, $p < 0.005$), *but not* egocentric localization ($F_{(2,56)} = 0.664$, $p > 0.10$). Follow up t-tests revealed that this effect of emotion during allocentric localization was driven by significantly increased response accuracy during trials paired with a negative auditory cue, relative to trials paired with a neutral or positive auditory cue ($p < 0.01$ and $p < 0.005$ respectively). No significant differences were found between trials paired with positive or neutral auditory cues. Importantly, a series of one-way repeated measures ANOVAs conducted on the response accuracy data for individual sounds within each emotional sound category identified no significant main effects (Negative $F_{(1.548,43.355)} = 1.642$, $p > 0.10$; Neutral $F_{(3,84)} = 0.026$, $p > 0.10$; Positive $F_{(3,84)} = 0.389$, $p > 0.10$). This suggests that earlier effects cannot be driven by a single anomalous exemplar within an emotion category.

Table 3.1 Emotional Effects on Localization Behaviour

Localization Type	Emotion	Response Time (ms)[a]	Localization Error (mm)[b]
Allocentric Localization	Negative	2108.2 (629.0)	57.6 (15.9)
	Neutral	2209.3 (627.2)	66.5 (21.7)
	Positive	2172.8 (597.1)	66.9 (23.9)
Egocentric Localization	Negative	2197.2 (603.6)	63.8 (18.9)
	Neutral	2086.9 (499.9)	63.3 (21.4)
	Positive	2156.1 (606.7)	62.9 (19.4)

[a] No significant effects of Localization Type, Emotion, or Localization Type by Emotion interaction were identified in the response time data. [b] A main effect of Localization Type and a Localization Type by Emotion interaction were identified in the Localization Error data ($p < 0.01$).

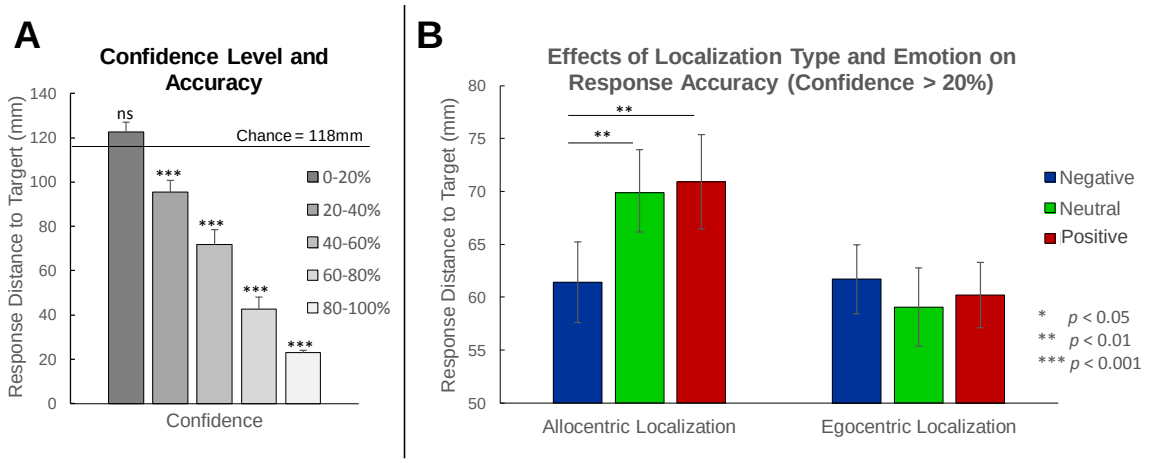

Figure 3.2 Effects of confidence, localization type, and emotion on localization response accuracy.

Accuracy is measured as the distance between a touch response and the centre of a visually presented target. A) Evident here is the effect of perceived task difficulty on deviation from chance. Participants performed at chance levels for those trials in which the confidence level ratings were no greater than 20%. B) This graph illustrates the nature of the Localization Type X Emotion interaction. For allocentric blocks, accuracy was significantly greater for trials paired with negative, compared to either positive or neutral auditory cues. In contrast, no significant effects of emotion were identified during trials involving egocentric localization.

3.4 Discussion

Considerable evidence suggests that emotional cues can influence stimulus processing (Vuilleumier and Driver 2007). Specifically, within the visual domain, emotion has been shown to impact a number of different identification and recognition behaviours (Pessoa et al. 2006; Phelps et al. 2006). The extent to which these effects are mediated independently by the ventral and dorsal visual streams, however, remains unclear. The present study sought to begin to address this gap in knowledge. Participants localized a visual target stimulus embedded within a background array presented to a single side of a display by utilizing either allocentric localization, (a process thought to rely on predominantly ventral stream contributions) or egocentric localization (a predominantly dorsal stream-mediated process). Simultaneously, a positive, negative or neutral auditory cue was presented to set an emotional context for each trial. We found that during allocentric localization, response accuracy, as measured by the distance of the response to the centre of the target, was significantly enhanced when the trials were paired with negative rather than neutral or positive sounds. In contrast, emotion did not significantly influence response accuracy during egocentric localization. Importantly, these results cannot be explained by task difficulty effects or a speed-accuracy trade-off, since the two localization tasks did not differ significantly in overall RT. These results support our hypothesis that negative emotional contexts may differentially modulate ventral versus dorsal stream-mediated behaviours.

Emotion can have heterogeneous effects on behaviour (Vuilleumier and Huang 2009). The present study raises the possibility that one potential source of these differential effects may be the relative involvement of the ventral versus dorsal visual system in the output behaviour. Indeed, functional and anatomical evidence suggests that the ventral stream has strong reciprocal connections with emotion-related structures like the amygdala (Morris et al. 1998; Freese and Amaral 2005), while only sparse connections exist between parietal cortices and the amygdala (Baizer et al. 1993). Nevertheless, recent evidence suggests that activity in dorsal visual stream areas (inferior parietal sulcus and superior parietal lobule) is enhanced for emotional relative to neutral movie scenes (Goldberg et al. 2014). It is important to note that in this latter study, the relative amount of motion in the emotional versus neutral stimuli was not explicitly

matched, and so it is possible that cross-category differences in motion (rather than emotion per se) may have driven these effects. This is particularly relevant given that parietal areas are also strongly activated by complex stimulus motion (Andersen 1997) and motion imagery (Goebel et al. 1998). Additional research utilizing both neuroimaging and refined behavioural measures are needed to clarify the impact of emotion on the visual processing streams.

The cross-modal design of the current study utilized auditory stimuli to create an emotional context during a visual localization task. It may seem counter-intuitive that task-irrelevant negative sounds might enhance performance on a visual task. However, the presentation of temporally synchronous auditory and visual cues have been demonstrated to cause the perceptual salience of sounds to transfer to associated visual objects, augmenting their representation and modulating behaviour and perception (Stein et al. 1996; Frassinetti et al. 2002). In the current study, the emotionally salient auditory cues likely augmented the salience of the array in the ventral visual stream. Importantly, this augmentation of object information selectively benefitted allocentric representation of visual space (a ventral stream-mediated process). An intriguing possibility is that this selective effect is mediated by the extensive anatomical and functional connections between ventral visual areas and the amygdala (Freese and Amaral 2005), which has fewer connections with dorsal visual areas (Baizer et al. 1993; Amaral et al. 2003).

It is also important to note that the beneficial effects of emotion in this context were conferred to negative but not positive auditory contexts. In some respects, this is not surprising. Previous work has demonstrated that some valence-specific emotional effect may only be present during block designed tasks (Schepman et al. 2012), of which the current task was not. In addition, although both positive and neutral emotional stimuli elicit enhanced amygdala activity, negative stimuli appear to produce more consistent and robust effects on tasks of spatial attention (Pourtois and Vuilleumier 2006). As a consequence, the observed effects are likely due to an enhancement of the representation of the spatial components within the array (i.e., an emotionally augmented attention effect) in the allocentric condition. In contrast, egocentric localization behaviours did not benefit from this augmentation of attention because they did not rely on a mental

representation of space independent of the observer as the allocentric actions did. Although the data are consistent with this interpretation, further work involving neuroimaging or virtual lesion techniques are warranted to clearly delineate the specific underlying neurocognitive processes. The possibility should also be acknowledged that the observed effects in the allocentric condition were due to low-level stimulus properties other than emotion that effect attention. We believe this is unlikely given that the acoustic properties and length of the stimuli were well-matched, and the well-replicated effects of emotion on ventral stream processes. Nevertheless, it is interesting that overt behaviours that are so similar could be differentially susceptible to such properties, and the results may have implications for the design of human-machine user interfaces.

3.5 Conclusions

Emotion is known to influence the representation of visual stimuli in the ventral visual stream; however, its relative effects on behaviours mediated by the ventral versus dorsal streams were unknown. In the present study, negative emotional context was found to enhance the accuracy of allocentric localization (a behaviour mediated predominantly by the ventral stream) but not egocentric localization (a behaviour mediated predominantly by the dorsal stream). The results are consistent with evidence that emotion-related brain areas have extensive modulatory connections with the ventral visual stream (Amaral et al. 2003; Tamietto and de Gelder 2010), as well as studies from the auditory domain which suggest that emotion is represented in the putative ‘what’ but not ‘where’ stream of auditory processing (Kryklywy et al. 2013). This study highlights the complexity of emotion-cognition interactions, indicating how emotion can have a differential impact on almost identical overt behaviours that happen to be governed by different neurocognitive systems.

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CHAPTER 4

4. Imaging Emotional Motion: interactions between emotional content visual and motion perception.

Abstract:

Emotional information can impact the representation and perception of visual information. This impact appears most pronounced in the ventral visual stream, with dorsal stream and dorsal stream-related behaviour less susceptible to emotional modulation. Adaptive behaviours such as threat detection, however, are known to utilize visual motion cues; yet little is known about how emotion influences activity in motion-processing areas. This study investigated the influence of emotional information on motion-based visual illusion. While undergoing fMRI, motion after-effects were induced on static emotional images to identify the effect of emotion on motion perception, and the effect of perceived motion on the subjective perception of emotional intensity. A separate localizer scan isolated neural regions sensitive to visual motion (i.e., area V5/MT+) independent of emotion for each participant. Activity in this region was modulated by both the existence of a motion aftereffect during the experimental task, and the emotional nature of the presented images; however, these factors did not significantly interact. In addition, this area displayed patterns of functional connectivity with the amygdala that were modulated by the emotional content of an image. A whole brain analysis of data identified large regions of ventral occipital, temporal and frontal cortex sensitive to emotional information. Of note, enhanced activity was elicited within both the amygdala and visual areas (ventral visual stream and V5/MT+) for emotional compared to neutral images. An interaction between emotion and perceived motion was identified within dorsal regions of the frontal pole, characterized by preferential responding to non-desirable outcome (i.e., approaching negative stimuli or receding positive stimuli). Overall, these data are consistent with the idea of emotion augmenting activity in motion-sensitive regions during the presentation and give valuable insight into the role of frontal cortex in representing the incentive value of an active situation.

4.1 Introduction

Emotion can impact perception of our environment from the very early stages of sensory processing. In the visual system, emotional information has been demonstrated to influence stimulus representations as early as primary visual cortex (Vuilleumier & Driver, 2007; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Emerging evidence suggests, however, that emotion does not have a uniform effect throughout the visual system; ostensibly similar visual localization behaviours have been found to be differently affected by emotional information depending on contributions from the ventral versus dorsal stream (Kryklywy & Mitchell, 2014). In particular, emotional information has profound effects throughout the ventral visual stream (Vuilleumier, 2005). This is supported by extensive functional and anatomical connectivity between these regions and emotion-related structures, such as the amygdala (Amaral, Behniea, & Kelly, 2003; Freese & Amaral, 2005; Morris et al., 1998; J. L. Robinson, Laird, Glahn, Lovallo, & Fox, 2010). In contrast, the dorsal visual stream appears less susceptible to emotional influence (Kryklywy & Mitchell, 2014). In line with this finding, anatomical investigations suggest that the dorsal visual stream has very limited connectivity to emotion-related structures (Amaral et al., 2003; Freese & Amaral, 2005).

Adaptive behaviours such as threat detection are known to utilize visual motion cues to guide behaviour (Parasuraman & Galster, 2013; van Boxtel & Lu, 2012). Thus, it is reasonable to predict that neural regions utilized in processing these cues should be influenced by the emotional nature of a stimulus. Nevertheless, little is known about the impact of emotion on activity in motion-processing areas (e.g., V5/MT+). Interestingly, V5/MT+ is not definitively categorized into either the dorsal and ventral stream framework for visual processing (Born & Bradley, 2005; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). While projections from this region feed into the dorsal visual stream (Arall, Romeo, & Super, 2012; Born & Bradley, 2005; Buchel & Friston, 1997; Cloutman, 2013), V5/MT+ also displays patterns of connectivity and behavioural responding consistent with ventral stream structures. In particular, V5/MT+ displays anatomical and functional connectivity with the amygdala (Amaral et al., 2003; Furl, Henson, Friston, & Calder, 2013; Young, Scannell, Burns, & Blakemore, 1994), a region

noted for its role in emotional processing (Dolan & Vuilleumier, 2003; Kryklywy, Nantes, & Mitchell, 2013; J. E. LeDoux, 1992; Pessoa, 2008; Phelps, 2006; Vuilleumier, 2005). Similar connections are not found in the dorsal visual stream, yet are quite characteristic of ventral processing regions (Amaral et al., 2003; Baizer, Desimone, & Ungerleider, 1993). Furthermore, while ventral visual processing is susceptible to a number of optical illusions, dorsal visual processing is relatively insensitive to these cues (Haffenden & Goodale, 1998). Interestingly, activity in V5/MT+ has been linked to illusionary visual motion (Antal et al., 2004; He, Cohen, & Hu, 1998; Tootell, Reppas, Dale, et al., 1995), displaying illusion sensitivity more consistent with the ventral than the dorsal visual stream.

Recent work examining the impact of emotion on visual area V5/MT+ while viewing dynamic facial expression has found that activity in this region is modulated by the emotional category of dynamic facial expressions, and suggested a series of feed forward projections from the amygdala to visual motion-sensitive regions as a likely mechanism underlying this effect (Furl et al., 2013). In addition, activity in V5/MT+ appears to be modulated by emotion during the perception of emotional actions (Van den Stock et al., 2011), while activity in inferior parietal cortex appears to be modulated by emotion presented in dynamic movie scenes (Goldberg, Preminger, & Malach, 2014). Of note, the amount of motion and the stimuli familiarity in the latter study were not controlled and consequently may be confounding the emotion-based result. Furthermore, emotional cues in previous studies were either directed to alternate objects in the environment, or did not change the distance of the emotional object relative to the observer. Both of these characteristics are important considerations when investigating the impact of emotion on motion systems involved in threat-detection. It remains unclear the extent to which emotional content can modulate the activity of motion-sensitive regions, particularly V5/MT+, while experiencing motion through complex visual scenes.

In the current work, we investigated the interaction between emotion and visual motion perception utilizing a motion-aftereffect paradigm. We varied perceived motion while keeping the visual stimulus constant by presenting our target stimuli after a prolonged pattern of consistent motion thus creating illusory motion aftereffects. This

allowed for greater control of low-level visual characteristics across conditions relative to presenting stimuli with real motion, which necessitate a change in visual angle to create the perception of an approaching and receding object. In addition, an independent functional localizer scan was performed for each participant to identify the bilateral motion-sensitive area V5/MT+. Changes in V5/MT+ activation were investigated with respect to both changes in the direction/presence of a motion aftereffect and changes in the emotional nature of the visual stimulus. We reasoned that because of the evolutionary importance of visual motion in threat detection and response, V5/MT+ would display increased activation for emotional compared to neutral images. In addition, we expect that activity in extended regions of the ventral visual stream, including lateral occipital cortex and fusiform gyrus, will also be modulated by emotion, while motion sensitive regions of the dorsal visual stream beyond V5/MT+, including V3a, V7, and inferior parietal lobe, will not be. To manipulate emotional context, the target images were chosen from a standardized data base of emotional images and fell into three distinct categories: positive, negative and neutral. In addition, following each trial, participants rated the quality of the visual illusion (i.e., the extent to which the target image was perceived to be moving) and the emotional intensity of the target image (i.e., the arousal level elicited by the image). We predicted that the emotional images would significantly increase the level of illusory motion, and that approaching images would elicit higher emotional intensity ratings.

4.2 Methods

4.2.1 Subjects

Nineteen healthy human subjects participated in the experiment (13F/6M) with a mean age of 22.6 (SD = 3.70). All participants were without history of neurological or psychiatric illness and were right-handed, had normal hearing, normal or corrected-to-normal vision and were fluent English speakers. The study was approved by the Health Science Research Ethics Board at the University of Western Ontario.

4.2.2 Stimuli and Apparatus

Four unique motion video clips were created for this study in VPixx (VPixx Technologies). Two unique video clips were utilized to induce the motion after-effect in

the main experimental task. These consisted of concentric circles (7.2mm width; alternating black/white), which contracted or expanded relative to a central fixation point at a constant rate of 2 Hz. After-effects created by these stimuli are a linear perceptual drift of images in the opposite direction of the initial movement (Bowditch & Hall, 1882). A third video, consisting of concentric circles with both contracting and expanding motion patterns alternating at 2 Hz was used as a no-after-effect control condition. A fourth video was created for the V5/MT+ localizer consisting of 200 short line segments randomly oriented either vertically or horizontally and moving at a constant pace in one of eight directions for 20s.

Twenty-seven images were chosen from the *International Affective Pictures System* (IAPS) stimulus set. To aid in the selection of these images, a pilot study (n=10) was conducted to ensure that the spatial layout of visually salient features did not vary between emotional categories. For this study, participants were presented with 78 potential IAPS images (35 positive, 25 neutral and 35 positive) for two seconds, and instructed to freely view each image. Eye-behaviour was monitored using a fast video-based eye-tracker at 1000 Hz (EyeLink 1000, SR Research). Subsequent analysis examined the percentage of time spent fixated within the centre of the image (<20° from the midpoint) in contrast to the periphery (>60° from the midpoint) for each image, (reported as %C - %P). From these initial images, nine pictures were chosen from each emotional category that allowed for the best matched spatial salience between categories (positive v. neutral: $t_{(16)} = 0.122$; $p > 0.10$; negative v. neutral: $t_{(16)} = 0.146$; $p > 0.10$; positive v. negative: $t_{(16)} = 0.289$; $p > 0.10$). Following this, subsequent analyses were conducted to ensure that the resulting positive and negative stimuli were balanced for valence levels (positive = 7.56, negative = 2.86, absolute neutral = 5 (0); $t_{(16)} = 1.52$; $p > 0.10$) and arousal levels (positive = 5.40, negative = 5.52; $t_{(16)} = 0.471$; $p > 0.10$). In addition, physical properties were compared between image categories to ensure a match on low level visual features by subjecting each image to a wavelet analysis similar to that outlined in Delplanque et al., (2007). For this, each red, green, blue and grayscale layer of the image was decomposed into eight frequency bands (512, 256, 128, 64, 32, 16, 8, 4, and < 2 cycles per image). An examination of the energy within each band indicated no significant differences between the negative or neutral stimuli (all corrected *p*s > 0.10).

Furthermore, absolute luminance levels did not significantly differ between categories (positive v. neutral: $t_{(16)} = 0.069$; $p > 0.10$; negative v. neutral: $t_{(16)} = 0.886$; $p > 0.10$; positive v. negative: $t_{(16)} = 0.933$; $p > 0.10$). In addition, eight different neutral IAPS images were selected for use in a pre-scan practice task. A final image was created for the V5/MT+ localizer consisting of consisting of 200 short static line segments randomly oriented either horizonally or vertically.

All scanned images were presented using a Silent Vision^{TM} Extended Range XR Fiber Optic Visual System (SV-7021). In addition to allowing binocular stimuli presentation with little extraneous visual information, this system was paired with a Real Eye Model^{TM} Eye Imaging System (RE-4921). The pre-scan task was conducted on a Lenovo ThinkPad W540 (1920 X 1080 pixels, refresh rate 60hz).

4.2.3 Procedure

Pre-Scan Practice

Participants completed a task designed to induce perceptual motion after-effects on static images of varying emotional content. Specifically, participants viewed a constant pattern of visual motion for a fixed duration before being presented a static neutral image. The pre-scan training consisted of a single testing run lasting ~5 minutes (2 motion direction X 8 target images).

To begin each trial, participants were presented a stationary fixation cross lasting 500ms. Following this, a pattern of constant visual movement (contraction or expansion) was presented for a period of ten seconds. After the completion of the video, a target image appeared immediately, and remained visible for 3000ms. The constant pattern of visual motion induced a pattern of illusory motion in the opposite direction on the subsequent target image. This effect is referred to as the motion-after effect. During the presentation of both the motion pattern and target image, participants maintained fixation on a red centre fixation cross. Once the target image disappeared, two questions were asked in random order. One question required the participant to indicate to what extent the target image appeared to move, while the other required the participant to rate the emotional arousal level of the target image. All responses were given using a 5-point Likert rating, ranging from ‘Very Little’ (1) to ‘Very Much’ (5). All button presses were

made with the right hand. The presentation of all motion patterns and target images were randomized within the pre-scan experiment.

MT+ Localization

Prior to the anatomical scan and experimental task, participants completed a single functional localizer run to identify area V5/MT+ (Figure 4.1a). In the scanner, participants were presented with alternating 20s motion video and 20s static image. This was repeated 8 times, with a fixation cross of variable duration (1.5-2.5s) separating each visual presentation.

Experimental Procedure

In the scanner, participants completed an "emotional motion-aftereffect task" with a very similar design to that outlined in the pre-scan practice procedure (Figure 4.1b). To begin each trial, participants viewed a 500ms static fixation cross, followed by a motion video (10 seconds; contracting, expanding or alternating). Immediately after the cessation of this video, one of 27 target images was presented for 3000ms. During the presentation of both the motion video and the target image, participants maintained fixation on a centrally located red fixation cross. After presentation of the target image, a black fixation cross appeared for 1500, 2000 or 2500ms (randomized between trials) followed by two questions in random order: "To what extent did the image move [towards you/away from you/around]?" and "How emotionally arousing was the image?". All responses were given on a 5-point Likert rating, ranging from 'Very Little' (1) to 'Very Much' (5) and collected with an MRI-compatible 5-response button box. A single run consisted of an image from each emotional category (positive, negative, neutral) presented following each of the motion patterns (contracting, expanding, alternating) three times, resulting in 27 trials per run. Participants completed six experimental runs (162 total trials, 18 per motion-emotion condition), with each image paired with each direction twice. Functional images were collected for the duration of the experimental task.

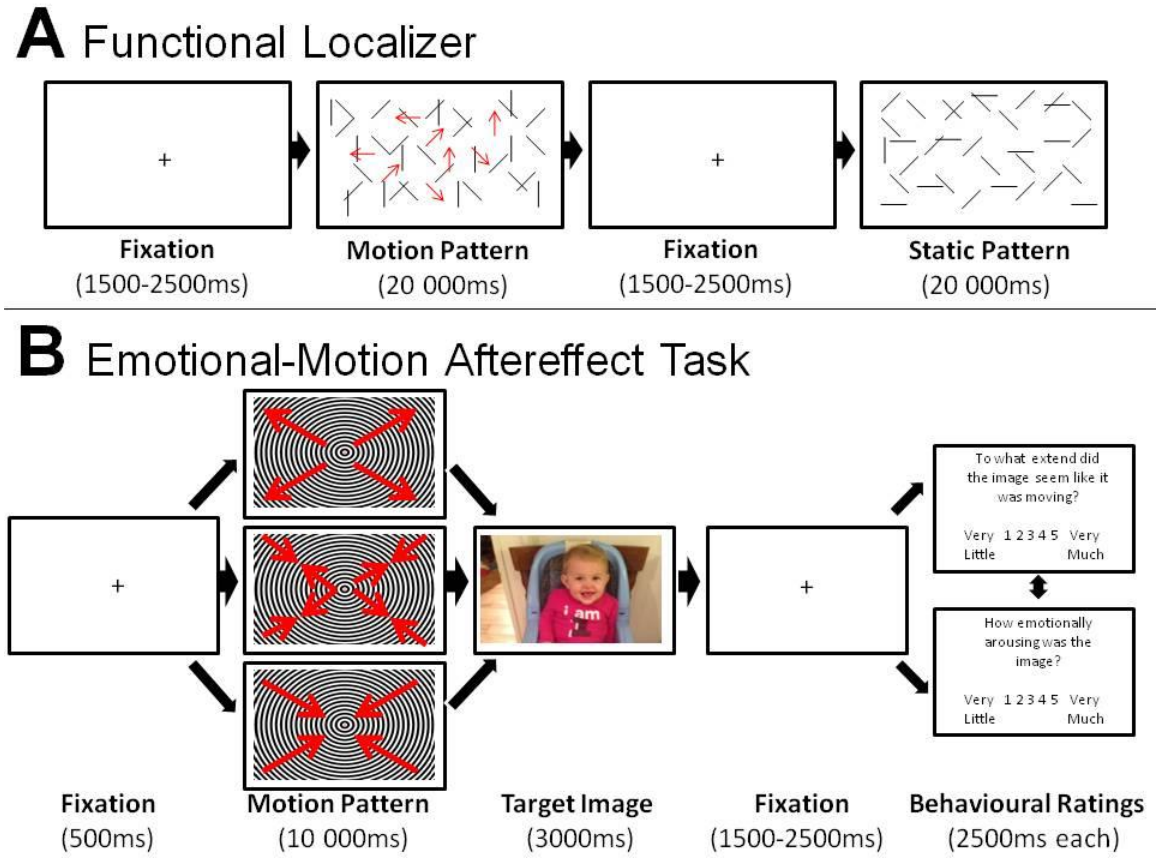

Figure 4.1 Trial schematics for functional neuroimaging tasks.

A) Twenty second of dynamic motion was alternated with 20 seconds of static images, separated by a fixation cross of variable duration. Both sets of visual stimuli consisted of an array of short line segments. B) Following fixation, participants were presented a pattern of consistent motion that was expanding from, contracting to, or flickering around a central fixation point. This induced a motion aftereffect on a subsequently presented target image. Following this, two questions were presented to assess the impact of direction and emotion on the perception of illusory motion and emotional arousal. The order of these questions was randomized between trials.

4.2.5 Behavioural Analysis

The primary behavioural outcome measures for this task were the emotional arousal rating, and illusionary strength rating for the target images. To assess the impact of emotion on motion perception, participants were required to rate the intensity of the after-effect for each image presentation. Similarly, to assess the impact of perceived motion on emotional intensity, participants were required to rate each image for its level of emotional arousal. For the analysis, trials were segregated based on two factors; the direction of motion aftereffect, and the emotional nature of the target picture. Two separate 3 (Direction of Aftereffect: approach, recede, static) X 3 (Emotion: negative, neutral, positive) repeated measures ANOVAs were conducted; one for each the post-trial illusion-strength ratings, and the post-trial arousal ratings.

4.2.6 Imaging Acquisition and Analysis
MRI Acquisition

Subjects were scanned during the task using a 3T Siemens Scanner with a 32 channel head coil. fMRI images were taken with a T2*-gradient echo-planar imaging sequence (repetition time [TR] = 1250ms, echo time [TE] = 30ms; field of view [FOV] = 192mm, 96 x 96 matrix). Scan parameters were chosen that would optimize the signal-to-noise ratio for the amygdala based on recent recommendations in the literature (Morawetz et al., 2008; S. Robinson, Windischberger, Rauscher, & Moser, 2004). All scanner images were acquired during a single scanning session. For all functional runs during the experimental task, complete brain coverage was obtained with 57 interleaved slices of 2.0mm isovoxels. A series of 268 functional images were collected during the V5/MT+ localizer run, and 468 for each experimental run. A whole-brain, high resolution T1-weighted anatomical scan was obtained between the functional localizer scan and the emotional motion-aftereffect runs (TR = 2300ms, TE = 4.25ms; FOV = 25.6cm, 192 axial slices; voxel size = 1mm isovoxels; 256 x 240 matrix).

Data Analysis

All analysis of fMRI data was conducted using Analysis of Functional NeuroImages (AFNI) software (Cox, 1996). The data were analyzed using both a region of interest (ROI) and whole-brain approach. The ROI analysis focused on a functionally

defined V5/MT+ region identified by an independent localizer scan at the individual subject level. In addition, a series of group-based ROIs derived from regions of cortex with activity modulated by motion versus no motion contrasts were identified. Following Swallow Braver, Snyder, Speers, and Zacks (2003), a multi-stage process was used to identify the V5/MT+ at a single subject level. First, general linear models were used to contrast single subject activity during the perception of motion videos and static imagery from the functional localizer task. At a threshold of $p < 0.001$, a significant cluster containing V5/MT+ was contiguous with significant activation in additional early visual areas, including V1, V2 and V3 in eighteen of nineteen participants. To remove these visual areas, which are not specifically motion sensitive regions (Tootell, Reppas, Kwong, et al., 1995), thresholds were adjusted until the resulting ROIs appeared the appropriate size ($<1000mm^3$) and location as V5/MT+, as described by Tootell and Taylor (1995). The percent signal change during the emotional motion-aftereffect task was extracted from all of ROIs (individually-derived V5/MT+ ROIs and group-derived ROIs defined as motion NE static) for each condition of interest as outlined in the model above. To determine the relative extent to which activity within V5/MT+ was driven by both the presence of a motion aftereffect and emotional content of a stimulus, a 3 (Direction: approaching, receding, static) X 3 (Emotion: negative, neutral, positive) repeated-measures ANOVA was conducted on the percent signal change derived for each of the conditions of interest. Follow-up paired t-tests were conducted to investigate any significant effects. Similar ANOVA and follow-up tests were performed on the data from each of the group-based ROIs as well.

In addition, a similar 3 X 3 repeated-measures ANOVA was conducted on the whole brain EPI data involving factors consistent with those presented during the ROI analysis. Relevant percent signal change was extracted from any significant clusters and subject to follow-up paired t-test to help determine the nature of these effects. To help clarify effects in the amygdala and thalamus, activity in these regions was isolated from larger significant clusters using anatomically-derived (TT Daemon atlas) bilateral amygdalar and thalamic masks. To correct for multiple comparisons, a spatial clustering operation was performed using 3dClustSim with 10000 Monte Carlo iterations on the whole brain EPI matrix. Additionally, any significant cluster identified within the

amygdala or thalamus was subject to a small volume correction using 3dClustSim, with 10000 Monte Carlo iterations, conducted on the anatomical masks.

Connectivity

Context dependent functional connectivity analysis with a V5/MT+ seed region was conducted using generalized psychophysical interactions (gPPIs; McLaren, Ries, Xu, & Johnson, 2012). The voxel of peak intensity in right V5/MT+ for each person (as identified by the functional localizer) was utilized as the seed region in all analyses, and each was performed in native space. Whole brain connectivity was identified during each motion direction (approaching, receding, static) at all of the emotional states (negative, neutral, positive). Connectivity maps were subsequently transformed to the standard space of Talaraich and Tournoux for group analysis. To investigate the impact of emotion on amygdala connectivity to V5/MT+ during motion processing, a secondary set of connectivity maps were generated by subtracting the baseline (static/no motion) connectivity from both the approaching and receding connectivity maps. A subsequent 2 (Direction: approaching, receding) X 3 (Emotion: negative, neutral, positive) repeated-measures ANOVA was conducted on the whole brain data to identify context dependent patterns of connectivity during stimulus motion. Significant clusters located within the amygdala were subject to small volume correction. Results are presented at $p < 0.005$ (corrected to $p < 0.05$).

4.3 Results

4.3.1 Behavioural Results

A 3 (direction) X 3 (emotion) ANOVA conducted on the Illusion Quality Ratings (Table 4.1) yielded a significant main effect of direction ($F_{(1.48,26.71)} = 52.065$, $p < 0.001$), wherein the approaching and receding aftereffects were rated to be significantly more robust (i.e., created a stronger illusion of motion) than the static aftereffects ($t_{(18)} = 8.501$; $p < 0.001$ and $t_{(18)} = 4.785$; $p < 0.001$ respectively; Figure 4.2a). In addition, approaching images were indicated to have significantly more apparent motion than receding images ($t_{(18)} = 6.256$; $p < 0.001$). No significant main effect of emotion ($F_{(1.12, 20.20)} = 0.599$, $p > 0.10$) nor direction X emotion interaction ($F_{(4, 72)} = 2.220$, $p > 0.05$) were identified with these data.

A similar analysis (3X3 repeated measures ANOVA) was applied to the emotional arousal data (Figure 4.2b; Table 4.1). This yielded a significant main effect of emotion ($F_{(3,36)} = 54.290$, $p < 0.001$), characterized by significantly greater arousal ratings for both negative and positive images compared to neutral images ($t_{(18)} = 7.504$; $p < 0.001$ and $t_{(18)} = 4.529$; $p < 0.001$ respectively) as well as significantly higher emotional arousal ratings for negative images compared to positive images ($t_{(18)} = 3.268$; $p = 0.007$). This effect was not present in standardized ratings (Lang, Bradley, & Cuthbert, 2005) of the negative and positive images selected for this experiment ($t_{(16)} = 0.471$; $p > 0.10$). Furthermore, while no main effect of direction was identified, a significant direction X emotion interaction emerged ($F_{(4,72)} = 4.785$, $p < 0.005$). During trials containing negative images, ratings of emotional arousal were significantly increased for approaching images compared to both receding and static images ($t_{(18)} = 2.187$; $p = 0.042$ and $t_{(18)} = 2.414$; $p = 0.027$ respectively). During the presentation of neutral images, trials with either approaching or receding aftereffects were rating as significantly more emotionally arousing than static trials ($t_{(18)} = 2.142$; $p = 0.046$ and $t_{(18)} = 4.360$; $p < 0.001$ respectively). Emotional arousal ratings for positive images were not significantly altered by the perceived direction of motion ($p > 0.10$ for all contrasts).

4.3.2 Imaging Results

ROI Analysis: Individually defined V5/MT+

Initial analyses aimed to address the question of whether emotional images augmented activity in V5/MT+, similar to their augmentation of the ventral visual stream. To isolate these regions, we contrasted the activity elicited by motion patterns with that elicited by static imagery during the V5/MT+ functional localizer task, as described above. A 3 (Direction; approaching, receding, static) X 3 (Emotion: negative, neutral, positive) repeated measures ANOVA was conducted on the percent signal change data in V5/MT+ during the subsequent emotional-motion task. This analysis was performed individually on ROIs identified in the left and right hemisphere (Figure 4.2a for representational mask example and Table 4.2 for individual mask details). A significant main effect of direction (right: $F(1.47,26.54) = 12.753$, $p < 0.001$; left: $F(2,36) = 11.057$, $p < 0.001$) emerged within these data. For both hemispheres, this effect was characterized by significantly enhanced V5/MT+ activation

Table 4.1 Emotional Effects on Localization

Illusory Motion Direction	Emotion	Illusion Quality[a] (1 = low, 5 = high)	Emotional Intensity[b] (1 = low, 5 = high)
Approach	Negative	3.06 (0.71)	3.53 (0.63)
	Neutral	2.92 (0.80)	1.55 (0.51)
	Positive	2.99 (0.56)	2.75 (0.75)
Recede	Negative	2.52 (0.71)	3.36 (0.67)
	Neutral	2.56 (0.77)	1.58 (0.53)
	Positive	2.42 (0.60)	2.82 (0.75)
Static	Negative	1.49 (0.63)	3.34 (0.71)
	Neutral	1.30 (0.48)	1.44 (0.50)
	Positive	1.44 (0.65)	2.85 (0.77)

[a] A significant main effect of direction were identified in the Illusion Quality ratings data.

[b] A significant main effect of emotion and a direction by emotion interaction were identified in the Emotional Intensity ratings data (*see figure 4.2 for additional details*).

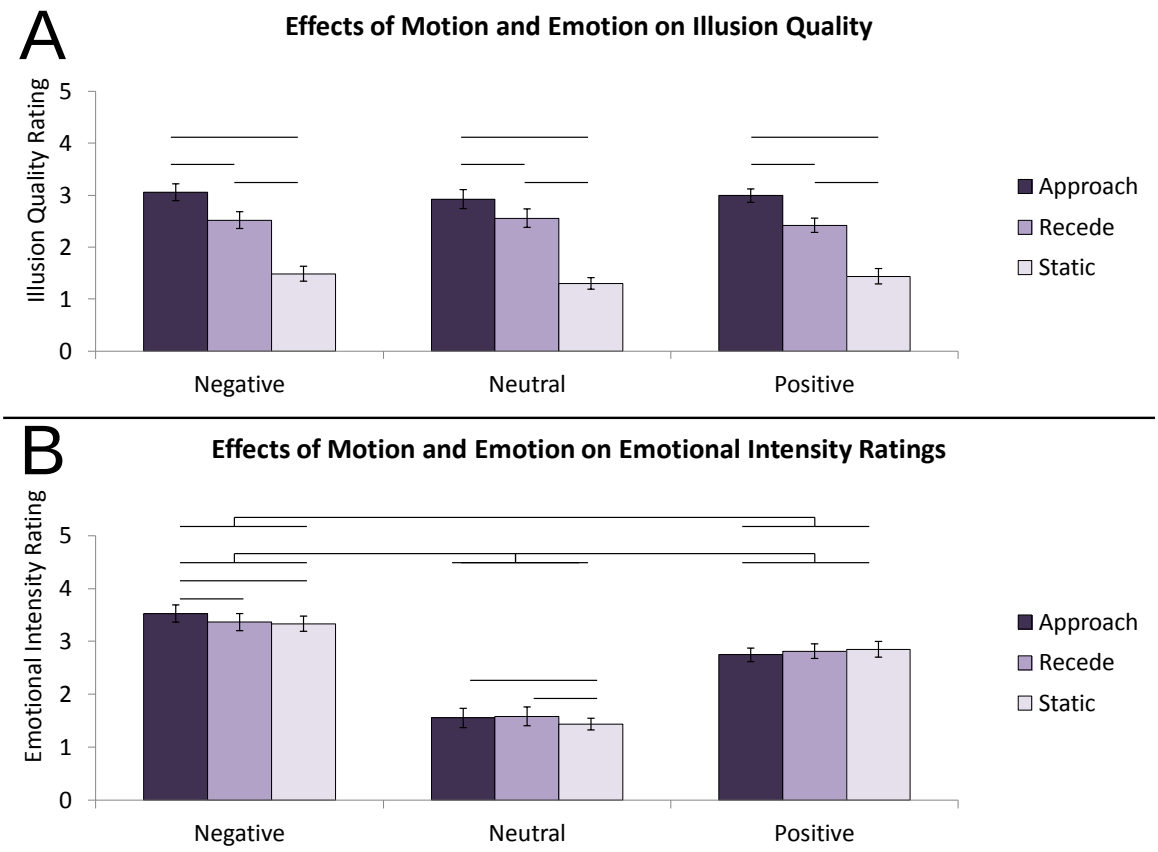

Figure 4.2 Impacts of emotion and direction on perceptual ratings during the illusory motion aftereffect.

A) Illusory direction was found to significantly impact illusion quality ratings. Approach and recede trials (i.e., contracting and expanding acquisition videos) were found to elicit significantly stronger aftereffects than static trial (i.e., alternating acquisition videos). In addition, approaching trials were rated to have significant more perceptual motion than receding trials. B) Ratings of perceived arousal was highest for negative stimuli, followed by positive, and then neutral stimuli. Within the negative stimuli, approach trials received higher ratings of arousal that either recede or static stimuli. In addition, within neutral trials, stimuli presented in either motion conditions (approach or recede) received higher arousal ratings than when presented in the static condition.

to motion (approaching or receding trials) compared to static displays (all *p*s < 0.005; Figure 4.2b). In addition, a significant main effect of emotion emerged in both hemispheres (right: $F_{(2,36)} = 6.298$, $p = 0.01$; left: $F_{(2,36)} = 5.245$, $p < 0.001$). This was characterized by significantly greater activity for trials containing an emotional target image, positive or negative, compared to trials containing a neutral target image (all *p*s < 0.05; Figure 4.2c). No significant differences were noted between the emotional categories (negative vs. positive) in either hemisphere (*p*s > 0.10). No significant Direction X Emotion interaction emerged (right: $F_{(4,72)} = 0.576$, $p > 0.10$; left: $F_{(4,72)} = 0.415$, $p > 0.10$).

ROI Analysis: Group Derived Motion vs. Static

A paired t-test was performed on the whole-brain data of all participants to identify regions with differential activation for moving versus static imagery (Figure 4.4). Data were thresholded to allow for the identification of bilateral V5/MT+ separate from early visual areas ($p < 0.0005$; corrected to $p < 0.05$). At this level, two separate regions of dorsal occipital lobe were also identified (V3a and V7), as well as one region along the parahippocampal gyrus, one on the precentral gyrus, and extensive regions encompassing early visual processing areas (Table 4.3). A 3 (Direction; approaching, receding, static) X 3 (Emotion: negative, neutral, positive) repeated measures ANOVA was conducted on the percent signal change data extracted from each of the group defined ROIs.

Within the group defined ROIs, both right and left V5/MT+ were modulated significantly by the emotional quality of the image (right: $F_{(2,36)} = 10.510$, $p < 0.001$; left: $F_{(2,36)} = 26.174$, $p < 0.001$). Within both hemispheres, this effect was characterized by significantly greater activity for positive and negative stimuli compared to neutral stimulus (right V5/MT+: $p = 0.005$ and $p = 0.001$ respectively; left V5/MT+: both $p < 0.001$). In addition, a significant main effect of direction was identified within right V5/MT+ ($F_{(2,36)} = 13.399$, $p < 0.001$) characterized by greater activity for approaching and receding stimuli compared to perceptually stationary stimuli ($p < 0.005$ for both contrasts). No significant main effect of direction was identified in left V5/MT+ ($F_{(2,36)} = 1.520$, $p > 0.10$), nor was a direction by emotion interaction observed in either hemisphere (right: $F_{(4,72)} = 0.723$, $p > 0.10$; left: $F_{(4,72)} = 0.382$, $p > 0.10$).

Table 4.2 Individually defined V5/MT ROIs: Thresholds and Volume

Participant #	Threshold	Left ROI Vol. ($mm^{3)}$	Right ROI Vol. ($mm^{3)}$
1	$p < 3*10^{-23}$	636	999
2	$p < 4*10^{-12}$	999	584
3	$p < 8*10^{-45}$	921	999
4	$p < 3*10^{-5}$	986	831
5	$p < 7*10^{-26}$	999	844
6	$p < 7*10^{-25}$	973	441
7_a	$p < 2*10^{-23}$	752	N/A
7_b	$p < 1*10^{-35}$	N/A	402
8	$p < 5*10^{-15}$	221	999
9	$p < 8*10^{-32}$	363	999
10	$p < 6*10^{-18}$	831	999
11	$p < 0.002$	247	986
12	$p < 1*10^{-15}$	999	506
13	$p < 0$*	260	999
14	$p < 1*10^{-29}$	999	286
15	$p < 3*10^{-12}$	960	999
16	$p < 0$*	727	662
17	$p < 2*10^{-37}$	999	857
18	$p < 5*10^{-14}$	675	999
19	$p < 2*10^{-34}$	986	311

Note: All thresholds were set to the most liberal threshold which allowed for an identification of bilateral V5/MT+ clusters each > $1000mm^3$. This was not possible for Participant #7 and as such, unique thresholds were used for each hemisphere.

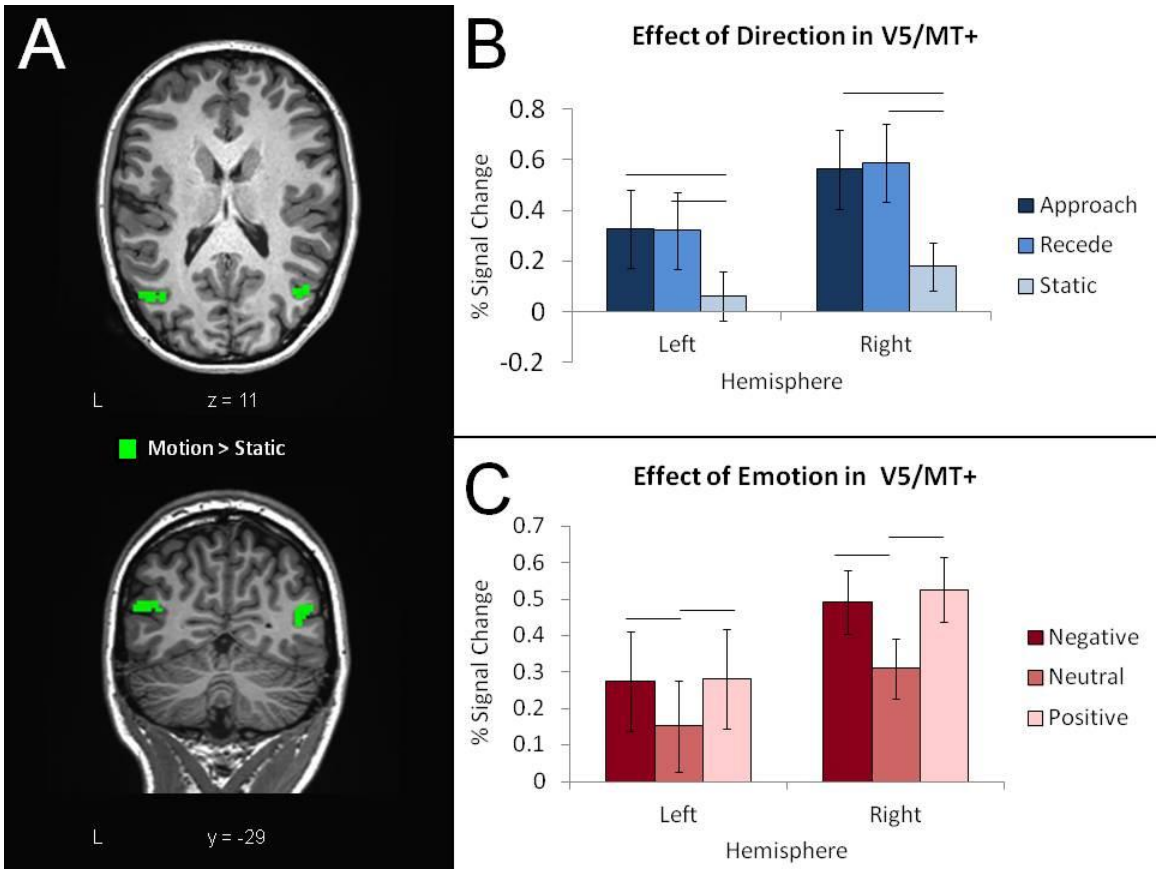

Figure 4.3 V5/MT+ responses to emotion and perceived motion direction within individually-defined ROIs.

A) Representational example of single subject ROIs containing bilateral V5/MT+ (Participant #3). B) Activity in bilateral V5/MT+ was modulated as a function of illusory motion, with both approach and recede trials eliciting significantly more activity than static trials. C) Activity in this region was also modulated as a function of emotion. Both positive and negative trials elicited significantly more activity than activity than neutral trials. No emotion by direction interaction was identified.

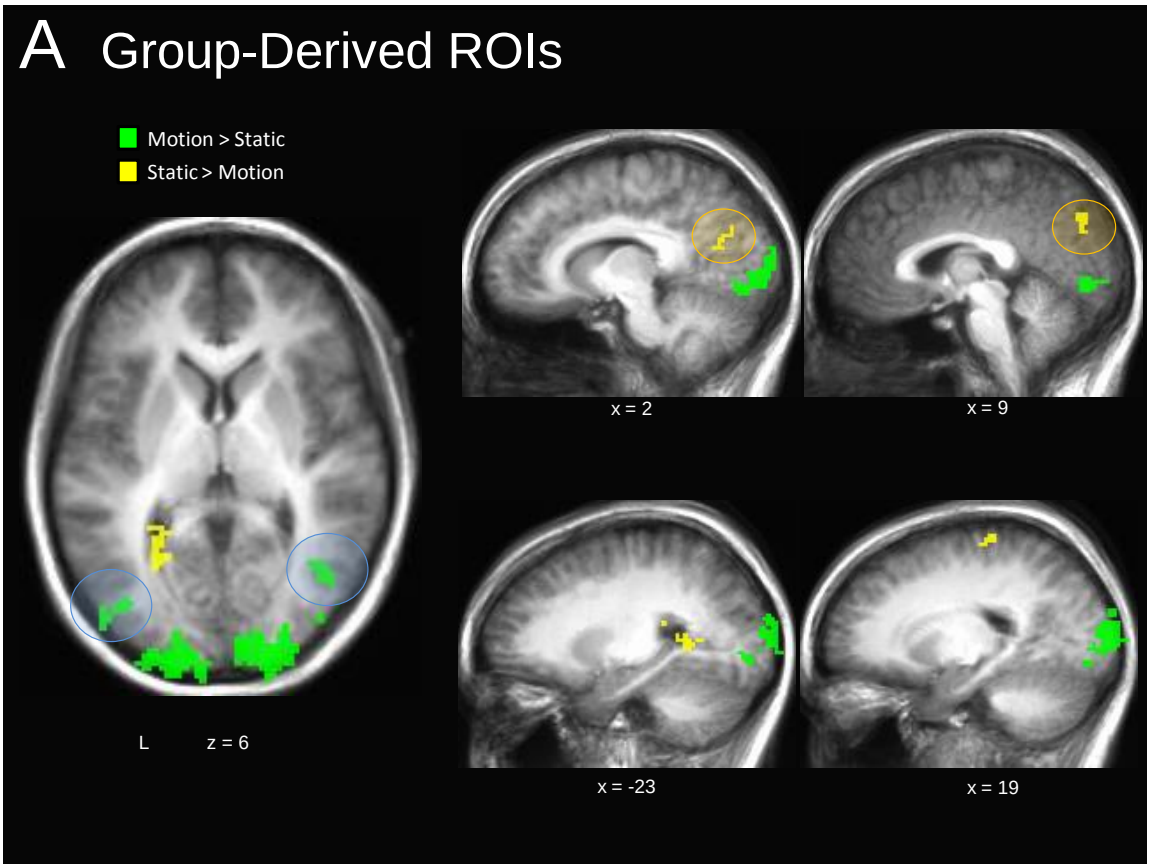

Figure 4.4 Group defined ROIs.

Group-defined ROIs were identified by contrasting neural activity in motion versus static viewing conditions during the functional localizer. A paired t-test performed on the localizer data in standardized space identified large regions of occipital and middle temporal lobe which respond preferentially to moving, but not static imagery (green). Independent bilateral V5/MT+ regions were identified separate from this cluster (blue circles). In addition, areas of dorsal occipital lobe (V3a and V7; orange circles), parahippocampal gyrus, and post-central gyrus displayed preferential activation to static imagery (yellow).

Interestingly, while a similar pattern of effects were observed within a bilateral ROI in early visual areas (marginal ME Direction: $F_{(2,36)} = 3.140$, $p = 0.055$; significant ME Emotion: $F_{(1.401,25.215)} = 6.136$, $p = 0.005$; non-significant interaction: $F_{(2.844,51.199)} = 0.365$, $p > 0.10$). This effect did not propagate into dorsal visual regions, as no significant main effects of direction or emotion, or significant direction by emotion interactions were identified in V3a, V7, or the precentral gyrus. Furthermore, no significant main effects or interaction involving emotion were identified within the parahippocampal gyrus.

Whole Brain Analysis

A 3 (direction) X 3 (emotion) repeated-measures ANOVA was conducted on the whole brain EPI data collected from the main experimental task. All clusters presented in this analysis are significant at $p < 0.005$ (corrected to $p < 0.05$). While the direction of the motion aftereffect was not found to significantly alter patterns of activation, emotion was found to significantly alter activation throughout widespread areas of cortical and sub-cortical regions (Table 4.4). Of particular note, a broad inferior temporal and frontal region was identified as having significantly greater activity elicited by negative compared to neutral and positive stimuli ($t_{(18)} = 6.084$; $p < 0.001$ and $t_{(18)} = 3.420$; $p = 0.003$ respectively), as well as positive compared to neutral stimuli ($t_{(18)} = 2.164$; $p = 0.044$). As this cluster subsumed many individual sub-regions, anatomically defined ROIs were generated to further investigate effects in targeted sub-regions. This included bilateral regions of the amygdala (Figure 4.5a), and thalamus (Figure 4.5c). Within bilateral amygdala, negative target images elicited significantly greater activation than neutral images (left: $t_{(18)} = 4.323$; $p < 0.001$; right: $t_{(18)} = 5.312$; $p < 0.001$). In addition, activity in the right amygdala was significantly greater for positive compared to neutral target images ($t_{(18)} = 3.621$; $p = 0.002$) while activity in the left amygdala was significantly greater during negative compared to positive target images ($t_{(18)} = 3.270$; $p = 0.004$; Figure 4.5b). Similarly, within bilateral thalamus, negative target images elicited significantly greater activation than neutral images (left lateral: $t_{(18)} = 3.398$; $p = 0.003$; left medial $t_{(18)} = 3.239$; $p = 0.005$; right: $t_{(18)} =$; p = 0.001). Furthermore, left lateral regions of the thalamus also displayed significantly greater activity during the

Table 4.3 Group-derived ROIs identified in Motion vs. Still contrast.

Contrast	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
Motion	R/L	Cuneus/MOG/LG	19	4	-90	5	16495
>	R	MTG/MOG	37	42	-62	6	441
Still	L	MTG/MOG	19/37	-43	-78	6	415
Still	R/L	Precuneus/pCC/V3a	31	9	-67	23	519
>	L	PhG	39	-23	-50	5	516
Motion	R/L	Cuneus/Precuneus/V7	18/19	2	-77	32	286
	R	PreCG	4	20	-26	62	156

Significant clusters are thresholded at $p < 0.0005$ (corrected to $p < 0.05$).

MOG = middle occipital gyrus; LG = lingual gyrus; MTG = middle temporal gyrus; PhG = parahippocampal gyrus; pCC = posterior cingulate cortex; PreCG = precentral gyrus.

Note: XYZ are Talairach coordinates and refer to centre of mass.

presentation of negative compare to positive target images ($t_{(18)} = 2.693$; $p = 0.015$; Figure 4.5d) while right thalamus displayed significantly more activation for positive compared to neutral images ($t_{(18)} = 2.978$; $p = 0.004$). Also of note, multiple clusters in regions of ventral visual cortex displayed significantly greater activity during the presentation of negative and positive compared to neutral images (see Figure 4.5e/f).

In addition to the extensive main effect of emotion, a significant direction by emotion interaction was found in a dorsal region of the right frontal pole (BA10; Table 4.4; Figure 4.6a). Initial investigation of this effect focused on the changes in activity related to perceived motion direction within each emotional category (Figure 4.6b). It was found that during the presentation of negative images, approaching images elicited significantly more activity in BA 10 than either the receding or the static images ($t_{(18)} = 2.931$; $p = 0.009$ and $t_{(18)} = 2.946$; $p = 0.009$ respectively) while during the presentation of positive images, approaching images elicited significantly less activation than the static images ($t_{(18)} = 2.132$; $p = 0.047$) and marginally less than the receding images ($t_{(18)} = 1.946$; $p = 0.067$). No significant differences were identified between perceived motion directions during the presentation of neutral images in this area.

Following this analysis, the interaction effect was also investigated with respect to the impact of emotion within each perceived motion direction. In right BA 10, negative approaching images were found to elicit significantly greater activity than positive or neutral approaching images ($t_{(18)} = 3.150$; $p = 0.006$ and $t_{(18)} = 2.564$; $p = 0.02$ respectively) while negative receding images elicited significantly less activation than positive receding images ($t_{(18)} = 2.331$; $p = 0.032$) and marginally less activation than neutral receding images ($t_{(18)} = 2.049$; $p = 0.055$). No significant effects of emotion were identified during static images within either region.

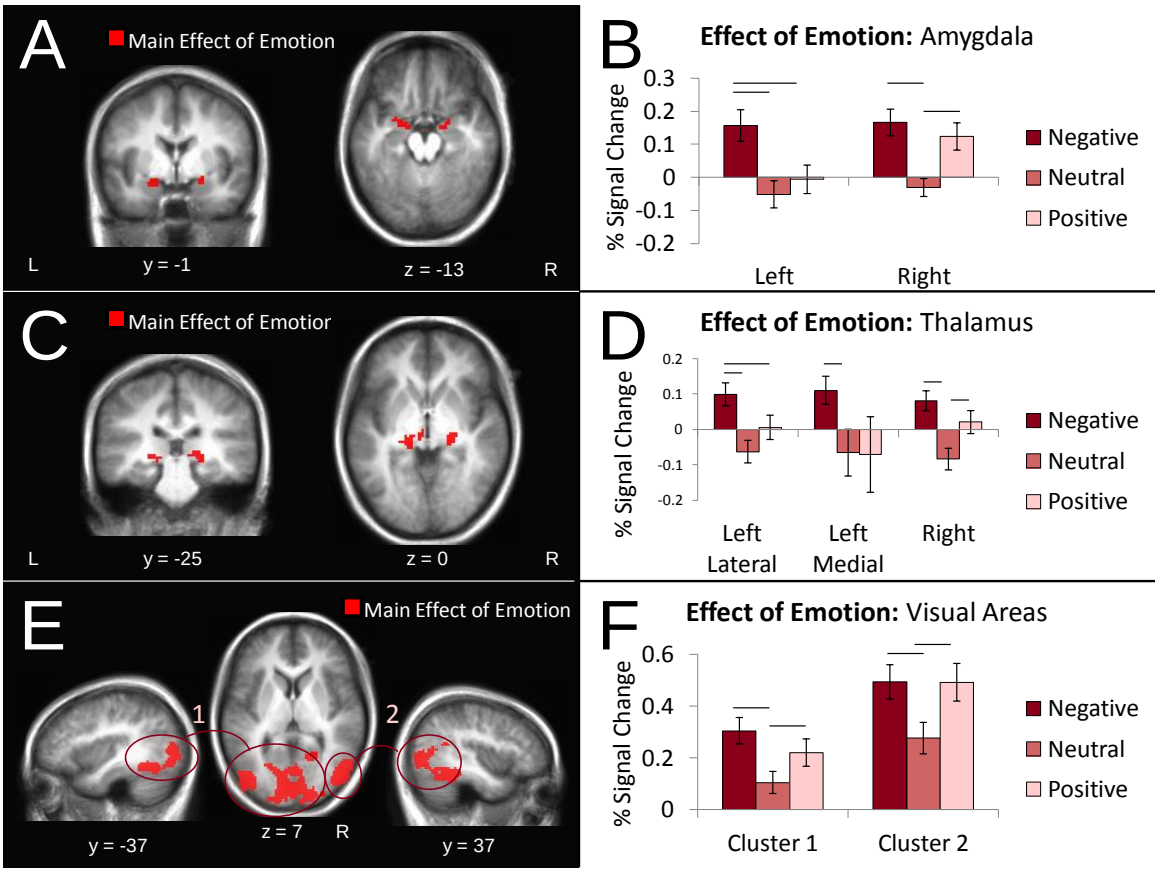

Figure 4.5 Impact of emotion during the motion aftereffect.

A/B) Regions of bilateral amygdala were modulated by the emotion during motion-aftereffects. Activity in bilateral amygdala was greater for negative compared to neutral stimuli, and in right amygdala, also greater for positive compared to neutral stimuli. C/D) Thalamic regions displayed activation patterns modulated by emotion. Left hemisphere regions were isolated from a larger cluster, while the right hemisphere region was independently identified (Table 4.4). Activity across all regions was significantly greater for negative compared to neutral images. E/F) Two large clusters were identified within visual cortices encompassing much of the ventral visual stream, as well as the motion processing area V5/MT+. These areas displayed significantly higher activation for emotion (both negative and positive) images compared to neutral images.

Table 4.4 Effect of Emotion and Direction during Illusory Motion.

Effect	R/L	Location	BA	X	Y	Z	Vol. (mm^3)
Ng >P> Nu	R/L	IOG/MOG/FG/LG/MTG	17/18/19/37	-15	-78	3	24489
	R/L	Amy/Thal/PhG/PAG/OFC	28/45/47	5	2	-8	7397
Ng/P > Nu	R	IOG/MOG/FG/MTG	19/37	40	-62	0	12459
	R	MTG/Uncus	21	36	1	-30	678
	R	Thal/PAG		19	-23	1	623
	L	MTG/Uncus	21	-33	-6	-30	350
Ng > Nu	L	IFG	45/47	-40	24	-2	623
Ng > P/Nu	R	IFG/MFG	45/46	48	29	10	675
Ng > P	L	PhG/pCC	30	-16	-50	5	350
P > Ng/Nu	R/L	OFC	10	3	41	-15	584
Ng/Nu > P	R	PhG	36	26	-40	-3	1324
Nu > Ng/P	L	PhG	36	-26	-40	-7	1778
	R	PreCG/PostCG	4/6	55	-14	26	675
	L	PostCG/IPL	2/40	-59	-29	44	441
	L	PreCG/PostCG	4	-58	-7	23	350
	R	IFG	44	57	10	20	350
	L	IPL	40	-65	-26	32	289
Emotion By Direction	R	dFP	10	19	58	12	376

Table 4.4 continued

Significant clusters are thresholded at $p < 0.0005$ (corrected to $p < 0.05$). All regions in the upper portion of the chart were identified as displaying a main effect of emotion. The nature of this effect is outlined for each. Activation from Clusters 1, 3, 10 and isolated sections of Cluster 2 (i.e., amygdala and thalamic regions) are further explored in Figure 4.5.

IOG = inferior occipital lobe; MOG = middle occipital gyrus; FG = fusiform gyrus; LG = lingual gyrus; MTG = middle temporal gyrus; Amy = amygdala; Thal = thalamus; PhG = parahippocampal gyrus; PAG = periaquaductal gray; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; PreCG = precentral gyrus; PostCG = postcentral gyrus; OFC = orbitofrontal cortex; IPL = inferior paraietal lobe; pCC = posterior cingulate cortex; dFP = dorsal frontal pole.

Notes: XYZ are Talairach coordinates and refer to centre of mass.

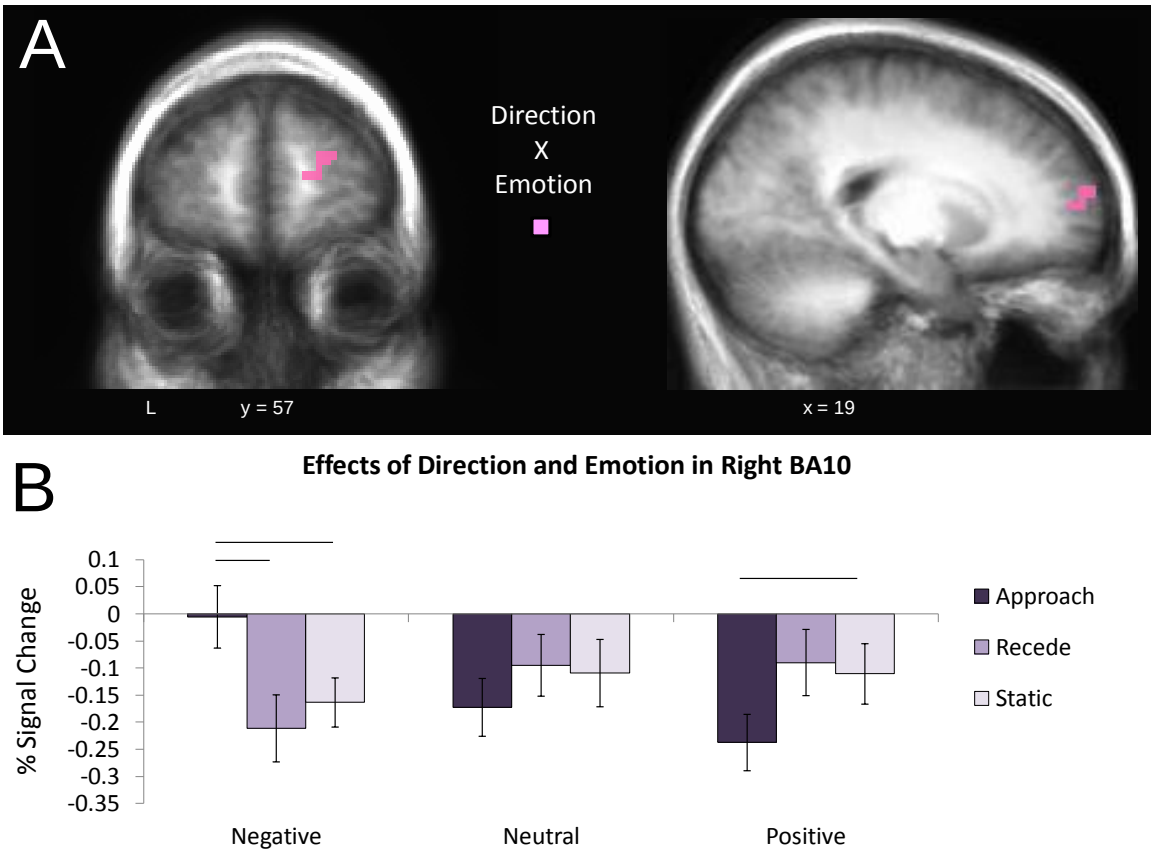

Figure 4.6 Direction by Emotion interactions during the motion aftereffect.
A) A significant direction by emotion interaction was identified in the right dorsal frontal pole (BA 10; shown in coronal and sagittal views). B) Activity in this region was greatest for conditions containing a non-desirable outcome (i.e., approaching negative scenes, or receding positive scenes) compared to other conditions. No effects were identified between directions or emotions in either the neutral or static conditions.

V5/MT+ Connectivity Analysis

To assess the functional connectivity changes in V5/MT+ across changes in motion direction and emotional content, whole brain connectivity using a right V5/MT+ seed was determined for each participant using gPPIs performed on the entire dataset from the main experimental task. The seed region was defined for each participant as the voxel of peak activity from the right V5/MT+ ROI. A 2 (Direction: approaching, receding) X 3 (Emotion: negative, neutral, positive) ANOVA was conducted on the whole brain connectivity maps. A significant main effect of direction was identified within the superior occipital gyrus in the motion area V3a (Ahlfors et al., 1999; McKeefry, Burton, & Morland, 2010; Figure 4.7a) with activity in this area significantly higher for receding compared to approaching images ($t_{(18)} = 3.019$, $p = 0.007$; Figure 4.7c). No significant direction by emotion interaction was identified.

Connectivity between V5/MT+ and the right amygdala (Figure 4.7b) was discovered to be significantly modulated by the emotional content of the scene. This effect was characterized by enhanced connectivity for both negative and positive compared to neutral images ($t_{(18)} = 3.532$, $p = 0.002$ and $t_{(18)} = 2.278$, $p = 0.035$ respectively; Figure 4.7d) and significantly stronger connectivity while viewing negative compared to positive images ($t_{(18)} = 3.799$, $p = 0.001$). In addition, functional connectivity between right V5/MT+ and anterior regions of BA 9 (Figure 4.5b) was also modulated by the emotional nature of the image. This was characterized by significantly stronger connectivity while viewing both negative and positive images compared to neutral images ($t_{(18)} = 3.333$, $p = 0.004$ and $t_{(18)} = 2.874$, $p = 0.01$ respectively; Figure 4.7d) as well as marginally stronger connectivity while viewing negative compared to neutral images ($t_{(18)} = 1.972$, $p = 0.064$).

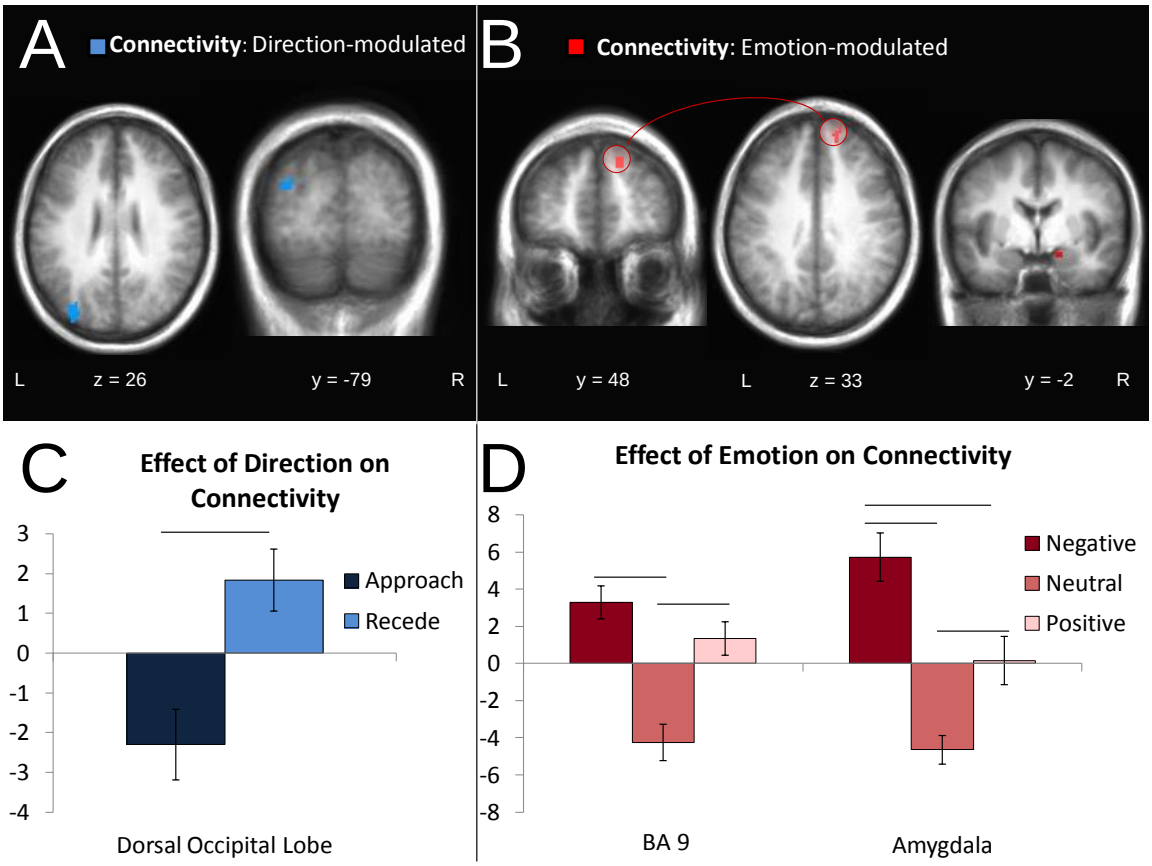

Figure 4.7 Context-dependent changes in connectivity with a right V5/MT+ seed during motion imagery.

A/B) A main effect of direction was identified on connectivity between right V5/MT+ and the superior occipital gyrus. Connectivity between these two regions was stronger during the perception of receding compared to approaching aftereffects. C/D) A main effect of emotion identified on connectivity strength between right V5/MT+ and both right prefrontal cortex (BA 9), and the right amygdala. In both regions, connectivity was stronger with V5/MT+ during the perception of emotional compared to neutral images. In addition, connectivity between right V5/MT+ and the right amygdala was also stronger while viewing negative compared to positive images.

4.4 Discussion

Emotional information is able to influence both behaviours and neural activation associated with visual processing. Many of these are related to processing within the ventral visual stream (Morris et al., 1998), while the dorsal visual stream appears to be less susceptible to emotional interference (Kryklywy & Mitchell, 2014). Early dorsal visual areas, such as V5/MT+, however, share a number of similar characteristics to ventral visual stream, including a susceptibility to perceptual illusions, and connectivity to emotion-related subcortical regions. The present study aimed to determine the impact of emotion on the motion processing region V5/MT+ associated with the early dorsal visual stream. Both individually-defined and group-defined bilateral V5/MT+ ROIs displayed patterns of activation responsive to both the presence and direction of illusory motion, and the emotional nature of a presented image. Specifically, activation in V5/MT+ was increased for illusory motion compared to perceptually static imagery, as well as for emotional compared to neutral images. Furthermore, whole brain analysis of the data found that numerous cortical and subcortical regions were also modified by the emotional nature of the images presented. Of particular interest, extensive areas of visual cortex responded to the emotional nature of the images, as well as bilateral amygdala. This effect was not consistent across all visual processing areas, but rather limited to ventral structures, and V5/MT+. It was not observed within any dorsal processing areas modulated by motion (i.e., V3a or V7). In addition, functional connectivity between V5/MT+ and the amygdala was found to be greater for trials with emotional compared to neutral stimuli, suggesting a possible mechanism for the increased activation of this motion-sensitive region during these trials. These results suggest a potential role of emotion in the preparation for, and representation of, motion in visual processing areas.

4.4.1 Emotional Motion: Changes in perception.

Casual observation would suggest that the subjective and perceptual experience we associate with an object may depend on the nature of the interactions we have with that object. In line with this, the current study found that the emotional intensity of an image was modulated by both the valence of the image, and the direction of perceived motion. While previous work has demonstrated increased rating of arousal for dynamic compared to static facial expression (Sato & Yoshikawa, 2007), the current work

interrogated this effect in relation to the direction of the motion relative to the viewer as well. Of particular interest, negative images were found to elicit the highest emotional intensity rating while perceived as approaching. This arousal may be dependent on the negative image acting as an impending and approaching threat, still requiring a behavioural response, rather than a retreating object requiring no action. This is consistent with studies investigating proximal versus distal threats (Mobbs et al., 2010), wherein the closer a threatening object (tarantula) was placed to an observer, the more arousing the object was rated. Also of note, neutral images were rated as significantly more arousing during perceive motion in either direction compared to static imagery. Notably, a similar effect has been observed in dynamic versus static environmental scenes, wherein greater preference was afforded to the scenes with visual motion (Heft & Nasar, 2000).

4.4.2 Neural Responses to Emotion

Large areas of inferior occipital and middle temporal lobe dedicated to visual processing (Milner & Goodale, 2006) displayed significantly greater activity for emotional compared to neutral objects. Consistent with previous work investigating emotional imagery, this activation was identified predominantly over areas normally associated with the ventral visual stream (Goodale & Milner, 1992; Kravitz et al., 2013; Lang et al., 1998; Morris et al., 1998; Vuilleumier & Driver, 2007). Anatomical and functional connections between these areas and the amygdala (Amaral et al., 2003; Amaral & Price, 1984; Furl et al., 2013) are thought to underlie much of these effects (Furl et al., 2013; Morris et al., 1998). Notable, however, this activity was not limited to what are typically considered ventral visual structures. Significant emotion-related changes in activation were also identified in bilateral V5/MT+, a region traditionally associated with dorsal stream processing (Born & Bradley, 2005; Buchel & Friston, 1997).

Furthermore, the emotional content of an image was demonstrated to modulate activity in many regions implicated in general emotional processing, including orbitofrontal cortex (Golkar et al., 2012; Rempel-Clower, 2007; Rolls, 2004; Tsuchida & Fellows, 2012), inferior frontal gyrus (Grecucci, Giorgetta, Bonini, & Sanfey, 2013), and

the amygdala (Bickart, Dickerson, & Barrett, 2014; Cahill, Babinsky, Markowitsch, & McGaugh, 1995; J. LeDoux, 2003, 2007; Ohman, 2005; Phelps, 2006; Whalen, 1998). Interestingly, closer visual inspection of the emotion-sensitive thalamic clusters indentified in the current study suggest that they may overlap with the periaqueductal gray (PAG), a midbrain region implicated in threat processing (Coker-Appiah et al., 2013; Johansen, Tarpley, LeDoux, & Blair, 2010; Mobbs et al., 2007). Previous studies have demonstrated this region to be particularly responsive to looming or approaching threats (Coker-Appiah et al., 2013; Mobbs et al., 2007) and reactive aggression (Blair, 2001). Comparable midbrain regions identified in the current study (i.e., those described as thalamic clusters with extensions into PAG; Table 4.4) displayed greater activation for negative compared to neutral or positive imagery, supporting the role of this area in threat assessment and response. Of note, however, activity in these areas were not impacted by the apparent proximity or perceived direction of movement of the stimulus, as may be predicted from previous work (Coker-Appiah et al., 2013; Mobbs et al., 2007; Mobbs et al., 2010). Strategies used to handle a threatening situation are influenced by the proximity and imminency of the threat (J. Panksepp, 1990). It has been suggested that as a threat approaches, our threat response strategies shift from cognitive mechanisms to more instinctive and unconditioned responding (Jaak Panksepp, 1998). Each of these strategies recruit a different set of neurocognitive structures, with the distal involving more prefrontal regions (e.g., ventral-medial prefrontal cortex; Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010), and proximal threats involving subcortical and brainstem regions (e.g., PAG; Coker-Appiah et al., 2013; Mobbs et al., 2007; Mobbs et al., 2010). Detection of accurate signal in the latter areas often requires the optimization of scanning parameters to reduce physiological noise (Brooks, Faull, Pattinson, & Jenkinson, 2013), which may contribute to the difference in observed effects. That said, however, the use of strategy and volition to avoid consequence is another potential mechanism which may underlie the discrepancy between the current results and previous work in the field. While previous studies required participant to actively assess the threat during presentation (Coker-Appiah et al., 2013), or placed them in situation with tangible negative consequences (Mobbs et al., 2007; Mobbs et al., 2010), the current design required viewing of emotional images unpaired with tangible feedback (e.g., shock;

Mobbs et al., 2007). Future work should aim to increase the active component of the task during target image presentation while optimizing scan parameters to detect signal in midbrain regions.

4.4.3 Emotional Motion: V5/MT+ activation and connectivity

Area V5/MT+ is generally considered highly relevant to the processing and representation of moving visual objects (Ahlfors et al., 1999; Riecansky, 2004; Thakral & Slotnick, 2011). Indeed, the current study utilized a functional localizer scan contrasting moving stimuli to static objects to reliably define this regions independently for all participants. As predicted from previous work (Antal et al., 2004; Culham et al., 1999; Fawcett, Hillebrand, & Singh, 2007; Hogendoorn & Verstraten, 2013; Tootell, Reppas, Dale, et al., 1995), V5/MT+ displayed preferential responding to the presence of apparent motion in an image. In addition, the traditional role of V5/MT+ as an important relay for motion-based information in the dorsal visual stream (Born & Bradley, 2005; Buchel & Friston, 1997) was supported by analysis of its functional connectivity. Connectivity strength modulated by perceived direction of motion was identified between a V5/MT+ seed region and V3a, a motion-sensitive area of the dorsal visual stream (Ahlfors et al., 1999; McKeefry et al., 2010). The role of V5/MT+, however, was not limited to the representation of visual motion. This region was also responsive to the emotional content of an image, with increased activation to both negative and positive compared to neutral imagery. A similar effect had been demonstrated once prior, wherein the presentation of dynamic emotional faces elicited greater activity in V5/MT+ than dynamic neutral faces (Furl et al., 2013); however, these stimuli did not vary in their apparent distance from the participant, but were rather cinematic displays of a facial expression changing from neutral to a particular emotion.

Interestingly, a significant direction by emotion interaction in this area was not observed. One possibility is that the lack of interaction reflects an emotional priming of V5/MT+, wherein increased emotional relevance leads to a preparation of the visual system for motion and stimulus detection. This is consistent with theories of threat response that suggest a physiological response towards increased physical readiness in times of heightened emotion or stress (Saper, 2002; Tsigos & Chrousos, 2002) and

suggests a possible preparation of our motion processing systems for relevant information when in an arousing or emotional situation, thus allowing for faster detection and identification of subsequent objects. Supporting this idea, V5/MT+ displayed significant emotion-dependent functional connectivity to the prefrontal cortex and the amygdala; regions which are both implicated in threat detection and monitoring (Mobbs, Hagan, Dalgleish, Silston, & Prevost, 2015). Increased V5/MT+ activation observed in the current experiment, however, was not associated with any changes in the subjective experience of illusory motion. This implies that any preparatory activity in V5/MT+ must be below the threshold of perception.

The emotion-related augmentation of activity in V5/MT+ observed in the current experiment may be mediated by the connections of this region to emotion-sensitive subcortical structures (Amaral et al., 2003; Young et al., 1994). Consistent with previous work (Furl et al., 2013), the current study identified emotion modulated functional connectivity between the V5/MT+ and the amygdala, with enhanced connectivity between these regions during emotional compared to neutral imagery. As the amygdala is highly responsive to the emotional nature of a visual scene (Breiter et al., 1996; Kapp, Whalen, Supple, & Pascoe, 1992; Kryklywy et al., 2013; Lane, Chua, & Dolan, 1999; Sander, Grafman, & Zalla, 2003), this connectivity is likely the mechanism by which emotional augmentation of V5/MT+ occurs. These effects mirror similar observations in traditional regions of the ventral visual stream, wherein backward projections from the amygdala to visual areas result in augmented visual cortical activity (Morris et al., 1998).

Similarly, feedforward projections from V5/MT+ to the amygdala may impact the perceived intensity emotion of the images as a function of its apparent direction of movement. In the current study, subjective ratings of emotional arousal were modulated by both the image valence and the direction of apparent motion. It has been demonstrated that the perceived intensity of an emotional object is significantly correlated with amygdalar activation (Cunningham, Raye, & Johnson, 2004; Kryklywy et al., 2013; Phan et al., 2003; Phan et al., 2004; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). As such, it is possible that increased activity in V5/MT+ during trials containing a motion after-effect may lead to changes in amygdala responsivity resulting in the increases of emotional arousal observed during neutral images, as well as impact the direction-

emotion interactive effects on arousal observed during negative imagery. Again, these effects mirror those observed in the areas traditionally associated with the ventral visual stream, wherein there is a positive linear relationship between ratings of emotional arousal and activation in amygdala and ventral visual regions (Sabatinelli et al., 2005).

4.5 Conclusion

The current study investigated the impact of emotion and perceived motion on perceptual assessment and neural responding to complex visual scenes during motion aftereffects. To investigate the impact of these features in early motion-sensitive areas of visual cortex, a functional localizer was utilized to identify V5/MT+ within each subject. Activity in this region was found to be significantly modified by both the emotional nature, and the perceived motion direction of the image. Specifically, both approaching and receding images were found to elicit significantly more activity than static images, while both and negative and positive images elicited significantly more activation than neutral images. Importantly, no similar effects were identified in ROIs encompassing alternate regions of the dorsal visual stream. A whole brain analysis identified large areas of the ventral visual stream also sensitive to the emotional nature of the image. Analysis of V5/MT+ functional connectivity using gPPIs identified significant emotional modulation of connectivity strength between this region and the right amygdala. This was characterized by greater strength of connectivity while viewing emotional compared to neutral images. It is possible that the increases in activation of V5/MT+ to emotional images may in part be driven by this connectivity. Overall these data provide evidence that emotional information is capable of influencing visual motion processing in area V5/MT+, in a manner reminiscent of ventral visual stream functioning.

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CHAPTER 5

5. Discussion

Our investigation of the representation of emotion in dual stream models of sensory processing identified a stark dissociation between dorsal and ventral streams for both audition and vision. Within the auditory domain, emotional information was found to influence neural activation of the anterolateral "what" pathway, but did not modulate activation within the posterior-medial "where" pathway (see 2.3.2). Early auditory processing regions, including primary auditory cortex and parts of secondary auditory cortex, however, displayed activity, or patterns of activity, that were impacted by both emotional quality and source location of a sound. Furthermore, tertiary projections of auditory processing streams displayed patterns of activity consistent with a dissociable role of emotion; activity patterns in anterior temporal lobe were predictive only of *emotion*, while patterns of activity in motor and premotor regions were predictive only of *location* (see 2.3.3). This notion of a dissociable effect of emotion in sensory systems was supported when investigating behaviours dependent on the dorsal and ventral visual system (i.e., egocentric and allocentric localization, respectively). It was found that dorsally mediated localization of a target was not impacted by the emotional context of a trial, while ventrally mediated localization was impacted (see 3.3.2). Specifically, participants displayed greater accuracy for target localization during the presentation of adverse emotional sounds compared to neutral sounds. To refine this model within the visual system, neuroimaging was used to investigate the impact of emotion on visual regions that do not categorize cleanly into the *two-visual system hypothesis*. Motion aftereffects were induced during the presentation of emotional images to enable the delineation of emotion-related influences on V5/MT+ functioning and activation. Activity in V5/MT+ was found to be influenced by the emotional content of the picture, similar to what would be expected of ventral stream structures. While this did not impact the perceived robustness of the illusory motion (see 4.3.1), the perceived motion did lead to valence-specific changes in arousal (see 4.3.2). Overall, these findings suggest an added role for emotion in motion processing in our visual systems in addition to its involvement in object feature processing undertaken by the ventral visual stream. Taken together, the three studies that comprise this dissertation provide evidence in support of a

role for emotion in modulating object perception and identification pathways of sensory processing, but not in action and direct localization pathways.

5.1 Effects of Emotion on Neural Activation

5.1.1 Auditory Activation

Individual patterns of neural activation were independently identified for both spatial- and identity-based processing within the auditory system (see 2.3.2), consistent with a dual pathway 'what' and 'where' model of audition (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Bushara et al., 1999). Areas of temporal lobe posterior and lateral to primary auditory cortex have been implicated in the processing and representation of sound location (Arnott, Binns, Grady, & Alain, 2004; Harrington, Stecker, Macpherson, & Middlebrooks, 2008; Rama et al., 2004; Rinne, Ala-Salomaki, Stecker, Patynen, & Lokki, 2014), while areas of temporal lobe anterior and lateral to primary auditory cortex have been implicated in sound identity processing (Kusmierek, Ortiz, & Rauschecker, 2012; Obleser et al., 2006; Russ, Ackelson, Baker, & Cohen, 2008; Wessinger et al., 2001). This dissociation, however, does not arise immediately within auditory cortices; primary auditory cortex and early secondary regions along the posterior superior temporal gyrus (STG) and transverse temporal gyrus (TTG) have been implicated in both location and sound identity processing (Arnott et al., 2004). Beyond these early processing regions, the auditory 'where' and 'what' pathways are believed to diverge into the posterior medial and anterior lateral portions of STG. Further projections of each pathway extend beyond the temporal lobe; the 'where' pathway into IPL and SFS (Ahveninen et al., 2006; Krumbholz, Eickhoff, & Fink, 2007), and the 'what' pathway into the inferior frontal gyrus (IFG; Alain et al., 2001; Arnott et al., 2004).

In Study I, it was identified that regions of the 'where' pathway (defined by regions sensitive to location change of a white noise burst in an independent scan), displayed activity that was significantly modulated by spatial aspects of natural sound. Univariate analyses performed on these data found that activity in this pathway was not modulated by the emotional characteristics of the localized sound. Interestingly, additional multivariate analyses found that regions of primary and secondary auditory

cortices (but not later stages of location processing) which showed selective sensitivity for location in the univariate analyses (see 2.3.2) did exhibit fine-grain patterns of activity predictive of both the emotional nature of a sound and its source location (see 2.3.3). This suggests a greater overlap of location-emotion representations during early auditory processing than initially identified. This is consistent with numerous previous studies, which find dual representations in these regions (for review, see Arnott et al., 2004). Both univariate and multivariate analyses, however, found that spatial information was being processed independent of emotion in latter areas of the dorsal visual stream during localization of naturalistic sounds, including areas of IPL and the postcentral gyrus.

Activity in regions of the 'what' pathways, identified in an independent scan and located in the anterolateral portions of auditory cortex, was modulated by both auditory emotion and auditory spatial location. This region overlapped with areas of both primary and secondary auditory cortices, as outlined in prior models of dual processing pathways in audition (Ahveninen et al., 2013; Ahveninen et al., 2006; Warren & Griffiths, 2003). Specifically, the auditory 'what' pathway displayed enhanced activation for emotional sounds, consistent with previous studies in the field (Ethofer et al., 2012; Fecteau, Belin, Joanette, & Armony, 2007). Furthermore, while univariate analyses of the data from Study I identified emotion sensitive activation in areas entirely anterior and lateral to primary auditory cortex, multivariate analyses provided evidence to suggest that there is greater representation of emotion in regions posterior to this as well, though the representation of emotion in each area may mechanistically differ. Taken together with the localization results, these data suggest a greater representation of emotion within the auditory 'what' pathway compared to the auditory 'where' pathway, along with additional representation of emotion in early regions of both.

5.1.2 Visual Activation

Cortical activity throughout early visual areas of the brain has routinely been demonstrated to be modulated by the emotional quality of a stimulus (Amting, Greening, & Mitchell, 2010; Lang et al., 1998; Morris et al., 1998; Vuilleumier & Driver, 2007; Vuilleumier & Pourtois, 2007). Indeed, during Study III, emotion sensitivity was observed throughout early visual areas V1, V2 and V3. In addition, emotion was

demonstrated to modulate activity in several regions of the inferior occipital and temporal lobes (see 4.3.2), consistent with many neuroimaging studies. Most of this activity was located in regions that are firmly believed to be subsumed by the ventral visual stream (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013) and utilized for conscious visual perception (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991). Of note, however, was the observation that area V5/MT+ also displayed activity modulated by the emotional content of an image. Though traditionally believed to be a dorsal visual stream structure (Born & Bradley, 2005; Goodale & Milner, 1992; Rizzolatti & Matelli, 2003), the pattern of activity identified in V5/MT+ is strikingly different than activity in the rest of the processing pathway. In particular, this area displayed increased activity during the presentation of emotional relative to neutral stimuli, and this activity was unaffected by the perceived direction of motion. While additional dorsal visual regions displayed sensitivity to movement versus stationary visual arrays, only V5/MT+ (of dorsal-related structures) was sensitive to emotion. (see 4.3.2) This result is consistent with studies of dynamic face perception, which has implicated V5/MT+ in the processing of dynamic emotional expression (Furl, Henson, Friston, & Calder, 2013), as well as studies investigating emotional actions (Van den Stock et al., 2011).

Interestingly, the augmentation of activity observed within V5/MT+ did not depend of the presentation of perceptual motion (see 4.3), nor the direction of motion, suggesting a potential role of emotional priming within this structure to enhance the representation of subsequent information. When viewed as a threat response, this pattern of activity would suggest enhanced preparation of our motion processing systems for relevant information in arousing or emotional situations, allowing for faster detection and identification of subsequent objects. Such an adaptation would clearly be beneficial to an animal, aiding in threat detection and response in emotional or high-risk situations.

5.1.3 Amygdala Activation

Numerous studies have identified increased amygdala activation to emotional objects presented in both visual (Adolphs, 2002; Anderson & Phelps, 2000; Kryklywy, Nantes, & Mitchell, 2013; Pessoa, 2008; Vuilleumier & Huang, 2009) and auditory domains (Fecteau et al., 2007; S. K. Scott et al., 1997). Study III identified a pattern of

activity consistent with this effect. Increased activation was found bilaterally in the amygdala for negatively valenced emotional scenes compared to neutral scenes, while increased activity in the right amygdala was found for positive scenes compared to neutral scenes (see 4.3.2). This is consistent with previous work, which has identified robust activation of the amygdala to negative emotional objects (Breiter et al., 1996; Fecteau et al., 2007; Kryklywy et al., 2013; J. LeDoux, 2003; Machado, Kazama, & Bachevalier, 2009) and during fear-related learning (Barad, Gean, & Lutz, 2006; Johansen et al., 2010; J. LeDoux, 2003; Ohman & Mineka, 2001), as well as to positive emotional objects, albeit less robustly (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Hoffman, & Kilts, 2002; Paton, Belova, Morrison, & Salzman, 2006). The reduction in activational strength elicited by positive emotional stimuli may be reflected by the unilateral effects identified for this valence category. It has been suggested that feedback projection from the amygdala to early visual areas mediate this effect (Furl et al., 2013; Morris et al., 1998). In line with this notion, functional connectivity between the right amygdala and right V5/MT+ was found to be modulated by the perceived direction of motion for emotion scenes, such that in situations with undesirable outcomes (i.e., when either approaching negative or receding positive scenes) enhanced connectivity was found between these regions. This supports the idea of a direct interconnection between the amygdala and visual regions mediating the effects of emotion on perception.

The pattern of connectivity identified between the amygdala and V5/MT+ is reminiscent of findings demonstrating reciprocal patterns of connectivity between the amygdala and numerous regions of the ventral visual stream. Robust pathways have been elucidated between the amygdala and ventral visual areas, involving both anatomical (Amaral, Behniea, & Kelly, 2003; Freese & Amaral, 2005) and functional (Foley, Rippon, Thai, Longe, & Senior, 2012; Furl et al., 2013; Morris et al., 1998) connectivity. In addition, functional connectivity between the amygdala and V5/MT+ has also been demonstrated to be modulated by emotion (Furl et al., 2013), while there exists no evidence of connectivity between the amygdala and the dorsal visual stream.

Auditory emotional cues have also been shown to elicit increased amygdala activity (Fecteau et al., 2007; Sander, Brechmann, & Scheich, 2003). Although Study I did not identify a similar effect, emotional effects in sensory cortices remain consistent. It should be noted, however, that scan parameters used in Study I were not optimized to identify amygdala activity (Morawetz et al., 2008; Robinson, Laird, Glahn, Lovallo, & Fox, 2010) as they were in Study III, and therefore responses in this area may have gone unnoticed. We cannot rule out the possibility, however, that an alternative mechanism may be utilized to process emotional information in the auditory system, rather than direct connectivity to the amygdala as found in ventral visual processing. One potential mechanism may relate to the physical characteristics of a sound which carry emotional information in the auditory domain and how our neural representations are tuned to recognize these. Multiple studies have suggested that the fundamental frequency of a sound can impact its emotional content (Arias, Busso, & Yoma, 2014; Kramer, 1963; Lieberman & Michaels, 1962; Protopapas & Lieberman, 1997) and that auditory cortex is able to process these features independently from emotion-related subcortical regions (Kaas, Hackett, & Tramo, 1999; Rauschecker & Tian, 2000). Likely, this mechanism functions alongside amygdala modulation of auditory processing, but additional research is necessary to further delineate the contributions of each.

5.2 Effects of Emotion on Behaviour

Interestingly, the impact of emotion on the behavioural measure in each study did not follow a consistent pattern of change. In Study I (2.3.1), emotional sounds, both positive and negative, were associated with significantly longer localization times compared to neutral sounds, suggesting a detrimental effect of emotion on localization. Study II (3.3.2), however, found that localization during negative emotional trials was significantly more accurate than during positive emotional or neutral trials. Though the emotional effect in Study I was not impacted by valence direction (i.e., there was a similar effect for both positive and negative vs. neutral stimuli), a lack of effect for positive compared to neutral stimuli is Study II is not unprecedented. While negative emotional objects have robust and consistent effects on neural activation during spatial

processing, the impact of positive emotional stimuli is relatively inconsistent (Pourtois & Vuilleumier, 2006). Nonetheless, these results do suggest a beneficial role of auditory emotion on visual localization behaviour during Study II; a striking contrast to the behavioural results presented in Study I, wherein auditory emotion impaired intra-modal localization. Varied results of emotion on behaviour appear to be a recurrent feature within the emotion literature (Vuilleumier & Huang, 2009).

Task-irrelevant emotional information can impair performance on a number of cognitive and behavioural tasks (Blair & Mitchell, 2009; Mitchell et al., 2008; Turatto, Mazza, & Umilta, 2005; Vuilleumier & Driver, 2007) consistent with the results from Study I. Emotion in this task was not associated with the task-relevant feature of the object (source location), and, as such, could theoretically act to shift mental processing resources away from sound localization towards the emotionally-relevant process of sound object identification. This mechanism is similar to a biased-competition model of attention (Desimone, 1998; Lee, Sakaki, Cheng, Velasco, & Mather, 2014; Shinn-Cunningham, 2008) applied to individual features of a stimulus rather than to its gestalt (i.e., competition for representation between stimulus A, feature A vs. stimulus A feature B, rather than stimulus A vs. stimulus B). The current work suggests that in the auditory domain, the neural correlates of this representational competition are likely early auditory regions, particularly primary and early secondary auditory cortex. These regions display sensitivity to both location and emotion information, while latter areas are increasingly separate in their functional specialization. This does not necessarily imply that additional competition and convergence cannot occur within higher order cortical association areas, but is rather intended to highlight a possible role for early sensory regions, as suggested by the current findings. Additional neuroimaging work is necessary to further determine if and where this representational competition may occur.

Study I investigated emotional influence on auditory processing, yet similar disruption of behaviours are often observed in the visual domain. During operant response paradigms, orientation and motor responding to exogenous cues is significantly delayed by the presence of emotional images compared to neutral images (Mitchell et al., 2008; Tipples & Sharma, 2000). In addition, during emotional Stroop tasks, wherein a

person is required to verbally report the font colour of a word rather than the word itself, it has been demonstrated that responding is significantly delayed when the presented word has an explicit emotion-related rather than neutral meaning (McKenna & Sharma, 1995, 2004). Of note, when the emotional Stroop task is performed under a state of increased emotional arousal, the normally observed behavioural impairments are suppressed (Mathews & Sebastian, 1993). This suggests that detrimental effects of emotion on behaviour may be minimized by increasing baseline activity in emotion-processing systems, thus minimizing the relative intensity of emotional versus neutral words.

Interestingly, there exist some instances where intra-modal emotional information can facilitate rather than impair behavioural performance. These tasks include lexical decision making, wherein participants are able to more quickly judge the validity of an emotional versus neutral word (G. G. Scott, O'Donnell, & Sereno, 2014), and continuous flash suppression, wherein emotional faces are more likely than neutral faces to reach both perceptual and subliminal awareness (Oliver, Mao, & Mitchell, 2015). Of note, facilitated performance by emotion observed during lexical decision-making may potentially be explained by an augmented and facilitated representation of the emotional versus neutral word, similar to that observed in an emotional Stroop paradigm, resulting in increased semantic salience and facilitated recognition of the word. Similarly, awareness of a repressed stimulus during continued flash suppression may be facilitated by any perceptual enhancement of the stimulus; thus, the emotional content may facilitate awareness of a facial expression by augmenting the general perceptual representation of the object, rather than specific features. An additional example of facilitated performance by emotion is observed during memory formation; retention of information is enhanced for information presented in emotional compared to neutral contexts (J. E. LeDoux, 1994; MacKay & Ahmetzanov, 2005; Mather, 2007; Shafer, Iordan, Cabeza, & Dolcos, 2011; Todd, Talmi, Schmitz, Susskind, & Anderson, 2012). Interestingly, during Study III, activity in task-related (i.e., motion processing) regions was augmented by the emotional nature of the stimuli, yet no reported behavioural effects were noted on motion perception. Overall, additional research is still necessary to fully understand the effects intra-modal emotional information on stimulus processing.

In contrast to Study I, Study II, a cross-modal paradigm, identified a beneficial impact of emotion on stimulus localization. This is consistent with multiple previous studies demonstrating stimulus augmentation during emotional processing (Calvo & Nummenmaa, 2008; Fox et al., 2000; Frischen, Eastwood, & Smilek, 2008). Interestingly, while many studies identify perceptual amplification for emotional objects while the emotion cue is task-relevant (Frischen et al., 2008; Lamy, Amunts, & Bar-Haim, 2008; Morris et al., 1998), participants in Task 2 were explicitly instructed to ignore the presented sounds. It is possible, however, that the cross-modal emotional presentation of the sound bypassed any attentional competition, given that the localization task and its emotional representation did not demand overlapping attentional resources. Instead, the emotional content of the sound appears to augment processing in the ventral visual stream, thus increasing the mental representation of the visual world. This type of auditory augmentation of visual perceptual has been observed during both emotional (Brosch, Grandjean, Sander, & Scherer, 2009; Zeelenberg & Bocanegra, 2010) and non-emotional sensory integration paradigms (Iordanescu, Guzman-Martinez, Grabowecky, & Suzuki, 2008; Stein, London, Wilkinson, & Price, 1996). Again, additional work is needed to determine the contribution of intra-modal and cross-modal emotional information on representation competition and stimulus processing.

5.3 Implication on Models of Sensory Processing and Perception

Together, the studies comprising this dissertation highlight the role of emotion in modulating processes involving the identification and perception of objects; specifically, processes mediated by ventral sensory pathways. In contrast, emotion does not appear to influence neural processing in dorsal sensory pathways. This dissociable impact may help to explain some of the diverse effects of emotion on both visual and auditory tasks (Gerdes, Wieser, & Alpers, 2014; Luo & Yu, 2015; Vuilleumier & Huang, 2009).

As may be predicted from the emotional augmentation of ventral sensory pathways outlined above, increased emotional arousal has indeed been demonstrated to enhance sensory perception in healthy individuals (Calvo & Nummenmaa, 2008; McTeague, Shumen, Wieser, Lang, & Keil, 2011; Phelps, Ling, & Carrasco, 2006). Of

particular note, some of the perceptual enhancements have been identified utilizing ventral visual tasks that have analogous behaviours mediated by the dorsal visual steam. For example, changing the emotional context during an orientation discrimination task was demonstrated to affect the level of contrast necessary to make accurate orientation judgements (Phelps et al., 2006). It would be interesting, however, to investigate whether a similar effect is observed if participants were require to demonstrate the orientation using direct visually guided action to the stimuli rather than indirect report. This could help further delineate the degree of dissociation between the emotional impact on dorsal versus ventral sensory pathways, and how they are translated into behaviour. Interestingly, in non-human primates, activity in parietal neurons associated with the dorsal visual stream is not modulated by the reward value of the targeted object (Rolls et al., 1979). Similarly, in humans, visually-guided implicit learning in the sensorimotor system is not mediated by reinforcement feedback, but rather by movement error feedback, (Cashaback, McGregor, Mohatarem, & Gribble, 2016; Cashaback, Mohatarem, McGregor, & Gribble, 2016), while planned but not automatic visually guided action is impacted by the presence of fear-invoking adjacent objects (Ta, Liu, Brennan, & Enns, 2010). These studies again support the idea of dorsal-stream insusceptibility to explicit reward and valence information.

5.4 Limitations and Future Directions

While the current work represents a step forward towards understanding the role of emotion in our on-line perceptual experience, it also provides a platform for additional research questions. Within Study I, the identification of a task independent auditory ‘what’ pathways was conducted in a subset of the sample population, while the auditory ‘where’ pathway was identified within the whole sample. This eliminated the use of individualized regions of interest, and potentially diminished the anatomical accuracy of the processing pathway location. It would be interesting for future work to use individually-defined regions of interest to address this issue. Similarly, Study II was unable to identify the precise neural pathways involved with direct and indirect localization. While theory supports our interpretation of reduced dorsal and increased

ventral stream involvement during indirect action, adapting the task to be completed while undergoing fMRI would allow for a greater understanding of the current effect.

Overall, the current results invite a number of interesting potential research questions. For example, the augmentation of ventral sensory pathways plays a role in a number of cognitive functions beyond the initial representation and perception of an object, such as the encoding and consolidation of episodic memories. Memory retention has been demonstrated to be increased for emotional compared to neutral stimuli (Kensinger & Corkin, 2003; Nielson, Yee, & Erickson, 2005) in a phenomenon known as emotionally enhanced vividness (Todd, Schmitz, Susskind, & Anderson, 2013; Todd et al., 2012). Augmentation of stimulus representations at an early sensory and perceptual level may be a mechanism by which memory encoding is enhanced for emotional rather than neutral objects. Indeed, it has been suggested that similar mechanisms to those discussed here for emotional enhancement of perception are involved in memory encoding; specifically, amygdala connectivity has been implicated in the enhanced encoding of emotional imagery (Cahill, Babinsky, Markowitsch, & McGaugh, 1995; McGaugh, 2004; Murty, Ritchey, Adcock, & LaBar, 2010). To further elucidate the contribution of a dissociable emotional impact in sensory streams on memory function, it would be intriguing to investigate whether the enhanced memory was also observed for memory processes recruiting dorsal sensory pathways for encoding (e.g., size-weight illusion, weighted motion fields). If real-time augmentation of sensory information in part underlies emotionally enhanced vividness, then the lack of emotional modulation in dorsal sensory pathways would suggest that these memories would not share the same enhanced encoding as ventrally-mediated episodic memory.

5.5 Conclusions

In conclusion, the results presented here provide important advancement towards our understanding of the influence of emotion in dual pathway models of sensory processing. During auditory localization, we identified a dissociable effect of emotion within the anterior lateral auditory ‘what’ and posterior medial ‘where’ pathway, such that emotion was demonstrated to impact activity through nearly all of the former and little to none of the latter. Subsequently, we determined that the presentation of emotional

auditory cues was related to increased visual localization accuracy for behaviours mediated by the ventral, but not the dorsal visual stream. This suggests a dissociable representation in visual pathways paralleling those previously identified in audition. Finally, utilizing an innovative emotional motion-aftereffect paradigm, we observed modulation of neural activity within both visual area V5/MT+ and large regions of the ventral visual stream. Importantly, activity in visual areas associated with the dorsal stream (V3a and V7) was not modulated by the emotion of the image. Furthermore, emotional modulation of functional connectivity between V5/MT+ and the amygdala was identified. This suggests that in addition to affecting ventral visual and anterolateral auditory pathways, emotion may also impact motion detection and representation. Together, these findings demonstrate an important role of emotion in the perceptual representations of sensory information, while suggesting that direct action and spatial representation may, in part, be immune to these effects. Furthermore, the totality of these studies emphasize the importance of emotion as a saliency characteristic of stimuli, and highlight the pervasive effect it may have on human perceptual experience.

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Appendix B: Formal License for material used with permission for Study II

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Appendix C: Research Ethics and Approval Number for Study I

Western Research

Research Ethics

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Dr. Derek Mitchell
File Number:4702
Review Level: Delegated
Approved Local Adult Participants:265
Approved Local Minor Participants:0
Protocol Title: The neurobiological basis of affective and social dysregulation
Department & Institution: Schulich School of Medicine and Dentistry\Psychiatry,London Health Sciences Centre
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: August 22, 2012 **Expiry Date:**August 31, 2014
Documents Reviewed & Approved & Documents Received for Information:

Document Name	Comments	Version Date
Revised Study End Date		

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the University of Western Ontario Updated Approval Request Form.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

[redacted]

Signature

Ethics Officer to Contact for Further Information

X Janice Sutherland (jsutherl@uwo.ca)	___ Grace Kelly (grace.kelly@uwo.ca)	___ Shantel Walcott (swalcot@uwo.ca)

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Appendix D: Research Ethics and Approval Number for Studies II & III

Research Western

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Dr. Derek Mitchell
File Number:102711
Review Level: Delegated
Approved Local Adult Participants:200
Approved Local Minor Participants:0
Protocol Title: The impact of salient stimuli on the senses and behaviour
Department & Institution: Schulich School of Medicine and Dentistry\Psychiatry,London Health Sciences Centre
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: July 30, 2012 **Expiry Date:**June 30, 2017
Documents Reviewed & Approved & Documents Received for Information:

Document Name	Comments	Version Date
Western University Protocol		
Advertisement	Flyer	
Letter of Information & Consent		2009/09/16

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the University of Western Ontario Updated Approval Request Form.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

[redacted]
Signature

Ethics Officer to Contact for Further Information

Janice Sutherland (jsutherl@uwo.ca)	Grace Kelly (grace.kelly@uwo.ca)	Shantel Walcott (swalcot@uwo.ca)

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Curriculum Vitae

Name: James H. Kryklywy

Education

2010-16 Ph.D., University of Western Ontario, London, ON
Department: Neuroscience, Brain and Mind Institute
Supervisor: Dr. Derek Mitchell, Ph. D.

2005-09 B.Sc**.,** University of Western Ontario, London, ON

Awards and Honours

2013-16 *Natural Science and Engineering Research Council* (NSERC)
- Post-Graduate Scholarship

2015 *Canadian Institutes of Health Research* (CIHR)
- National Research Competition Nominee

2015 *London Health Research Day;* Academic Poster Competition Winner

2010-15 *University of Western Ontario;* Graduate Research Scholarship;

2013 *Ontario Graduate Scholarship* (declined)

Peer-Reviewed Publications

Kryklywy, J.H., MacPherson, E.A. and Mitchell, D.G.V. Decoding spatial and emotional information within individualized virtual auditory environments using multi-voxel pattern analysis. *In Preparation*

Kryklywy, J.H. Vieira, J.B., and Mitchell, D.G.V. Emotional motion: Investigating the impact of emotion on motion processing regions in visual cortex. *In Preparation*

Roach, V.A., Fraser, GM, Kryklywy, J., Mitchell, D.G.V. and Wilson, T.D. Perfect Timing: How do time limits impact eye movements during spatial reasoning? *Anatomical Sciences Education, Under Review*

Roach, V.A., Fraser, GM, Kryklywy, J., Mitchell, D.G.V. and Wilson, T.D. Do the eyes have it? How eye-tracking can reveal accuracy in a timed test of spatial reasoning. *Cognitive Science, Under Review*

Roach, V.A., Nguyen, N., Eagleson, R. de Ribaupierre, S., Kryklywy, J., Mitchell, and D., Wilson, T.D. The Eye of the Beholder: Can patterns in eye movement reveal aptitudes for spatial reasoning? *Anatomical Sciences Education, In Press*

Kryklywy, J.H. and Mitchell, D.G.V. (2014). Emotion modulates allocentric but not egocentric stimulus localization: Implications for dual visual systems perspectives. *Experimental Brain Research,* 232, 3719-1726.

Kryklywy, J.H., Nantes, S., and Mitchell, D.G.V. (2013). The amygdala encodes the level of perceived fear but not emotional ambiguity in visual scenes. *Behavioral Brain Research,* 252, 396-404.

Kryklywy, J.H., Macpherson, E.A. Greening, S.G., and Mitchell, D.G.V. (2013). Emotion modulates activity in the 'what' but not 'where' auditory processing pathway. *Neuroimage,* 24, 295-305.

Meredith, M.A., Kryklywy, J., McMillan, A.J., Malhotra, S., Lum-Tai, R. and Lomber, S.G. (2011). Crossmodal reorganization in the early-deaf switches sensory, but not behavioral roles of auditory cortex. *Proceedings of the National Academy of Science,* 108, 8856-8861.

National/International Conference Presentations

Kryklywy, J.H., & Mitchell, D.G.V. Evidence for dissociable neurocognitive systems subserving emotion recognition and emotional intensity encoding. Poster to be presented at the annual Canadian Student Health Research Forum, Winnipeg, MB. June 2-4th, 2015.

Kryklywy, J.H., & Mitchell, D.G.V. Emotion modulates ventral but not dorsal visual stream-mediated behaviours. Poster presented at the annual meeting of the Cognitive Neuroscience Society, Boston, Mass. April 4-April 8, 2014.

Kryklywy, J., Macpherson, E.A., Greening, S.G., and Mitchell, D.G.V., Impact of valence on the dual pathway model of audition. Poster presented at the 19th annual meeting of the Cognitive Neuroscience Society, Chicago, IL. March 31-April 3, 2012.

Lomber, S.G., Kryklywy, J., Hall, A.J., Lum-Tai, R., Malhotra, S. and Meredith, M.A. Crossmodal reorganization in the auditory field of the anterior ectosylvian sulcus (fAES) of postnatally deafened cats. Program No. 260.12, 2009 *Abstract Viewer/Itinerary Planner.* Chicago, IL: Society for Neuroscience. Online.

Related Work Experience

2014 Instructor, Brescia University College, Department of Psychology
2010-14 Graduate Teaching Assistant, UWO, Department of Psychology