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Developmental Trajectories of Social Signal Processing

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Submitted in fulfilment of the requirements for the
Degree of Doctor of Philosophy

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Dedication

For my Mum

Abstract

Most of the social cognitive and affective neuroscience in the past 3 decades has focussed on the face. By contrast, the understanding of processing social cues from the body and voice have been somewhat neglected in the literature. One could argue that, from an evolutionary point of view, body recognition (and particularly emotional body perception) is more important than that of the face. It may be beneficial for survival to be able to predict another's behaviour or emotional state from a distance, without having to rely on facial expressions.

If there are relatively few cognitive and affective neuroscience studies of body and voice perception, there are even fewer on the development of these processes. In this thesis, we set out to explore the behavioural and functional developmental trajectories of body and voice processing in children, adolescents and adults using fMRI, behavioural measures, and a wide range of univariate and multivariate analytical techniques.

We found, using simultaneously recorded point-light and full-light displays of affective body movements, an increase in emotion recognition ability until 8.5 years old, followed by a slower rate of accuracy improvement through adolescence into adulthood (**Chapter 2**). Using fMRI we show, for the first time, that the body-selective areas of the visual cortex are not yet 'adult-like' in children (**Chapter 3**). We go on to show in **Chapter 4**, that although the body-selective regions are still maturing in the second decade of life, there is no difference between children, adolescents and adults in the amount of emotion modulation that these regions exhibit when presented with happy or angry bodies. We also show a positive correlation between amygdala activation and amount of emotion modulation of the body-selective areas in all subjects except the adolescents. Finally, we turn our attention to the development of the voice-selective areas in the temporal cortex, finding that, contrary to face and body processing, these areas are already 'adult-like' in children in terms of strength and extent of activation (**Chapter 5**).

These results are discussed in relation to current developmental literature, limitations are considered, direction for future research is given and the wider clinical application of this work is explored.

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Author’s Declaration

I certify that this doctoral dissertation is my original work and that all references to the work of others have been clearly identified and fully attributed. Some of the work contained in this thesis has been previously published.

[1] Ross, P. D., B. de Gelder, F. Crabbe and M.-H. Grosbras (2014). "Body-Selective Areas in the Visual Cortex are less active in Children than in Adults." Frontiers in Human Neuroscience **8**.

[2] Ross, P. D. (2014). "Body form and body motion processing are dissociable in the visual pathways." Front Psychol **5**: 767.

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1 General Introduction

1.1 Social Signal Processing

Humans are social animals. We need the company of others, and progress is built upon a foundation of collective social endeavours. Like all social animals we have evolved a whole range of communicative abilities, both verbal and nonverbal, without which we would arguably not survive.

Argyle et al. (1970) suggested that whereas verbal communication is normally used to disseminate information about events external to the speakers, nonverbal cues are used to establish and maintain interpersonal relationships. This is perhaps not the whole picture, as nonverbal communication may also be threatening or aggressive, and hardly conducive to establishing or maintaining relationships. Argyle (1988) nevertheless concluded that there were 5 main functions of non-verbal behaviour in human communication, namely:

1. To express emotions,

2. To express interpersonal attitudes,

3. To accompany and support speech,

4. Self-presentation,

5. Rituals (Greetings/handshakes etc.).

These functions and categories are not mutually exclusive, but the seeming ease with which we interpret even the subtlest of these nonverbal cues has led to the longstanding assumption that there are areas of the cortex dedicated to the processing of social signals.

This ‘social brain’ hypothesis, as well as describing the neural basis of communicative skills, also incorporates an affective perception system (Brothers, 2002;Frith, 2007). An important function of this system is to filter incoming sensory information for the presence of socially relevant features (any stimuli that would represent a threat to the individual for example) and grant them priority access to higher-level areas of awareness and attention. For humans, (and other non-human primates, see de Gelder and Partan (2009) and Brothers et al. (1990)), the most salient emotional signals are often social in nature (an expression of fear would indicate a threat nearby; anger might indicate a direct threat of aggression towards the observer). These social stimuli can include facial expressions, body movement and posture, and the prosody and content of vocalisations.

This leads to the interesting question of when these abilities come to the fore. Are they innate or do they develop with experience? Are the developmental trajectories of these abilities similar across modalities?

For better or worse, most of the social cognitive and affective neuroscience in the past 15 years has focussed on the face. By contrast, the understanding of processing social cues from the body and voice has been somewhat neglected. Here, therefore, I will primarily focus on the development of the ability to process social cues from the human body, as well as the development of human voice perception. First, it is necessary to highlight the importance of the face-related research in this field, as well as making the case for more body-centric studies.

1.2 The Importance of the Face

Faces are special. They are arguably the most salient portrayer of social signals that we possess and both recognising and responding to the information contained in the human face is something we are adept at from birth. New-borns show greater interest in faces than objects (Johnson et al., 1991;de Haan and Nelson, 1999), and more interest in their mothers face than a strangers face (Field et al., 1984;de Haan and Nelson, 1997). Furthermore, the inversion effect for faces (in which inverted faces take longer to recognise than normally orientated faces; (Yin, 1969)) has been observed in non-human primates (Dahl et al., 2013) and infants as young as 4-months-old (Turati et al., 2004;Otsuka et al., 2007;Dobkins and Harms, 2014).

Currently, the literature is divided as to whether face processing is domain specific; that is, we possess an innate ability for the recognition of faces which is grounded in evolutionary theory (McKone et al., 2012b) or whether the pure experience of seeing faces makes us experts over time (see Gauthier and Tarr (1997) for initial ‘Greeble’ study).

The ‘specialness’ of faces in recognition is likely a combination of the two theories. Neuroimaging techniques including functional magnetic resonance imaging (fMRI), magneto-encephalography (MEG), electro-encephalography (EEG), event-related potentials (ERPs), trans-cranial magnetic stimulation (TMS) and single cell recordings in humans and primates have all highlighted specific areas in the visual cortex that are highly selective for faces. Perhaps the earliest example of functional selectivity for faces came from Sergent and Signoret (1992) who, using positron emission tomography (PET), identified activation in the fusiform gyrus and anterior temporal cortex when subjects undertook face-identity tasks (male-female face categorisation, familiar face identification etc.). In the mid ‘90s, Bentin et al. (1996) and Botzel et al. (1995) first described the N170. They found that EEG responses evoked by images of faces compared to other visual stimuli showed increased negativity approximately 170 ms after stimulus onset. The source of this potential was consistent with a later fMRI study by Kanwisher et al. (1997), who found that a region of the fusiform gyrus (and hinted at by the earlier work of Sergent and Signoret (1992)) dubbed the ‘fusiform face area’ (FFA) responded selectively to faces. Further support for the function of this region has also come from lesion studies describing patients with selective impairments for the identification of faces (Barton et al., 2002), resulting in prosopagnosia (impairment of facial recognition).

This would then seem to support a domain-specific model, in which the FFA is evolutionary preprogramed for face recognition. However, Gauthier and Tarr’s (1997) ‘Greeble’ studies demonstrated that familiarising oneself with an object could elicit responses in the FFA similar to that produced by faces. Gauthier also showed that the FFA was activated when bird and car experts were shown pictures of objects from their respective areas of expertise (Tarr and Gauthier, 2000). This then would call into question the evolutionary purpose of the FFA in identifying faces (but also see McKone et al. (2012b), who conclude that the role of experience in the development of the face identification mechanisms has been overestimated).

As an example of the complexity of the face-processing network, using fMRI and a face-recognition task, Zhen et al. (2013) produced a dendrogram and network model to explain the hierarchical structure of the face-processing network. They suggest that the face-processing network consists of 3 relatively independent sub-networks that correspond to the identity of the individual (Identification), the retrieval of personal knowledge (Semantic) and the analysis of the facial features and expressions (Expression). Their dendrogram shows these sub-networks as hierarchical clusters based on the strength of functional connectivity among the relative face-processing ROIs (Figure 1-1 A). These ROIs are displayed as nodes and edges on a standard brain template in Figure 1-1 B.

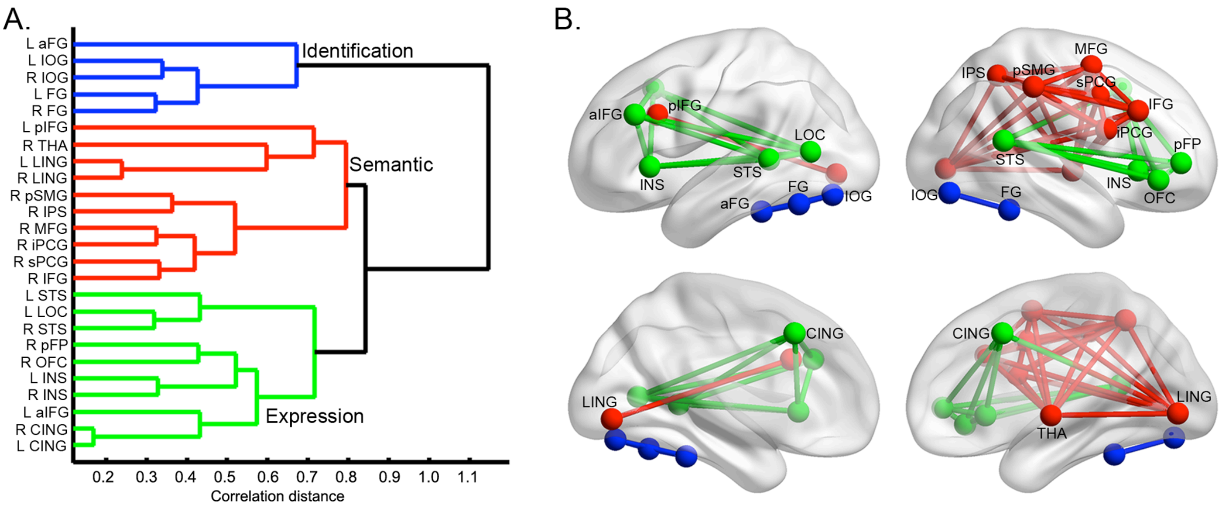


Figure 1-1 Hierarchically structured face-processing network.
Identification, Semantic and Expression sub-networks are presented in blue, red and green respectively. FG=Fusiform Gyrus; LING=Lingual Gyrus; STS=Superior Temporal Sulcus; IOG=Inferior Occipital Gyrus; LOC=Lateral Occipital Cortex; IPS=Intraparietal Sulcus; SMG=Supramarginal Gyrus; IFG=Inferior Frontal Gyrus; CING=Paracingulate Gyrus; THA=Thalamus; a=anterior; p=posterior; s=superior; i=inferior. Figure reproduced with permission under CC-BY license (Zhen et al., 2013).

The complexity of the processes involved in face perception is therefore well documented, with the face playing a key role in social interaction.

This work builds upon the Haxby et al. (2000) hierarchical model of face processing. The model is divided into a core system and an extended system. In the core system the occipital face area (OFA) analyses/encodes facial features, the STS deals with facial expressions and lip movements, while the FFA interprets the identity-related properties of the face. The extended system is then comprised of higher cortical areas that can be recruited to modulate or act with regions in the core system to extract meaning from faces. As we will see, recent models of body recognition mirror this face processing model.

The wealth of information contained in facial expression allows us to both convey and recognise a vast range of social detail and emotional content. This ability to recognise emotion in facial expressions has even been demonstrated in infants. Five-month-olds show little difference in attention when presented with a fearful or happy expression. When 7-month-olds perform the same experiment, they focus longer on the fearful face. They also show a stronger initial ERP component for the fearful face, indicating an increased cognitive and attention focus towards fear (Peltola et al., 2009).

This ability to understand the content of emotional facial expressions begins to become apparent in early childhood. Current research suggests that the functional mechanisms responsible for face recognition are present by the age of five years (Jeffery and Rhodes, 2011). Furthermore, Jeffery and Rhodes (2011) suggest that although children process faces in a similar way to adults, adults tend to process faces more efficiently. Several studies report that emotion modulation (the influence of emotional content on a stimulus or brain region) and ERP timing do change between childhood and adolescence (Batty and Taylor, 2006); even if the electrophysiological markers of the face perceptual process do not appear to change from 4 years of age onwards (Kuefner et al., 2010). Furthermore, brain-imaging studies suggest that the neural processing of faces does not appear fully mature in early adolescence (Golarai et al., 2010).

Behavioural and brain-imaging studies both also suggest non-linearity; that is, a steady increase in performance during childhood mentioned above, followed by no or very little change in emotion recognition ability in the early adolescent/mid-teenage years, and a subsequent improvement to adult levels in late-adolescence (Casey et al., 2008). Although still under-studied and ill understood, such non-linearity has been linked to changes in both structural brain development and cognitive strategies (Shaw et al., 2008). If one considers that changes in brain maturation of social brain regions and changes in social environments (starting secondary school etc.) occur in a non-continuous fashion, then this might be related to non-linear trends in the developmental trajectory of basic social skills.

1.3 Why the Body?

These new theories of the maturation of the social brain, however, have been primarily conducted when looking at recognition of facial expressions or recognition of speech prosody. Considering that there is over thirty years' worth of rich face recognition research, there is surprisingly little research with regards to the perception and recognition of the human body. In terms of affective neuroscience, a search of PubMed today, 15th December 2014, revealed over 7000 hits for emotions & face, and only 1400 for emotions and body. On closer inspection, most of the papers in the emotion & body category are related to eating disorders, well-being, sexual violence, organ donation and nursing. There were fewer than 40 cognitive and affective neuroscience studies of emotional body perception. There is even less work on the development of body perception. The development of speech prosody recognition is more neglected again, but we will revisit that aspect of the social brain briefly at the end of this chapter, and again in more depth in **Chapter 5**.

Focussing on the body, one could argue that, from an evolutionary point of view, body recognition (and particularly emotional body recognition) is as important than that of the face. One could speculate that it may be helpful for an individual to be able to predict what someone is about to do, based solely on their body language, rather than rely on facial expressions alone (see de Gelder et al. (2010)). Often people are seen from a distance, and one can perceive patterns of body motion, posture, form and gait long before cues from facial expressions are available.

Furthermore, compared with faces, emotion expression and potential action representation are two very important aspects of body representation. The former has an equivalent in faces, but the latter does not. de Gelder (2009) argues that while we typically relate a facial expression to an emotional feeling or mental state, we tend to associate a bodily expression with an action the person is involved in. This is important as even though the emotion expressed may be the same in both cases in terms of affective signals, they may elicit completely different responses in the observer. The facial expression of fear for example may produce empathy in the observer, while the body expression of fear may be interpreted as a call for action (de Gelder, 2009).

So although both bodies and faces (and voices) fulfil the role of conveying social interaction information effectively, they do so in different ways. This is why it is worthwhile spending just as much time exploring the structural and function systems behind body perception as it is for face perception. And, as we will see, this is even more important when one explores the developmental and maturational changes in these systems.

In terms of emotional body processing, recently Zieber et al. (2014) demonstrated that 6.5-month-olds could match happy and angry static body images with corresponding emotional vocalisations, whereas 3.5-month-olds did not exhibit such emotional knowledge. Similarly, Missana et al. (2014) presented infants with upright and inverted point-light displays of happy and fearful body expressions. They showed that orientation-sensitive and emotion-sensitive brain processes are present in infants of 8 months of age, but not in 4-month-olds. Despite this functional differentiation between emotions, it is doubtful that in face or body research the infants are aware of the emotional content encoded within these expressions, only that it is emotionally loaded. Further developmental studies of the body-selective areas involving older children and adolescents will be explored in more depth at the end of the sections outlining the extrastriate body area and fusiform body area.

1.4 Body Circuits

Before dealing with the body circuit models, the various visual pathways models, and their varying functional and structural trajectories, we will start by first defining and exploring each key component of the extrastriate cortex that has been involved in processing signals conveyed by other people’s bodies. These are illustrated in Figure 1-2.

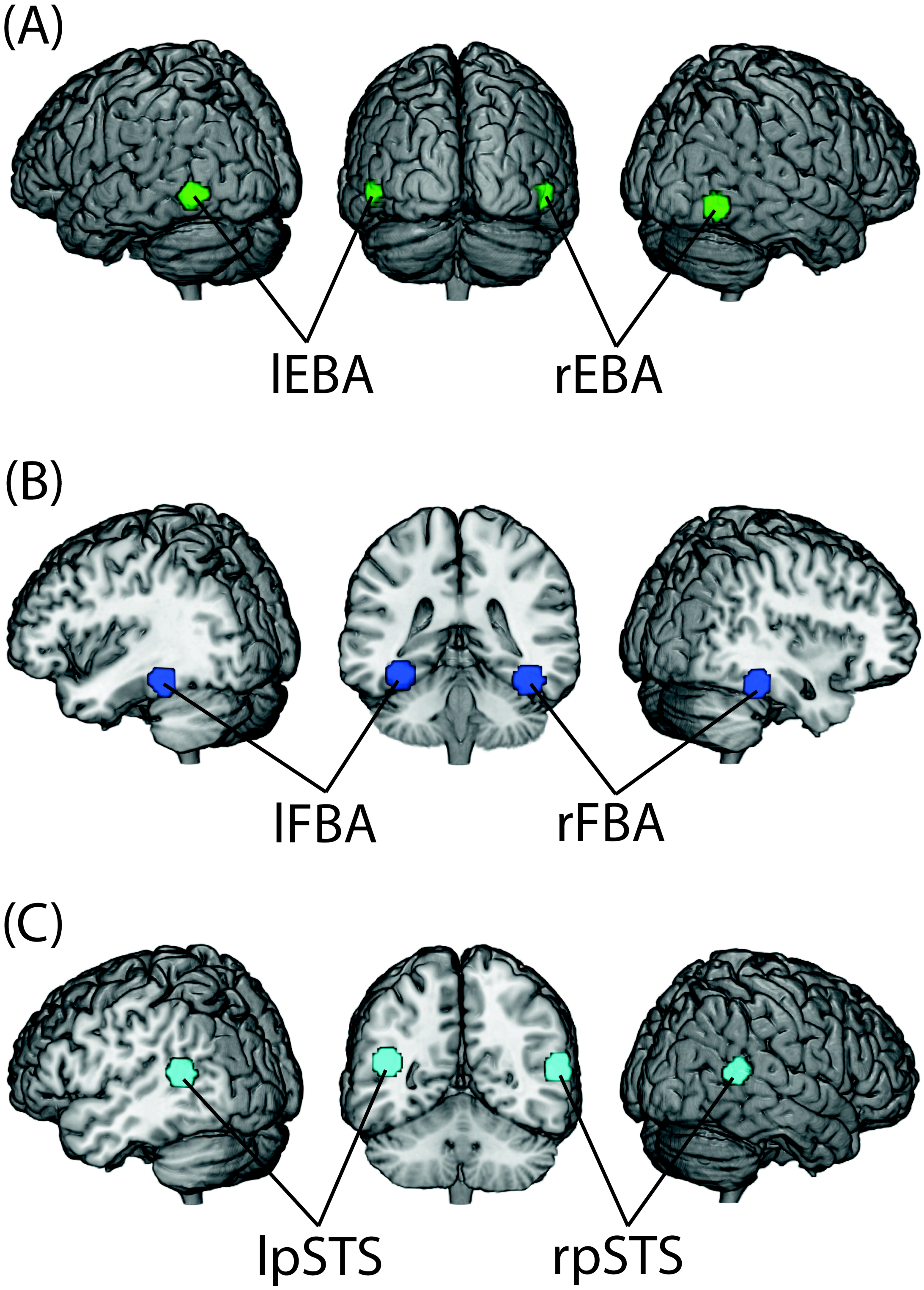


Figure 1-2 Anatomical locations of the EBA, FBA and pSTS

1.4.1 Extrastriate Body Area

The extrastriate body area (EBA) is a distinct cortical region in humans located in the lateral occipitotemporal cortex. It is a specialised neural system for the visual perception of static and dynamic human bodies and body parts (with the exception of faces). First identified by Downing et al. (2001), the EBA has also been shown to respond to goal-directed actions of participants, both imagined and executed (Astafiev et al., 2004). They found that both limb movements and saccades to a stimulus produced stronger activation than when subjects didn't perform any motor involvement. This suggests a potentially widespread influence of action on visual cortex. However, EBA has also been shown to significantly overlap with the human motion complex (hMT+), which could go some way to explaining this visual and sensory-motor integration (Weiner and Grill-Spector, 2011;Ferri et al., 2012;Ross, 2014;Vangeneugden et al., 2014b). Using evoked potential mapping, Arzy et al. (2006) showed that mentally embodied self-location is coded in the EBA. Furthermore, this activation was modified by the position in which the participants themselves were lying/sitting. So together with the temporoparietal junction (TPJ – an area involved in self-processing and the multi-sensory integration of body-related information; Leube et al. (2003); Blanke and Arzy (2005)), the EBA is crucial for the coding of the self as both embodied, and as spatially situated within the human body.

Since its identification, there has been one study that has used subjects with lesions to body form areas. Counter-intuitively, Gilaie-Dotan et al. (2015) found that biological motion could be processed normally when the ability to perceive the form of the actor performing the movements is impaired (but also see Moro et al. (2008) and Frassinetti et al. (2012)). Instead, for the most part, event-related rTMS studies have been used to inhibit the area transiently, leading to longer reaction times in the visual processing of body parts (Urgesi et al., 2004), reduced accuracy for inverted but not upright bodies (Urgesi et al., 2007a), gender differences in the aesthetic processing of human bodies (Cazzato et al., 2014),and reveals double dissociations of processing form and motion information (Urgesi et al., 2007b;Vangeneugden et al., 2014a).

1.4.1.1 Developmental Work

In terms of functional development of the EBA, there is little literature available. Peelen et al. (2009) and Pelphrey et al. (2009) report, using fMRI, activity in the EBA when viewing static images of bodies in children as young as 7 years old. Pelphrey, Lopez et al. (2009) went on to suggest that the selectivity for images of bodies did not differ between adults and children and that in terms of localisation and specificity, the EBA is already ‘adult-like’ in children as young as 7 years of age. These studies, however, each have their own limitations. Peelen et al. (2009) tested a participant group with a large age-span including pre and post-pubertal individuals (ages 7-17), which could have led to a masking of adult/child differences due to the presence of late adolescents in the sample. Pelphrey et al. (2009) on the other hand used a very lenient whole-brain analysis threshold ($p<0.01$ uncorrected) before using an index of activation based solely on this threshold (it is my opinion that taking the peak t-values in a given ROI is a superior method of gauging sensitivity than taking the mean activation in an ROI; not only does it discount the problems of less than stringent thresholding, but the peak is guaranteed to show the best effect of any voxel in the ROI).

Despite these apparent limitations, the findings of these studies demonstrate that the EBA does exist in children, with both studies suggesting that the EBA is equally selective in children as in adults. While Peelen et al. (2009) do acknowledge that their results were only significant when rEBA was defined at more lenient thresholds, both concur that more work is needed to confirm their findings.

Thus there is much more to be done in understanding developmental trajectories of the EBA in particular. We will explore this in much more detail in **Chapter 3** and **Chapter 4**.

1.4.2 Fusiform Body Area

First identified by Peelen and Downing (2005), the fusiform body area (FBA) is a region located in the mid-fusiform gyrus that responds selectively to images of bodies without faces. They found substantial overlap with the FFA, noting that the fusiform areas activated by contrasting bodies versus tools and faces versus tools were very similar. Individual subject analyses, however, showed the peak activation on the two contrasts to occupy distinct regions. A further interesting finding was that the FBA responded to stick figure depictions of bodies versus scrambled controls, suggesting that the body-selective response of the FBA extended to abstract image formats. This finding led Taylor et al. (2007) to posit the question of ‘Are the EBA and FBA analysing different aspects of the human body?’

Taylor et al. (2007) used the structure of the Haxby et al. (2000) face processing model as the framework for a body-processing model. They hypothesised that the EBA consisted of a group of neurons whose selectivity was primarily for parts of the body, whereas the FBA was primarily selective to the body as a whole (or larger segments of the body). They tested this by showing participants bodies in various hierarchical levels (i.e. finger – hand – arm – full torso). To control for the possibility of any observed activity being due to the increase in complexity in the image, they matched the body images with those of a tree (i.e. leaf – leaves – branch – trunk). They found that bilaterally the EBA showed a gradual increase in selective response, which was in proportion to the amount of body hierarchy that was visible. In contrast, the FBA showed no difference across the first 3 images, before a ‘step-like’ rise in the response to torso and headless bodies relative to the smaller body part images. These findings thus supported their hierarchical model of body processing.

This question of dissociative encoding is still open for debate, as both the EBA and FBA overlap with other regions associated with social signal processing. We will return to this question later in the chapter.

1.4.2.1 Developmental Work

Along with the development of the EBA, the main focus of Peelen et al.’s (2009) study was to examine the differential developmental trajectories of the FFA and FBA. Using subjects aged 7-32 years old they replicated previous findings that the rFFA increases in both selectivity and size with age (Golarai et al., 2007;Scherf et al., 2007). However, in contrast they found that the rFBA did not show these developmental trends. Instead, the region was comparable in children and adults. The finding that the rFBA was substantially larger than the rFFA in children, but not adults, supports the idea that the rFBA develops faster/earlier than the rFFA. Due to the overlap between these two regions, the lack of difference between adults and children in the rFBA could not be attributed to typical confounds found in developmental studies (i.e. differences in head motion, differences in variance in hemodynamic response function, variations in normalisation etc.; see Grill-Spector et al. (2008)) as these too would have effected the rFFA differences. So why do the face perception regions continue to develop while those dedicated to body perception do not?

Peelen et al. (2009) speculate that something as trivial as height may play an important role. Young children, when surrounded by adults, will typically use the body (and its movements) to infer identity, intentions and emotional state. Then, as people go through childhood and adolescence (and are attending various schools), they are exposed to many new faces, and thus may require an increase in the size and selectivity of the face-selective cortices in order to discriminate between them.

Again, it should be noted that Peelen et al. (2009) are terming ‘children’ here as anyone aged 7-17 years old. As with the EBA results, this inclusion of subjects in early and late adolescence has the potential to mask any prospective differences between adults and pre-pubertal children. Furthermore, to this author’s knowledge, there are no other investigations into the developmental trajectory of the FBA, so whether the FBA and EBA is indeed ‘adult-like’ by as young as seven years old has not yet been replicated.

1.4.3 Superior Temporal Sulcus

Anterior and dorsal to the EBA and FBA, the STS (primarily the posterior portion of the STS (pSTS)) has been found to be involved in the processing of human movements (review in Allison et al. (2000), Grosbras et al. (2012a)). In contrast to EBA and FBA activation (which increases towards bodies compared with objects regardless of whether or not the stimuli are in motion), it is thought that pSTS activity is related only to bodies in motion (Saxe et al. (2004); but also see Puce and Perrett (2003)).

Single cell recordings from anterior STS in macaque monkeys also show its responsiveness to biological motion as well as processing monkey body parts (Oram and Perrett, 1996). STS has also been found to be sensitive to emotional body expressions in non-human primates. Using rhesus monkeys and fMRI de Gelder and Partan (2009) found that, in line with the role of the STS in humans, the sulcus showed preferential sensitivity to threat signals in the stimuli.

Pelphrey et al. (2003) observed that studies prior to 2003 had used random motion controls (the studies in question used point-light display walkers and compared them to the same point-lights moving in an incoherent manner, Bonda et al. (1996), Grèzes and Decety (2001)) in identifying the selectivity of the STS, leaving open the possibility that coordinated and meaningful motion from non-biological stimuli may activate the same regions. This outcome would call into the question the STS's presumed specificity to biological processing. However, Pelphrey et al. (2003) found that the STS responded more strongly to biological motion than to complex but meaningful non-biological motion and non-meaningful complex non-biological motion. Puce and Perrett (2003) further noted that the STS also displayed robust neural activity when presented with eye and lip movements. This evidence seems to give the STS a more social role in body perception. Puce and Perrett (2003) go on to suggest that the STS may indeed play a role in enabling social behaviour and appropriate affective responses to the human body.

It should be noted that the eye and lip movements in Puce and Perret's review (2003) are socially relevant stimuli, in so much as they could allow an observer to predict the individual's social attention and potential speech respectively. Thus, all of these stimuli have something in common in that they are intentional actions. Saxe et al. (2004) elaborated on this, showing that the rpSTS is not sensitive to body motion per se, but is instead involved in the representation of intentional action. It is, in other words, sensitive to 'goal-directed' motion (Morris et al., 2008;Carter et al., 2011). Vander Wyk et al. (2012) demonstrated this by having participants view an actor looking at two objects and making either positive or negative facial expressions towards them. This created expectations in the observer as to which object the actor would then reach for. When these expectations were broken and the actor reached for the unappealing object, they observed an increase in rpSTS activity, suggesting that the region plays an active role in intention understanding.

As well as being involved in the processing of a wide range of social tasks (biological motion, intention and goal related actions) the STS also has a role in speech processing (which we will revisit in depth in **Chapter 5**). This wide range of processing dimensions led Redcay (2008) to propose that rather than intention being the driving force behind increased STS activation, it is the communicative significance of the stimuli. This is supported in the vocal processing domain by findings of increased STS activity to communicative human sounds (speech/laughter) compared with non-communicative human sounds (coughs/sneezes) (Specht and Reul, 2003;Shultz et al., 2012).

One of the problems with all of the above work on the STS, however, is determining whether all studies refer to the same region. The STS is a rather long sulcus and it isn’t always mentioned whether authors refer to the posterior, mid or superior portions. In this thesis then we will aim to be more unambiguous and will be mostly concerned with the pSTS.

1.4.4 The Amygdala and Emotion Modulation

One of the first studies to examine the effect of emotion modulation on the activation in body-selective areas found results similar to those observed in studies using faces; namely a connection between the fusiform gyrus (likely FBA in bodies and FFA in faces) and amygdala (Hadjikhani and de Gelder, 2003). Amygdala activity is linked with emotional processing and is commonly reported in fMRI studies of socially relevant facial expression perception (Grosbras and Paus, 2006;Fusar-Poli et al., 2009). It has, however, also been implicated in the processing of body movements and posture in the human (Bonda et al., 1996;Hadjikhani and de Gelder, 2003;de Gelder et al., 2004a;de Gelder, 2006;Grosbras and Paus, 2006) and non-human (Brothers et al., 1990) brain.

In terms of emotion modulation of visual cortical areas, a parametric relationship has been shown between amygdala damage and the level of emotional activation in the fusiform cortex when viewing pictures of fearful and neutral faces (Vuilleumier et al., 2004). Furthermore, contrary to healthy controls, subjects with damage to the amygdala showed no increase in activity in the fusiform and occipital cortices when presented with fearful faces. Thus, increased perceptual processing of emotional stimuli may result from direct feedback from the amygdala, ‘modulating’ cortical pathways (in this case the visual pathways) either in an additive or competitive manner with other higher cortical areas (e.g. attention and decision making regions in the frontal and parietal cortices)(Vuilleumier, 2005). Understanding this emotion modulation process is key to understanding emotion processing as a whole, both from a functional and behavioural point of view. Several factors could influence the proposed amygdala feedback system (attention, decision-making, and emotion signal strength), so understanding and controlling for these parameters will be essential in future work.

The results of emotion modulation of the EBA are varied. Using static images of fearful bodies with their faces blurred out, de Gelder et al. (2004b) and Hadjikhani and de Gelder (2003) found increased activation in the amygdala and the fusiform gyrus, but no evidence for the involvement of the EBA. They suggest that this indicates that the EBA is not differentially sensitive to the Happy, Fearful or Neutral body conditions used, but instead only implements the processing of the body shape/parts, while the fusiform gyrus and amygdala is sensitive to the expressions and emotions on display. van de Riet et al. (2009) again found no difference between emotional and neutral bodies using static body images, however, data using dynamic body expressions showed clear emotional modulation of the EBA (Grèzes et al., 2007;Pichon et al., 2008;Sinke et al., 2010;Kret et al., 2011).

This leads one to ask: What is the difference functionally between the processing of static and dynamic bodies? Which kinematic parameters contribute to the emotional content? To what extent are the different regions sensitive to these parameters? We will return to these questions later in the chapter.

Unlike the EBA, the FBA has shown strong emotion modulation when static bodies are used as stimuli (van de Riet et al., 2009). Using dynamic body stimuli, Peelen et al. (2007) showed that the emotion modulation of the FBA (and EBA) was proportional to the selectivity (computed by contrasting the response of bodies with the response to tools) of these areas to static body stimuli. They took a t-value for each voxel in the ROI reflecting body selectivity and a t-value for each voxel in the ROI reflecting emotion modulation and correlated these two sets of values. The emotion modulation in these two areas was also shown to correlate with emotion-driven increases in the amygdala using the same technique. These results seem to reflect the idea that the emotion modulation in the EBA and FBA, rather than reflecting direct encoding of the emotions present in the stimuli, is simply a result of the feed-back influence from sub-cortical areas.

Atkinson et al. (2012) showed that emotional content within point-light displays of bodies was sufficient to enhance the strength of activation in the bilateral EBA and rFBA. This finding further constrains the suggestion that emotional content within body movements modulate those regions that code for the viewed stimulus. It should be noted, however, that to date (and to my knowledge) no study has examined the explicit representation of emotion in these regions from a developmental point of view. Using a large sample of children and adolescents, correlation analyses and dynamic emotional body stimuli, we will return to this question in **Chapter 4.**

It should be noted (although they won't be the primary focus of this thesis) that there are other areas related with the perception of the human body. van de Riet et al. (2009) found, using emotional and neutral bodies, activation of motor related areas including the putamen and the inferior frontal gyrus (IFG). The latter region has been linked with action observation and execution (Grèzes and Decety, 2001;Hodzic et al., 2009), which perhaps suggests that the region contains 'mirror neurons' and represents other people's actions in relation to one's own actions (Rizzolatti and Craighero, 2004).

All of these regions obviously don't operate in isolation, but how might one create an integrative network of body processing? And furthermore, how might modulating the body with motion, goal or emotional information add to the complexity of the network?

1.4.5 Integration of Regions

Downing and Peelen (2011) identify five main functions of the body-selective areas; perceiving identity, emotion, body motion, actions and goals, and motor control. They propose, that instead of the EBA and FBA playing a high-level role that is specific to these representations, that the fMRI activation labelled EBA and FBA reflect relatively concentrated populations of neurons that respond selectively to the visual features that are highly typical of human bodies or body parts. These neurons jointly form a representation of perceived bodies and body parts, making this information available to other regions. They do this, they propose, by extracting some of the information about bodies that is implicit in 'early' retinotopic visual representations and making it explicit. It then contributes to computations in other areas. Conversely, they argue that the influence of activity in other regions on the EBA and FBA can mainly be explained as ‘attentional modulation’.

This suggests that the EBA and FBA serve no higher purpose other than the perceptual representation of body posture and shape. This information is then fed-forward to other regions interested in the social (or communicative) content (pSTS, amygdala, IFG, IFL, and PFC). Any subsequent feedback to EBA or FBA is simply a modulatory effect of a social construct leading to increases in perceptual representation.

Amoruso et al. (2011) add to this work and propose a functional neuroanatomical model for the processing of goal-directed actions using the body-selective areas, and the fronto-insular-temporal networks (or Social Context Network (SCN)). They suggest a multimodal system in which expectations (frontal areas) of a stimulus (in this case the body as processed by the EBA and FBA) interacts with the current internal motivational state (insula) and the stimuli’s semantic associations (temporal regions). This system could then be modulated by any emotional (amygdala) and communicative (STS) context. It is the functional development of emotion modulation in this system that we will examine in **Chapter 4**.

The main message here, however, is that the role of an area is best investigated, and perhaps only relevant, in relation to its role within a network.

1.5 Competing Pathway Models

Along with evolving models of body processing through modulation, feedback and feed-forward information, there are also models of body processing which involve differing pathways altogether. As mentioned above, in order to perceive the intentions, emotions and actions of others based on their body movements, we must be able to bring together information both from the body form, and the body motion of the individual. This, however, leaves open the question as to how body form and body motion can be differentiated.

1.5.1 Stimuli

There are several ways to explore the underlying neural pathways governing the perception of the human body. Along with changing the overall technique employed (fMRI, TMS, psychophysical, behavioural etc.), arguably more interesting is the change one can make to the stimuli themselves. Most of these changes are used to examine the finer details of perceptual processes. For example, comparing neural processing of static body images against bodies in motion can illustrate the contribution of the motion specific areas in the body perception network. The use of point-light and full-light displays can extract the form information from a body stimulus, leaving the observer with just the motion information to infer any intentional state of the stimulus. A combination of both the aforementioned techniques can allow for regions in the body-selective areas with very specific sensitivities to be identified. We can then ask questions of attention and memory, make the stimuli affective in nature, and chart the developmental trajectories of all of these processes. The methodological possibilities are vast, and in the scope of this thesis we will use both behavioural and brain imaging techniques as well as point-light, full-light, dynamic, and affective stimuli in various iterations.

1.5.2 Form and Motion Processing

There are two main theories as to how form and motion information is processed in the brain. One account posits that actions are recognised and processed as a series of static ‘snapshots’ that are concatenated to form motion. There is evidence of distinct neuronal populations encoding static body poses, but these findings do not rule out separate neuronal populations for the encoding of dynamic body actions (Lange and Lappe, 2006;Singer and Sheinberg, 2010). The alternative theory suggests that there are two parallel pathways consisting of a dorsal stream that analyses the motion information and ventral stream that analyses the form information (Giese and Poggio (2003); see Figure 1-4 (A) in ‘Section 1.5.2.2 Double Dissociations’ later in this chapter).

Taking the two pathways model for the time being, as we have seen above, the pSTS is hypothesised to be involved in processing body motion cues, while the EBA and FBA are hypothesised to be involved in processing body form cues.

Jastorff and Orban (2009) showed that EBA and FBA activation correspond to the initial stages in visual action analysis and that this occurs automatically, even in the absence of a task. They also show in humans (Jastorff and Orban, 2009) and monkeys (Jastorff et al., 2012), that pSTS activation depends on complexity of movements or task instructions.

Dissociating these two pathways, however, remains a contentious issue. Firstly, there is substantial cortical overlap between EBA and the human motion complex (hMT+). Secondly, body motion and form information are closely linked and integrated; body posture can convey information about intended movements (Cazzato et al., 2012) while body motion can give clues about body form such as gender, emotion and identity (Mather and Murdoch, 1994;Pollick et al., 2005;Peelen et al., 2006;Blake and Shiffrar, 2007;Schouten et al., 2013).

So with such overlap between these two visual cues, what techniques can we use in order to disentangle the perceptual and functional processes governing their perception?

1.5.2.1 Point-Light Displays

One way to differentiate between human form and motion is by using ‘point-light displays’ (PLDs) in which the body is represented by a small number of illuminated dots, positioned in such a way as to highlight the motion of the main body parts (example in Figure 1-3 is from **Chapter 2**). When static, the display appears at first glance as a seemingly meaningless configuration of points; yet, when moving, the display gives a striking impression of a moving body (Johansson, 1973).

Figure 1-3 Full-light display and it's respective Point-light display

In terms of function, PLDs of full body movements are known to activate EBA (Downing et al., 2001;Peelen et al., 2006), pSTS (Grossman and Blake, 2002;Puce and Perrett, 2003), FBA (Peelen and Downing, 2005) and PMC (Saygin et al., 2004). Indeed, neuropsychological studies show that STS and PMC have independent causal relationships with deficits in PLD perception (Saygin et al., 2004). Also, as previously mentioned, PLDs provide enough information (by way of motion and form-from-motion) for observers to gauge gender, emotional content, dominance, and identity (review in Blake and Shiffrar (2007)). To date, however, there has been no examination of the developmental trajectories of these abilities. This will be the focus of **Chapter 2**.

There is, however, a problem; due to dynamic PLDs giving the form-from-motion effect, it is hard to discern whether the cues used to infer affect from a PLD stimuli are due to the motion alone, the form-from motion alone, or a combination of the two.

Recent time course analyses have attempted to move past the anatomical localisation of regions that facilitate the various perceptual processes involved with PLDs and better understand the underlying neural mechanisms. Some ERP evidence suggests that the processing of biological motion begins in the range of the occipital-temporal N1 component (peak approximately 170-210ms after stimulus onset. Baccus et al. (2009) posit that this activity reflects the integration of form and motion information. However, Krakowski et al. (2011)

found that human motion can elicit a response as early as the P1 component (approximately 110ms after stimulus onset). They also showed that the P1 component was sensitive to the point-light walker (PLW) stimulus whether attention was directed to it or not. This may suggest an initial reflexive processing of biological motion, before any top-down attentional control mechanisms can influence the signal (perhaps from the body processing brain regions outlined in the **Integration of Regions** section above).

Buzzell et al. (2013) investigated this question of perceptual process speed using PLWs and scrambled PLWs to show that the P1 component could be modulated by motion. They found that dynamic PLWs resulted in a larger P1 compared to scrambled PLWs. Similarly, static PLWs were found to be more salient to P1 than static scrambled PLWs. This is interesting as it could mean that Krakowski et al.'s (2011) observed effect of P1 for dynamic PLWs may not be dependent on motion cues, but rather the visual system can extract form information with great speed, even from static PLWs. Buzzell et al. (2013) further found that the N1 component was sensitive to dynamic, but not static PLWs. Thus, they argue, the N1 component is a reflection of both motion and form information, and possibly (as Baccus et al. (2009) previously suggested) the integration of the two visual cues.

These results are also consistent with the Amoruso et al. (2011) brain model, in which the basic visual information (form) is processed first (P1) in the extrastriate and fusiform areas, before more complex contextual information (motion) is integrated from the pSTS at a later stage (N1).

However, the results also seem to support a 'snapshot' model of form and motion processing, insomuch as Buzzell et al.'s (2013) models suggest that the perception of biological motion arises from the temporal integration of the form present in individual frames of PLWs. In other words, it is the sequence of these static postures concatenated which gives the perception of motion. This somewhat reduces the importance of motion, as a visual cue in its own right, when it is simply imagined as 'concatenated form'. It certainly makes a paradox of the idea of 'form-from-motion', as Buzzell et al.'s (2013) conclusions make motion a by-product of form itself.

What then of the parallel processing model? None of the research above rules out the possibility of a separate pathway which analyses actions based on motion cues alone (although by definition the ‘motion’ may have to come from a form pathway). So given all of the integration between form and motion perception, can the underlying processes be empirically dissociated?

1.5.2.2 Double Dissociations

A recent study by Vangeneugden et al. (2014b) addressed the issue of dissociating form and motion in a novel way. They used a combination of fMRI, psychophysics and TMS to provide converging evidence for dissociable parallel processing of body form and body motion information. First, they tackled the issue of EBA/hMT+ overlap by localizing each ROI independently. Voxels selective for both body form and motion in both ROIS (and so would be included in both EBA and hMT+) were excluded from any further analysis. This effectively created two new functional regions which authors labelled EBA* and hMT+*.

Then, to look for evidence of a double dissociation in body form and motion processing, the authors used fMRI and MVPA to ask whether multivoxel patterns in EBA* and pSTS selectively carried information about the form and motion of whole body point-light display walkers (PLW). The MVPA results yielded a stark double dissociation: the EBA* carried information about the PLWs body posture but not motion, while the pSTS carried motion direction information, but no body posture information.

Next, the authors investigated whether the representations uncovered in the two ROIs causally contributed to behavioural discriminations of body form and motion. To address this question they created a novel set of stimuli of PLWs consisting of ellipses with variable alignments. This allowed the authors to manipulate form information while leaving the movement trajectories unaffected, and *vice-versa*. They found that elliptical misalignment (form manipulation) had a stronger effect on a facing orientation task than on a walking direction task, while stimuli duration (motion manipulation) gave the opposite effect. Thereby these results strongly indicate that body form and body motion processing rely on separate visual cues.

Finally, the authors used the same psychophysical tasks in a repetitive TMS experiment, during which they manipulated neural activity in either the EBA or pSTS. They observed a double dissociation, with TMS over EBA disrupting performance in the form discrimination task significantly more than TMS over pSTS, and *vice-versa* for the motion discrimination task.

These results provided converging evidence that the perception of body form and motion relies on distinct functional and neural pathways, in keeping with the parallel processing pathways model of body action perception. However, as I pointed out in a recent commentary article (Ross, 2014), there are a few caveats relating to this conclusion that are worth reiterating.

In separating the EBA and hMT+ into two regions containing only voxels that were selective to bodies and motion respectively (EBA* and hMT+*), Vangeneugden et al. (2014) have set the standard from which future work into the dissociation of form and motion processing in the visual system should adhere to. They have also, however, effectively made comparison with other papers exploring the EBA and hMT+ impossible. EBA* and hMT+* should be treated as distinct areas in their own right in future work, perhaps being renamed to avoid confusion (The Occipital Body Form Area (OBFA) and Occipital Motion Area (OMA) for example, see Figure 1-4 (B)).

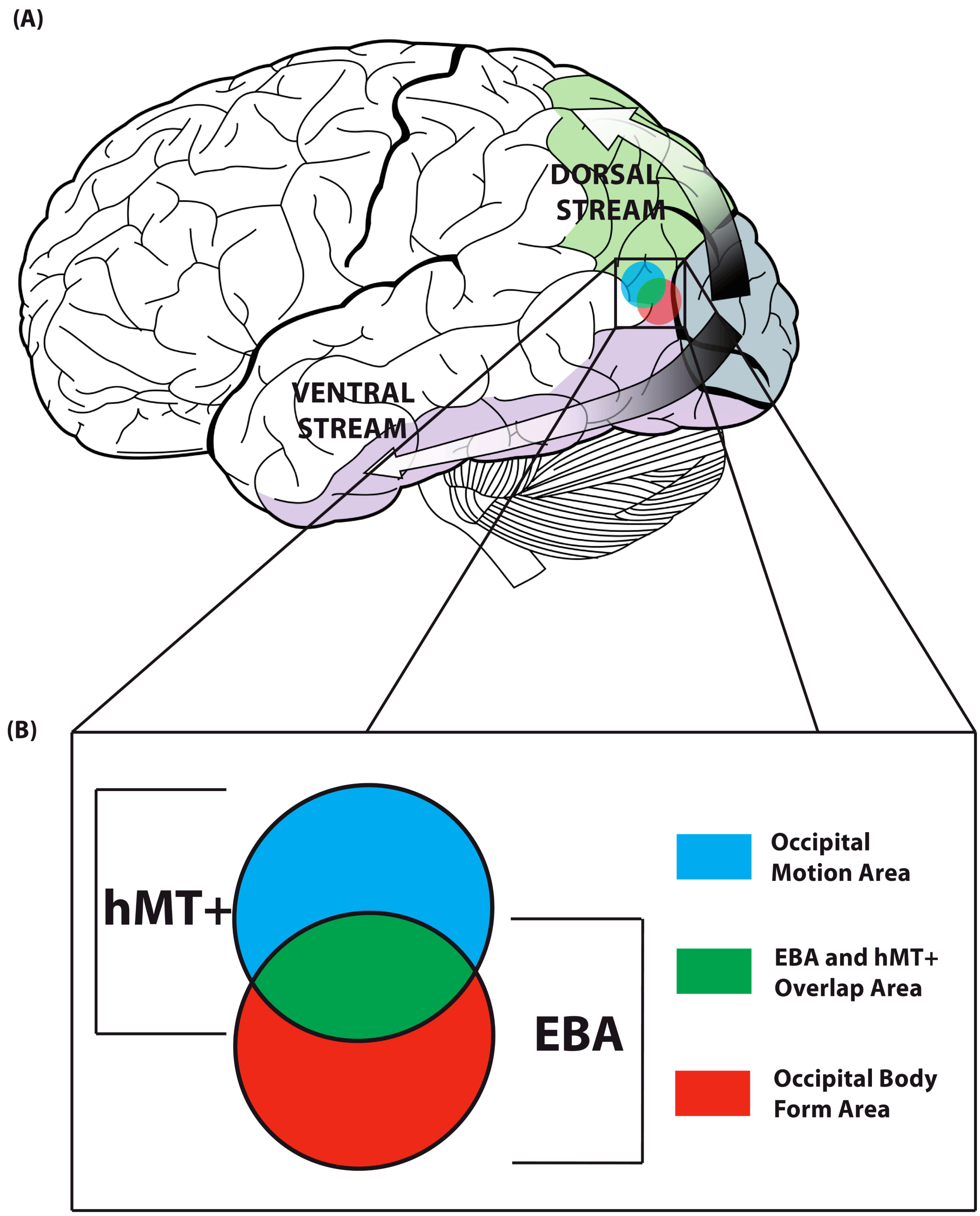


Figure 1-4 Dissociable Form and Motion Visual Pathways

(A) The dorsal (motion) and ventral (form) pathways of the visual system.

(B) The overlap of EBA and hMT+ is presented in Green. The Occipital Motion Area (formally hMT+*) is shown in Blue, and the Occipital Body Form Area (formally EBA*) is shown in Red.

Adapted from an image created by Lokal_Profil, CC-BY-SA-3.0.

This is significant because, as Vangeneugden et al. (2014b) duly acknowledge, the occipital area that they target in the TMS portion of their study also most likely contained hMT+. This could have led to disruption of motion processing in hMT+, although the authors give several reasons why hMT+ stimulation may not lead to impaired biological motion discriminations.

The main issue is that one could argue that the areas in which the double dissociations were observed in the fMRI and TMS portions of Vangeneugden et al's. (2014) study were not the same. This is important, as if future studies are to build upon this work effectively, they must make the distinction between EBA and hMT+, and EBA* and hMT+* (or OMA and OBFA).

Finally, Vangeneugden et al. (2014b) conclude that their results favour action perception models with distinct form and motion pathways over ‘snapshot’ models in which action perception relies solely on integrating a series of static body postures. However, by manipulating motion in their psychophysical experiment by varying the presentation duration, one could argue that their results also lend some support to the snapshot model. There is no noteworthy improvement in the form discrimination task as more frames (1 frame/17ms) are added to the sequence. Thus, a single snapshot is all that is needed to determine form information (in keeping with Buzzell et al. (2013)), at least in the facing direction recognition task used here. Conversely, there is continual improvement to the motion discrimination task as more frames are added, with performance just above chance with the 33ms stimuli. The longest stimuli in the motion discrimination task was also three times longer than the longest form discrimination stimuli, which could have led to the seeming lack of improvement in the form task.

Despite this, Vangeneugden et al. (2014b) conclude that the snapshot model is still unlikely given the converging dissociation results of the fMRI and TMS studies. So, given the evidence for a parallel processing model, we will assume that form and motion perception are dissociable, and explore the developmental trajectories of these processing abilities from a behavioural point of view in **Chapter 2.**

1.6 Voice-Areas of the STS

As we have seen, as well as being involved in several aspects of human communicative processing including biological motion perception (Allison et al., 2000;Puce and Perrett, 2003;Saxe et al., 2004;Vangeneugden et al., 2014b) and face perception (Haxby et al., 2000), the STS is also deeply involved in speech processing. In humans, bilateral regions in the STS respond preferentially to human vocal sounds compared to non-human sounds (Belin et al., 2000b). These 'temporal voice areas' (TVAs) have since been shown to be more selective to words rather than natural sounds, pseudo-words and tones (Roder et al., 2002;Specht and Reul, 2003). Following this, and based on Redcay's (2008) suggestions, Shultz et al. (2012) investigated whether the TVA regions of the STS are interpreting the communicative significance of their auditory signals rather than the basic signals per se. They used four categories of human vocal sound, infant-directed speech, adult-directed speech, communicative vocal non-speech (laughter, sounds of disapproval etc.) and non-communicative vocal non-speech (physiological vocalisations such as coughing/yawning etc.). They found that although the TVA was active for all vocalisation groups, it was especially sensitive to the three communicative groups compared with the non-communicative group in the bilateral middle to anterior STG and the right middle STS. Furthermore, they also found that the communicative sounds produced more activation than the non-communicative sounds in the left TVA but not the right. Interestingly, when rating of emotional content in the communicative sounds was added as a regressor, regions were no longer selective for communicative sounds. However, even though the adult-directed speech was rated as having significantly lower emotional content than the infant-directed speech, the beta values for the two were equivalent. The seeming selectivity in the left TVA to communicative sounds could instead be in line with the general left lateralisation of speech and language function (Vikingstad et al., 2000).

1.6.1 Developmental Work

To date, several studies have explored the functional development of the TVA in infancy (Grossmann et al., 2010;Blasi et al., 2011;Lloyd-Fox et al., 2012). Using near infrared spectroscopy (NIRS) they find that 7 month-olds, but not 4 month-olds show increased TVA activity (if one can call this region the TVA in an adult sense at this early stage of development) when listening to human voice compared with non-vocal sounds. They even show emotion modulation of the TVA, particularly in the right hemisphere.

To my knowledge, there has only been one study exploring the functional trajectory of the TVA in children and adolescents. Bonte et al. (2013) found a right lateralisation in voice-selective activity that was present in adults, adolescents and children, and which decreased with age. They also found that the TVA response to voices changed from being more spatially diffuse and less selective in children to highly selective and focal in adults. This is in line with a recent study by Belin et al., (Submitted) which identified 3 bilateral clusters found along the STS that make up the TVA. It remains to be seen, however, whether these clusters are found in children, or whether they are masked by the 'spatially diffuse' activity in children reported by Bonte et al. (2013). This will be the main focus of **Chapter 5**.

1.7 Methodological Issues in Developmental Studies

It could be argued that an issue of normalisation arises when one tries to compare data from children and adult subjects. Due to the individual differences in brain morphology, imaging data has to be spatially normalised to allow for inter-individual comparisons (Wilke et al., 2002). This is achieved by transforming an individual's brain imaging data into a standardised space (Toga and Thompson, 2001). However, due to anatomical and compositional differences between a child's brain and that of an adult, O'Shaughnessy et al. (2008) argue that the normalisation of images into a standard brain template can be problematic. Particularly as the most widely used spatial normalisation schemes use information based on adult brain data.

In attempting to address the question of applicability of adult brain templates for the spatial normalisation of child brain imaging data, Muzik et al. (2000) looked at 13 children with epilepsy. They determined the deviation of children's outer brain contours compared with adult's brains after spatial normalisation to a standard adult brain template. They found that there was much more variability in the outer contours of the children compared with the adults, and furthermore, that this result was age-dependent. They concluded that spatial normalisation to an adult template is feasible in children aged 6 years and older.

One of the problems with this type of research is that every year the software used to create the spatial normalisation improves and undergoes major revisions. This then makes inferences across analysis programs and time very difficult.

There is another issue in that even if it is feasible for children aged 6 or older to be normalised to the framework of a standardised space, as there are constant structural and functional changes occurring in the brain throughout childhood, it is hard to determine how much deformation of the child's brain will occur in applying it to the template. In other words, is a region showing some sort of activation in a child's brain the same region when the brain is normalised to standard space?

Burgund et al. (2002) assessed the effectiveness of the normalisation of children's brains into Talairach space by comparing the coordinates of major sulci in a group of healthy 7 and 8-year old volunteers to the coordinates of the same sulci in a group of adults. Twenty child and twenty adult brains were normalised into Talairach space and the coordinates of nine consistently identifiable sulci were recorded. Their results showed that of the nine sulci examined, only two differed significantly between children and adults. Having said this, the differences were comparatively small, with the largest significant difference being less than 3 millimetres. Their conclusions are therefore in line with those of Muzik et al. (2000), in that neuroimaging data gathered from children over the age of 6 may be effectively transformed into the same (Talairach) stereotactic space.

Also, at this age the hemodynamic functions used to model the fMRI signal do not seem to show any difference between adults and children (Kang et al., 2003;Wenger et al., 2004). Studies using paediatric templates show that the morphological differences that most affect the localisation of function occur between younger children (<7 years old) and adults and concern more “central” brain regions (close to the ventricles; see Fonov et al. (2011)). The occipitotemporal regions described in this thesis are less affected by gross morphological changes and as we have seen, several studies have shown that there is no significant difference in the locations of brain activation foci (Burgund et al., 2002;Kang et al., 2003) when children's brain data are warped to a common adult template. Thus, we can have confidence that normalising the children and adults to the same stereotactic template creates no confound of brain size and adults and children's activation strength and extent can be compared in this way. More practical problems involved in scanning children and adolescents are described in the General Discussion in **Chapter 6**.

1.8 Thesis Rationale

At this stage, it will be useful to summarise each experimental chapter and their subsequent rationales using information presented so far in the General Introduction.

1.8.1 Emotion Recognition from Full and Point-light Displays across Age

We have seen that the form and motion pathways in the brain are likely parallel in nature, i.e., form and motion information can be independently processed (Vangeneugden et al., 2014a). PLDs have been shown to be versatile stimuli for separating form and motion information (Blake and Shiffrar (2007)), albeit with some caveats relating to the problem of form-from-motion information. However, many studies using point-light displays and full-light displays (FLDs) have used different recordings for their different stimuli. Here then we have created a new set of point-light and full-light stimuli that are simultaneously recorded. This allows for direct comparison across lighting conditions, as the motion information contained in both is identical. We had actors portray four basic emotions (Happy, Sad, Scared and Angry) whilst being both filmed on a digital camera, and captured on motion capture cameras.

Several studies have explored the ability of children and adults to recognise emotions from body movements (Boone and Cunningham, 1998;Lagerlof and Djerf, 2009). In Experiment 1 of this thesis, and using this new set of stimuli, I will address for the first time whether information from motion (PLDs), or a combination of motion and form (FLDs), is sufficient for children, adolescents and adults to recognise the four basic emotions mentioned above. Using a large sample set, I will also be able to chart the differing developmental trajectories of emotion recognition from these two types of stimuli, and assess whether the benefit of the full information in the FLDs is similar across age. For instance, any interaction between age and the lighting condition would indicate that the differential use of socially relevant visual cues changes during development. If this is the case, then to understand the functional development of body perception, we must first ask: ‘Do children and adults process the human body differently on a functional level?’

1.8.2 Development of the Body-Selective Regions

To address the above question, I will first investigate the functional development of human body perception using fMRI, followed by exploring the emotion modulation of these body-selective regions by bodily expressions. This will lay the foundation for future studies wishing to extrapolate the results of **Chapter 2** using a brain-imaging paradigm. Such a study into the neural developmental trajectories of emotion judgements from body expressions will first need to be aware of the differences between adults and children in the functional development of the body-selective areas. Furthermore, any study determining the neural underpinnings of explicit (or implicit) emotional body recognition in adults and children will also require knowledge of any potential differences over age in the emotion modulation of the body-selective areas. This is the function that **Chapter 3** and **Chapter 4** serve; namely, as necessary groundwork for future studies wishing to directly expand upon the results of **Chapter 2**.

Only two studies have previously studied the development of the body regions of the visual cortex. Peelen et al. (2009) found that the FBA was ‘adult-like’ in children and adults. The children in their study, however, ranged from 7-17 years old. Similarly, Pelphrey et al. (2009) found the EBA to be ‘adult-like’ in terms of localization and specificity by 7 years of age. They used a very low random-effects threshold ($p<0.01$ uncorrected) that greatly increases the Type II error rate of the data. Subsequently, they find the rEBA in children to consist of 712 voxels, making it approximately 38,000 mm^3. So, in Experiment 2 of this thesis, using more stringent statistical thresholds and a more homogeneous sample of pre-pubertal children and adults, I will attempt to redress the shortcomings of previous work and address the question of the functional development of human body perception anew.

Further to this I will build upon work by Golarai et al. (2010), who found a distributed pattern of activity encoding faces which did not change over age. Using multivariate bayesian (MVB) techniques, I will explore the possibility that any differences found between children and adults in functional body recognition are due to a difference in the neural representation of the stimuli. As well as MVB allowing the comparison of different spatial encoding models, it is also possible to look for interactions across groups as to the most likely model of spatial encoding. This will allow a comprehensive comparison of the function of body-selective regions across age and allow us to ask whether the body areas are really ‘adult-like’ in children as young as 7 years old.

1.8.3 Emotion Modulation of Body-Selective Areas across Age

With so little previous research on the function development of body processing over childhood and adolescence, it is perhaps not surprising that there is currently no data regarding the effect of emotion modulation on the developmental trajectories of the body-selective areas.

Therefore, by using affective body stimuli and combining the emotion recognition work from Experiment 1 (**Chapter 2**) with the functional development work from Experiment 2 (**Chapter 3**), I will be able, for the first time, to explore this question. Using a large sample of over 40 children and adolescents in an fMRI study, I will be able to not only chart the developmental trajectory of the body-selective areas when viewing normal bodies (as in Experiment 2), but also the developmental trajectory of these areas when modulated by the emotional content of affective stimuli. If it is the case that the body-selective areas are in fact adult-like in children, the emotion modulation of these areas may still not be mature at this age. We will of course have the emotion recognition data obtained in Experiment 1 to use as a basis for hypothesis.

1.8.4 Functional Development of Temporal Voice Areas

So far, this thesis has been focussed on recognition of the body using various techniques. Experiment 4 will shift focus on to the third (and incidentally least studied) signal used in social interaction, the voice. Like the body, the voice literature has demonstrated the wide range of social information that can be gleaned from the information contained within the human voice. Also like the body literature, the work into the development of the voice-selective areas is extremely limited. The only study to look at the functional development of the TVA in children and adolescents found a right lateralisation for voice-selective responses in all age-groups that decreased with age (Bonte, Frost et al., 2013).

Thus, in Experiment 4, I will first set out to replicate this lateralisation result. Then I will explore whether the 6 focal regions outlined in Belin et al., (Submitted) exist in children, or whether children show the more diffuse activation observed by Bonte et al. (2013). Experiment 4 will thus be only the 2nd to date to chart the functional developmental trajectory of the bilateral TVAs in children and adolescents.

2 Developmental Changes in Emotion Recognition from Full-Light and Point-Light Displays of Body Movement

2.1 Introduction

Emotions play an important role in human development. They are an integral part of how our experiences are interpreted, organised and communicated. As such, the identification and recognition of other people's expressed emotions are important skills in the social and emotional development of an individual.

By the age of five, children are able to identify and name all basic emotions (Felleman et al., 1983); however, emotion recognition is not fully mature until early teenage years (De Sonneville et al., 2002;Herba et al., 2006;Tonks et al., 2007;Gao and Maurer, 2010). Existing research also points towards differences across emotions; while happy expressions seem to be interpreted accurately early on, anger and sadness are not recognized with maximum accuracy until late childhood/beginning of adolescence. Likewise, brain imaging studies indicate that the brain networks involved in recognizing others' emotions are not adult-like until late childhood or early adolescence (Thomas et al., 2001;Batty and Taylor, 2006;Shaw et al., 2008). Both kinds of studies, behavioural and brain imaging, also suggest non-linearity, with steady increase in performance or specialized brain activity during childhood until the beginning of adolescence followed by no or very little change in emotion recognition during the mid-teenage years and then subsequent improvement from late teenage years until adulthood. Although still ill-understood such non-linearity has been conceptually linked to changes in strategies as well as to structural brain development (Shaw et al., 2008). Indeed if both changes in social environments (such as starting secondary-school) and changes in brain maturation of social brain regions occurs in a non-continuous fashion, this might be related to non-linear trends in developmental trajectory of basic social skills.

Most of this research, however, has been conducted when looking at recognition of facial expressions or recognition of speech prosody. There is surprisingly little developmental research with regards to recognising emotion from the body. One could argue that, from an evolutionary point of view, this type of emotion recognition is even more important than those mentioned above. It must be helpful for an individual to be able to predict what somebody else is about to do from their body language, rather than relying on facial expressions (Walk and Homan, 1984;de Gelder et al., 2010). Often, people are seen at a distance, and one can perceive patterns of body motion, posture and gait before cues from facial expression are available. To address the ability of individuals to recognize emotions from body movement and form, several studies have used videos of actors or dancers portraying 'basic' emotions of happiness, sadness, fear, disgust and anger (Meijer, 1989;Boone and Cunningham, 1998;Atkinson et al., 2004;Lagerlof and Djerf, 2009). They all find that adults can identify basic emotions well above chance; although this can be influenced by context (Kret and de Gelder, 2010). Very few studies have looked at developmental changes in this ability. Two studies investigating the recognition of emotional meaning from dance movements have reported that by 8 years of age children have achieved adult performance in a matching (Boone and Cunningham, 1998) or in a forced-choice task (Lagerlof and Djerf, 2009). Using similar stimuli but asking participants to freely name the emotion, Van Meel and colleagues observed that 8-years old performed significantly worse than 12 years old (van Meel et al., 1993). It could be argued, however, that by using dance, the actions are exaggerated and are a more symbolic representation of the emotion in question. How this finding generalizes to everyday-life body movements remains uncertain.

Furthermore, this research raises questions regarding which body cues allow emotions to be perceived: biological motion direction and speed, or static form (McDonnell et al., 2009). This can be addressed by using 'point-light displays' in which the body is represented by a small number of illuminated dots, positioned in such a way as to highlight the motion of the main body parts. When static, the display appears as a meaningless configuration of points; yet, when moving, the display gives a striking impression of a moving body (Johansson, 1973). Point-light displays are sufficient for individuals to identify socially relevant features, such as gender of the actor (Mather and Murdoch, 1994;Hill and Pollick, 2000) or, more importantly in regards to this study, affective state (Dittrich et al., 1996;Pollick et al., 2001;Clarke et al., 2005;Pollick et al., 2005).

This may imply that people are able to perceive emotions from kinematic patterns without having to compute the detailed shape of the human form first.

The remarkable efficiency in extracting complex information from animate motion presented in point-light displays suggests that the detection of biological motion has a simple developmental trajectory (Kuhlmeier et al., 2010). Indeed, the ability to extract form from motion develops very early on, with an advantage for biological motion (Fox and McDaniel, 1982). Infants as young as 12 months can follow the ‘gaze’ of a point-light actor suggesting that they are able to interpret the action depicted (Yoon and Johnson, 2009); By five years of age, children perform as well as adults for identifying a body from moving dots (Pavlova et al., 2001). However, adding noise to the displays reveals that the sensitivity to biological motion continues to develop during adolescence (Freire et al., 2006;Annaz et al., 2010). Therefore, despite children possessing the ability to extract human form from the point-light displays, we might expect that the more complex analysis necessary to discriminate emotion from fine spatio-temporal patterns will continue to develop into late childhood and adolescence. Adults too recognize emotions better from full-light (normal video footage of an actor) than from point-light displays (Dittrich et al., 1996;Atkinson et al., 2004), which indicates a benefit from having the full complexity, yet one might expect children to be further impaired from impoverished information in the point-light display. Indeed, during development, social interactions change and inferences from body cues are made from further distances as a child gets older and one could expect that motion information becomes more important. Also, younger children spend a considerable amount of time interacting with the hands of their parents; and hands seem particularly important to convey emotion (Yoon and Johnson, 2009). Since this information is absent from point-light displays (due to the hands being represented by a single point-light point in the majority of PLD studies, but also see Pollick et al. (2001)) one might also expect children to be further disadvantaged compared to adolescents or adults. Consequently, we were interested in establishing the developmental trajectory of emotion perception from body movements, when only the simplified biological motion is present and additionally study whether the benefit from the full information is similar across ages.

We therefore probed basic emotion recognition from either point-light or full-light displays of short body movements in a sample of 107 primary and secondary school children (4-17 years old). We used angry, fearful, sad and happy expressions as these are the emotions that are most commonly used in emotion research (de Gelder, 2006). Importantly, we created both sets of stimuli from the same capture, thus avoiding confound between display condition and variability in emotion portrayal. In addition, contrary to previous studies, which have constrained stimuli into codified emotion expressions used in dance or mime (Boone and Cunningham, 1998), our actors were given more freedom and instructed to execute movements commonly produced when experiencing basic emotions (e.g. shaking fists in anger, retreating in fear, jumping for joy etc. See also (Atkinson et al., 2004).

In summary, we expect that the ability to recognise emotion from bodies will improve during adolescence, possibly in a non-linear trajectory as it has been proposed for the perception of emotion from faces (De Sonneville et al., 2002;Tonks et al., 2007;Lagerlof and Djerf, 2009;Gao and Maurer, 2010). Furthermore, the use of both full-light and point-light displays allows us to compare emotion recognition when both form and motion cues are present with performance when only biological motion information is present. Based on previous research with adult participants (Dittrich et al., 1996;Atkinson et al., 2004), we expect, on average, poorer recognition when viewing point-light displays compared to full-light displays. Any interaction between age and display condition, however, would indicate that the differential use of socially-relevant visual cues changes during development.

2.2 Materials and Methods

2.2.1 Participants

One hundred and seven primary and secondary school children (aged 4-17 years; *M*=9.89 years; *SD*=3.96, 57 girls) from after-school clubs in the West End of Glasgow (n=50) and the Shetland Islands (n=57) participated in the study. Permission was obtained from the managers of the after-school clubs, as well as consent from the children's parents or guardians a week prior to testing from the respective clubs. These clubs offered a homogeneous sample in terms of socio-economic status (assessed with range of tax-bands, level of education and employment figures from Glasgow Census Report Pupils Scotland 2008, and Shetland in Statistics published by Shetland Islands Council Economic Development Unit). All participants understood that participation was voluntary and gave their assent. As a comparison group, we tested a sample of 14 adult volunteers (aged 21-51 years; *M*=32.9 years; *SD*=11.1, 7 women) from the University of Glasgow.

2.2.2 Stimuli

The stimuli were created using a Vicon motion capture system (Vicon Systems, 2009) to capture the movements of two actors. Twelve Vicon MX Series Cameras were connected to two Vicon Ultranet units for the motion capture process.

Two male actors portrayed four emotions (happiness, sadness, fear, and anger). They were wearing dark tight-fitting suits with 31 reflecting balls attached at the location of major joints. They were instructed to move as they would if they were suddenly feeling anger, happiness, sadness or fear respectively, without exaggerating. The actors were given a few practice trials and then we recorded ten captures per actor per emotion. Thus, a total of 80 captures, each lasting between six and ten seconds, were obtained. Each clip was then examined in post processing and seven clips were selected for each emotion, based on the quality of the motion capture (Typically during motion capture, some information will be lost and in some cases reconstruction of the point-light image will be impossible; we selected the clips where reconstruction was possible for all the capture frames). Those 28 clips were subsequently rendered as point-light displays with 15 joint-centred coordinates using the Vicon Nexus software in combination with MATLAB scripts (MATLAB Version 7.12.0, The MathWorks Inc., Natick, MA, 2010). The clips were then cut down to the three seconds containing the main part of the movement using Adobe Premiere Pro.

The capture clips, which were rendered as point-light displays, were also captured simultaneously as full-light displays using a Basler Digital Video camera. When rendering the point-light displays, the view from which the participant saw the display was set to exactly the same angle and distance from which the full-light video camera was capturing the actors. In other words, both point-light and full-light displays were viewed from exactly the same position (See Figure 2-1 for screen captures of stimuli). In addition, both sets of videos ran at the same rate of 29 frames/second.

Figure 2-1 Full-light and Point-light display stimuli.
Two corresponding frames of a ‘Happy’ clip presented in both Full-light and Point-light display.

The 28 full-light captures which corresponded to the 28 chosen point-light captures were themselves post-processed using Adobe Premiere Pro. Firstly, the clips were edited to the exact same length (3-seconds long) as their point-light counterparts. Secondly, the actors’ faces were blurred out using Gaussian noise so that the participants could not determine any emotion from their facial expressions.

2.2.3 Procedure

Participants sat in front of a 17-inch laptop screen at a distance of about 50cm. The screen resolution was 1440x900 pixels, with video dimensions of 1022x680. E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used to present the stimuli. Point-light and full-light stimuli were presented in separate blocks, with the order counterbalanced across participants.

Each trial started with a fixation cross displayed for 1 second, followed by one of the videos and then a response screen prompting the participants to decide how the person in the video felt, with a choice of 'happy', 'sad', 'scared' or 'angry' respectively. Participants had to indicate their response by pressing a key (c, v, b, or n). Along with the words 'happy', 'sad', 'scared' and 'angry', emoticons were used to aid the younger children's responses. Stickers with those emoticons were also placed on the keyboard. Two different associations between keyboard key and respective emotion were used across participants in a counterbalanced order. The prompt for a response stayed on screen until the participant had responded, at which point the next video would start. Each block comprised 20 trials, randomly selected from the 28 clips produced (five per emotion). Participants completed five practice trials, with experimenter's feedback, before starting the experiment. Thus, our independent variables were lighting condition (Full-light and Point-light) as within-subject, and age as a continuous between-subjects variable. Emotion recognition score was the dependent variable.

2.2.4 Analysis

The averaged percentage of correct responses across emotion for each participant was computed. These scores were then entered into separate regression analyses for children and adults to investigate the effects of lighting conditions and age. Changes with age were also assessed using linear regression models. Finally, we analysed recognition performance separately for each emotion using mixed design ANOVA. Analyses were conducted using PASW Statistics 18, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL) and Matlab (Mathwork Inc).

2.3 Results

2.3.1 Gender and sample differences in recognition accuracy

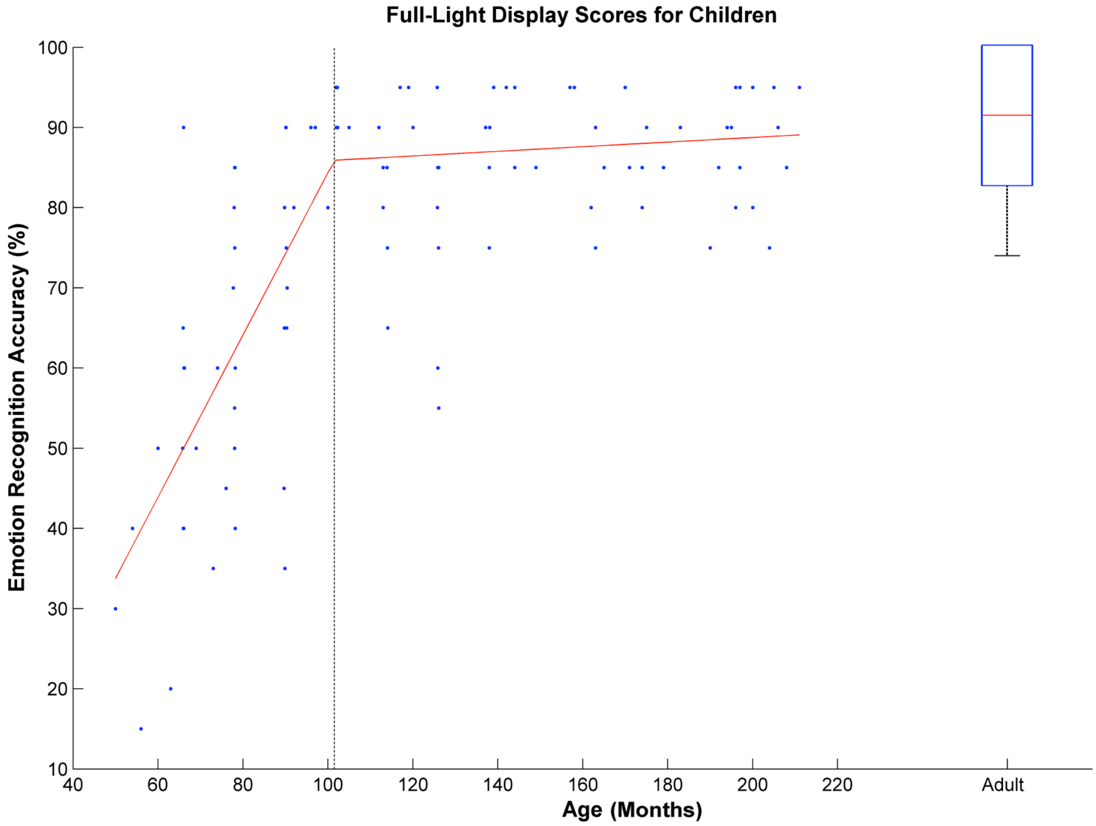
We first checked for any gender effect in the group of children across lighting conditions. We found neither a main effect of gender (F(1,105)=.879, p=.351) nor an interaction with lighting condition (F(1,105)=.065, p=.799). We thus did not consider this factor in subsequent analyses.

We also tested for any differences between the Glasgow and Shetland samples. We found no significant differences between groups (F(1,104)=2.74, p=.101), nor interaction between group and lighting effect (F(1,104)=0.221, p=.64). We thus did not consider this factor in subsequent analyses.

2.3.2 Emotion recognition changes with age and comparison to adults

In adults, as expected, performance under the full-light condition was significantly better than under the point-light condition (F(1,13)=4.98, $p<.001$) with no effect of age (F(1,13)=0.06, $p>.8$ for full-light and F(1,13)=1.17, $p>.29$ for point-light-light). Average performance was 94.3% for full-light and 81.1% for point-light. In comparison, the group of older teenagers (16-17 years old, N=15) achieved 90% correct and 68.7% correct for full-light and point-light conditions respectively. This was still significantly different from adults (F(1,27)=12.67, $p<.001$), with no interaction between the age-groups and lighting condition (F(2,27)=2.32, $p=0.14$).

In the children, using a General Linear Model approach, with recognition scores as the dependent variables, and lighting condition and age as fixed and continuous predictor variables respectively, we found a significant effect of age (F(1,105)=67.32, $p<.001$, partial $\eta^2=.391$) and lighting condition (F(1,105)=22.39, $p<.001$, $\eta^2=.176$). This indicated an increase in performance with age, with children performing significantly better under full-light than point-light (see Figure 2-2). We found no significant interaction between lighting condition and age (F(1,105)=1.38, $p=.24$). This indicates that the slopes representing the increase in performance with age were not different in the full-light and point-light conditions.



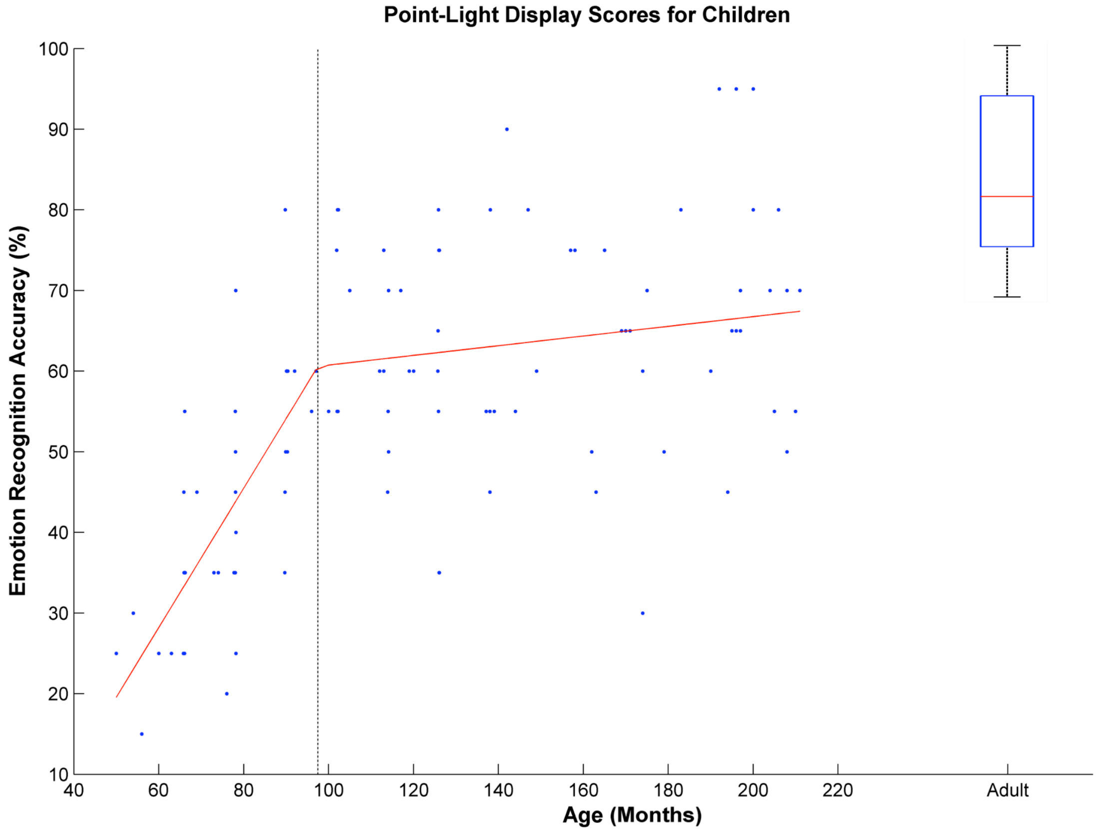


Figure 2-2 Emotion recognition scores from full-light and point-light displays of body movements.
Children's individual scores are presented as blue dots. The corresponding bilinear trend-lines are presented as a red line, with a black dashed line indicating the position of the knot in both cases. Adults' data are presented as a boxplot in both graphs, representing the median and upper and lower quartiles.

On inspection of the data, it is clear that it would be better described by two connected linear segments rather than a simple linear model. We therefore used a least-squares approximation algorithm with free-knot splines to determine the position of the knot (i.e. point of change of slope). The results of this piecewise regression analysis are illustrated in Figure 2-2.

Our data was best explained with two linear segments and a knot at 102 months (RSS=126.96, R^2=.60) for the full-light condition, and a knot at 98 months (RSS=132.06, R^2=.48) for the point-light displays. This model indicates a steep rise in performance (slope ß=1.03 F(1,44)=42.8, $p<10^{-4}$ for full-light condition and ß=0.87 F(1,44)=55.05, $p<10^{-4}$ for point-light condition) until about 8.5 years, followed by a much shallower slope through late childhood and adolescence (Full-Light: ß=0.07, R^2=0.063 F(1,62)=3.98, *p*=.050; Point-Light: ß=0.11, R^2=0.066 F(1,62)=4.24, *p*<.05).

2.3.3 Differences across emotions

We also tested differences in recognition scores for the different emotions using a 4x2 mixed design analysis of variance with emotion and lighting condition as within subject factors, age as a continuous between subjects variable and percentage of emotion recognition as dependent variable. We observed no significant difference across emotions and no 3-way or 2-way interactions. The same analysis of the adult's data yielded no significant differences across emotions and neither interaction. For illustrative purposes, we present the mean recognition score for each emotion under both lighting conditions arbitrarily grouping participants by age group (see Figure 2-3).

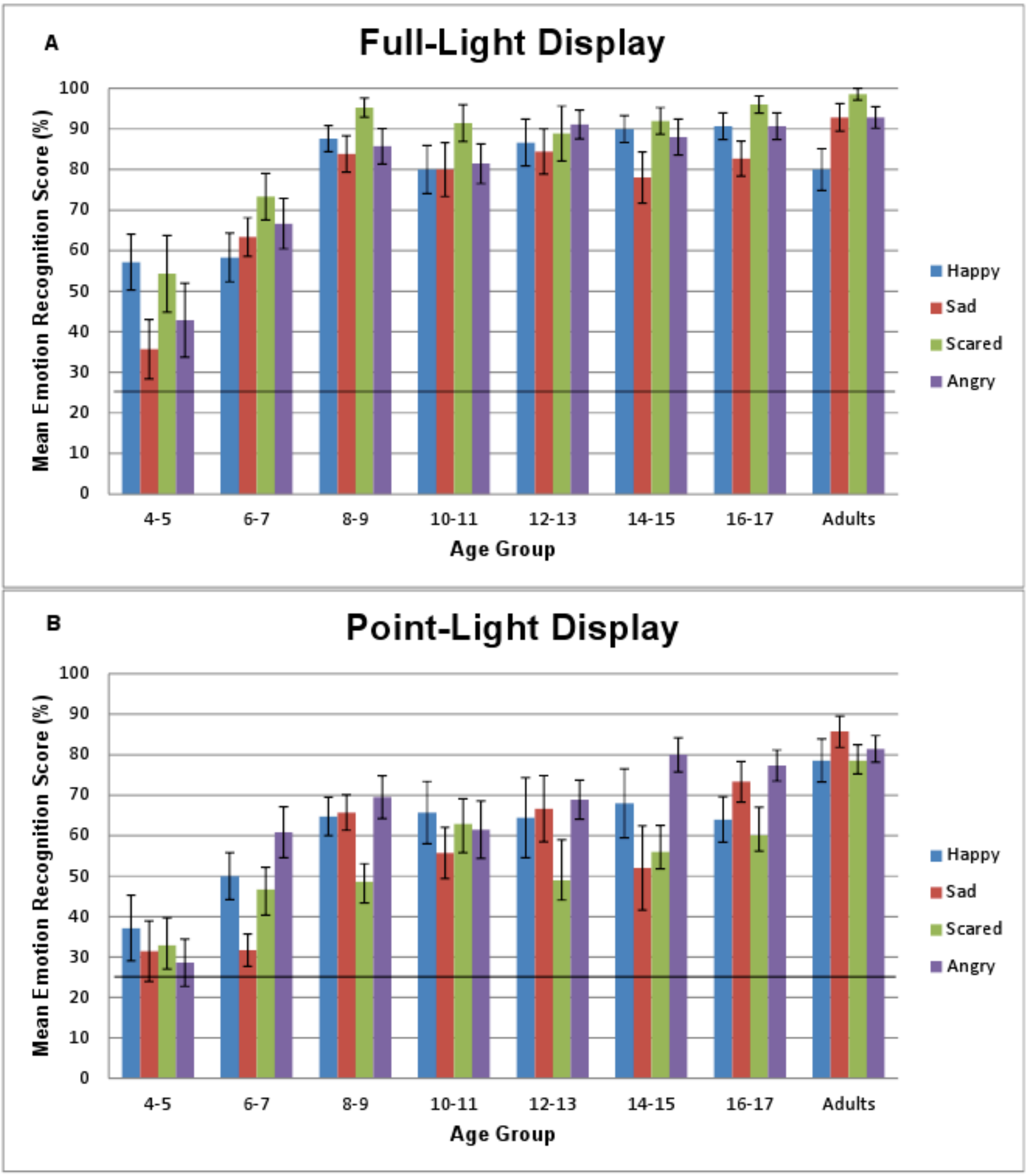


Figure 2-3 Recognition score for each emotion across age.
For display purposes children are grouped by age. Bars representing the mean recognition score (percent correct response) for each group and each emotion are shown under both Full-light Display (A) and Point-light Display (B). Error bars represent SEM. Level of chance marked at 25%. The seven age groups of children comprise 14 (4-5 years old), 24 (6-7 years old), 21 (8-9 years old), 14 (10-11 years old), 9 (12-13 years old), 10 (14-15 years old) and 15 (16-17 years old) subjects respectively.

2.4 Discussion

Using a forced-choice recognition task, we found that the ability to recognize basic emotions from body movements continues to improve during childhood and adolescence. The data could be well approximated with a bilinear developmental trajectory with a steep increase during childhood followed by a much slower rate of improvement after 8.5 years of age. Similar developmental trajectories were observed when the body movements were shown as full-light displays and when the biological motion was shown through point-lights and no differences were observed across the basic emotions we tested.

2.4.1 Changes in Emotion recognition accuracy with age

First our data confirms that children as young as 4 years old perform above chance in decoding affect from body language. Nevertheless, we observed that the refined development of emotion recognition occurs later than what had been described in studies using dance movements as stimuli: both Lagerlof and Djerf and Van Meel et al. suggested that 5-year-old children showed adult-like performance (van Meel et al., 1993;Lagerlof and Djerf, 2009). As dance uses highly codified language to convey emotion, the tasks might have been easier and relied on both true emotion perception and familiarity with such exaggerated movements. Also, the dance stimuli were much longer (between 14 and 96 seconds respectively) than ours, possibly confounded by narrative aspects and thus leading to an easier recognition task. Both of these reasons could account for the fact that we found adult-level performance much later than the aforementioned studies.

Emotion recognition from non-verbal cues has been most often studied using faces or prosody as stimuli. How do our results compare to teenage development for these modalities? While reports have implied that few significant changes in the ability to read facial expressions occur after mid-childhood (Herba et al., 2006;Wade et al., 2006), more and more studies indicate developmental changes well into the teenage years. Using a battery of tests assessing emotion reading from eyes, voice and faces in a cross-sectional design using children aged 9-15, Tonks and colleagues reported that highest performance was achieved at 11 (Tonks et al., 2007). Using a match-to-sample task with emotional faces or words, McGivern and colleagues showed that reaction times improved until about 13 years of age (McGivern et al., 2002). A number of older studies using photographs or dynamic faces also points towards adult's level of performance reached between 9 and 12 years of age (rev. in (Tonks et al., 2007)), with differences across studies being probably due to differences in tasks and material (Gosselin et al., 1995). Testing more subtle sensitivity to emotional cues with morphing techniques indicates a protracted development with adolescents aged 14-18 still displaying lower sensitivity to facial expression cues than adults, at least for negative emotions (Thomas et al., 2007). This suggests that some processes involved in facial expression decoding still develops in late adolescence, which is line with what we observed with our body movements stimuli. This protracted development might be linked to a combination of both a changing external social environment and continuing brain development during that time. Indeed brain regions involved in social and emotion perception, such as the superior temporal cortex, prefrontal cortex (Gogtay et al., 2004) and amygdala (Guyer et al., 2008) undergo developmental structural changes at least until the end of the second decade of life. Functional imaging studies also show different brain activity in adolescents and adults while viewing other people moving with an affective connotation (Thomas et al., 2001;Peelen et al., 2009). Event-related potentials (ERPs) studies have also shown that the signature of emotion processing when viewing faces is still different from adults at the age of 14 (Batty and Taylor, 2006). Thus, it seems that changes are still occurring at the end of the teenage years in the ability to recognize emotions from non-caricatural social stimuli. Further studies are needed to compare emotion recognition across different modalities and how this relates to brain development.

Interestingly, our data show a steep increase in the rate of improvement, followed by a slower improvement throughout late childhood and adolescence. This is in line with other reports of non-continuous development of social cognition abilities. Mann, Diamond and Carey (1979) observed that the ability to recognize unfamiliar voices increased steadily from 6 to 10 years of age, reaching adult levels, but then stalling slightly during the beginning of the teenage years to re-attain adult's level at the age of 14 . A similar change in the rate of development during the same age-range has been reported for recognition of facial identity (Carey et al., 1980;Rhona H, 1980) and for recognizing emotion from faces (McGivern et al., 2002). Using more complex affect processing tasks, such as cartoon matching tasks, Kolb and colleagues reported a slowdown in developmental trend between 8 and 13 years of age (Kolb et al., 1992). The origin of this change in performance improvement rate at the beginning of adolescence is unknown and is worthwhile investigating further. Similar non-linearity in development of cognitive abilities has been described and proposed to be linked to puberty (McGivern et al., 2002). Although the brake in improvement occurs around the same time that one would expect to observe pubertal changes, the fact that it happens at the same age for both sexes in all the studies cited, and that the exact age seems different for body, voice and face processing suggests that it is related to maturational events other than hormonal. The fact that this slowdown in development is observed for different aspects of human processing indicates instead that it might be linked to an individual attainment in social skills. It has been suggested that such a change in the slope of the developmental trajectory at the end of childhood/beginning of adolescence might be linked to a shift from one perceptual or cognitive strategy to a new one. During this transition, when the childhood strategy is abandoned, but when the adult strategy is not fully operational yet, performance doesn’t improve or can even be impaired (Carey et al., 1980). This explanation is in line with the observation that developmental slowdowns have been reported in other cognitive domains such as working memory (Rhona H, 1980) or response inhibition (McGivern et al., 2002). Interestingly, similar trajectories have been observed in fMRI measures of developmental changes of brain activity in relevant regions during emotion processing (supramarginal gyrus, (Shaw et al., 2008)) or during response inhibition (frontal lobe, (Luna et al., 2001)). Electroencephalography studies have also evidenced non-linearity in long-range synchrony changes pointing towards a reorganization of functional brain networks in late adolescence (Uhlhaas and Singer, 2011). Taken together, these data suggests that, perhaps, at the end of childhood individuals start to use new mechanisms to process social stimuli in relation to general changes in executive control abilities, but still do so in an inefficient manner. This would be compatible with the change in slope that we observe in the linear relationship between age and affective body language interpretation.

2.4.2 Differences in emotion recognition accuracy when viewing full-light or point-light displays

Our results corroborate the previous findings that basic emotions are identifiable from body movements, even when initial form information is eliminated by using point-light displays. The observation that emotion recognition is more accurate when viewing full-light displays compared to point-light displays replicates the results of both Dittrich et al's and Atkinson et al's studies (Dittrich et al., 1996;Atkinson et al., 2004). As with these studies, our results were achieved using stimuli in which body movements portrayed in the full-light and point-light displays were identical, as they were created from the same footage. This eliminated the possible confound of differences in movement between these conditions. Furthermore, as we used a computer model in the creation of the point-light displays, we were able to create an 'internal skeleton' of point-lights. That is, rather than point-light displays being achieved by attaching reflective strips to an actor's clothing, our light points could be artificially placed on the exact positions of the actors' bones and joints. This further minimised any unwanted form information, which may have been included in the point-light displays of other studies.

We found that the developmental trajectory of recognition scores was similar for emotion recognition from both kinds of stimuli, with the difference between the two not changing significantly across ages. This advantage of full-light over impoverished point-light stimuli might be due to over reliance on form information, which doesn't change significantly during childhood and adolescence. This suggests that emotion processing from form and motion information develop at the same time.

2.4.3 Differences across emotions

Previous studies have shown that children aged 4-5 are able to name and recognize all basic emotions from facial expressions (Felleman et al., 1983) and pointed towards differences across emotions. Happiness is most often reported as the emotion most easily recognised by young children, while sadness recognition seems to develop later (Meijer, 1989;Wade et al., 2006;Lagerlof and Djerf, 2009), (but see (Boone and Cunningham, 1998)). In our sample of primary and secondary school children, we did not observe any specific advantage for happiness. On average, sadness was less accurately recognised than the three other emotions, but this was not statistically significant. These discrepancies regarding the rate of development of other basic emotions might be related to tasks and stimuli factors, as well as inter-individual characteristics. In our experiment for example, solving the forced-choice task could rely on development of executive functions. As our experiment was a forced-choice between the four emotions, the process of elimination could have been used in order for the participants to deduce which emotion was presented, particularly in the case of an ambiguous clip (the head in our point-light display clips was represented by only one light point, meaning that some motion information, shaking of the head etc., was lost in a few of the sadness and angry clips). In a review paper on the development of deductive reasoning, Jansson states that logical and deductive reasoning is a characteristic of the concrete operational period, that is, between 7 and 11 years old (Jansson, 1974). This could influence how children solved the four alternatives forced-choice task, and perhaps mask differences across emotions.

2.5 Conclusions

This is the first study to our knowledge that explores the development of the ability to recognize emotion from naturalistic body cues presented as full-light and point-light displays during childhood and adolescence. Our data indicates that, like adults, children recognize emotion better from full-light displays than from point-light displays. This could be due to an over reliance on body form information in emotion recognition from an early age, which impacts upon social processing strategies. Furthermore, a change in these strategies could explain the change in rate of improvement: after a steep increase until 8.5 years of age, the ability to recognize body language then improves at a much slower rate through late childhood and adolescence. We believe that this research has important implications for understanding emotional development in children, both from typical and atypical populations.

3 Body-Selective Areas in the Visual Cortex are less active in Children than in Adults

3.1 Introduction

Perception of signals conveyed by other people's faces or bodies is still improving in late childhood (Thomas et al., 2007;Johnston et al., 2011;Ross et al., 2012). Along with an individual attainment in social skills and with endocrinological changes, this protracted development may be linked to a shift from one perceptual or cognitive strategy to another (review in McKone et al. (2012a)). Functional magnetic resonance imaging (fMRI) studies have revealed that face-selective regions in the occipitotemporal cortex show a particularly long developmental course, taking more than a decade to become adult-like (review in Grill-Spector et al. 2008; Scherf et al., 2011; but see McKone et al., 2012). In contrast, very few studies have looked at the development of the functional brain response to body perception. As the processing of body cues becomes particularly important during adolescence when social interaction becomes more complex (perception of dominance or aggression for instance), one might expect the cerebral processes involved in basic body perception to also change during this period as is the case for face processing.

Brain areas identified as being specialized for the recognition and interpretation of human form and motion include the extra-striate body area (EBA) located bilaterally in the lateral occipitotemporal cortex, the fusiform body area (FBA), areas in the inferior parietal lobe (IPL) and posterior superior temporal sulcus (pSTS) (Downing et al., 2001;Peelen and Downing, 2005;de Gelder, 2006;Grosbras and Paus, 2006;Weiner and Grill-Spector, 2011;Grosbras et al., 2012a). Previous fMRI studies have reported activity within those regions when children as young as 7 years old viewed static (EBA and FBA: Peelen et al., 2009; EBA: Pelphrey et al., 2009) or dynamic (pSTS and FBA: Carter and Pelphrey, 2006; Anderson et al., 2013) body stimuli. How this activity differs from that observed in adults is still unclear however, as this has only been tested using samples encompassing a large age-span including pre and post-pubertal individuals (Peelen et al., 2009) or using an index of activation that does not compare directly the height and spatial extent of the activation (Pelphrey et al., 2009). There is also evidence across modalities, of an initial right lateralisation in face (Golarai et al., 2010), voice (Bonte et al., 2013) and body (Pelphrey et al., 2009) selective areas, which decreases with age.

Hence, our first goal was to further investigate the recruitment of EBA, pSTS and FBA during body movement perception in pre-pubertal primary-school children as compared to adults in terms of its amplitude and recruited spatial territory. We also wanted to replicate the decreasing right lateralisation effects observed by Pelphrey et al., (2009) (i.e. larger rEBA than lEBA in the children, and vice-versa for the adults). Taking into account the pubertal stage of participants (PDS; Petersen et al., 1988), allowed us to focus on a more homogenous sample than previous studies. Furthermore, using a passive task allowed us to focus on the body-selective areas without any potential interference or modulation from motor or decision making regions (Witt and Stevens, 2013).

Secondly, global level inferences obtained using current univariate approaches may not tell the full developmental story. They negate interactions between voxels, which can only be observed if one looks at patterns of neural representation. For example, Morcom and Friston (2012) have shown that while the level of prefrontal activity during a memory task did not change with age, the spatial pattern of neural activity associated with successful encoding was more distributed in older adults, supporting the notion that ageing alters the spatial deployment of neuronal activity within specialized functional regions. Similarly, Golarai et al. (2010) showed that a sparse spatial representation best explained their face perception data, and that this spatial pattern did not change over age.

Here we applied a recently developed analytic method that allows multivariate Bayesian (MVB) model comparison across different patterns of activity both within, and across, regions (Friston et al., 2008). Using this approach, we were able to explore how body information is represented in the relevant brain areas. Specifically, using a similar approach to Morcom and Friston (2012), we compared a distributed and a clustered coding hypothesis. Distributed coding would indicate that most voxels within an ROI have little contribution, with a few making a large contribution. Clustered coding on the other hand would indicate that the voxels making the most contribution are clustered together.

We then could compare these differences across adults and children to explore whether the spatial pattern of activity within the body-selective regions changes with age. Or, in other words, how the brain neurally represents perceived body movements over age.

In summary we hypothesise, in line with face processing, that the body-selective areas will be right lateralised in children, but this effect will decrease over age. We further hypothesise, contrary to previous work in body recognition, that the neural representation pattern of body movements, along with the height and spatial extent of activation in the body-selective brain areas, will not be 'adult-like' in pre-pubescent children.

3.2 Materials and Methods

3.2.1 Participants

Twenty-Seven primary school children were recruited from schools and afterschool clubs in the West End of Glasgow (Scotland). Three children were excluded because of excessive head motion in the scanner. Therefore data from 24 children (aged 6-11 years: M = 9.08 years; SD = 1.59, 15 females) were included in the analyses. They were all at Tanner stage 1, that is, pre-pubertal, as assessed using the Pubertal Developmental Scale (PDS; Petersen et al., 1988), a sex-specific eight-item self-report measure of physical development (e.g. growth in stature, breast development, pubic hair etc.)) filled in by parents. Permission was obtained from the heads of the schools and the managers of the afterschool clubs in order to promote the study. Written consent was also obtained from the children's parents or guardians before the testing began. All participants understood that participation was voluntary and gave their assent. The study was in line with the Declaration of Helsinki and was approved by the local Ethics Committee. As a comparison group, a sample of 26 adult volunteers (aged 18-27 years: M = 21.28 years; SD = 2.11, 15 females) from the University of Glasgow also took part.

3.2.2 Stimuli

We used 45 short video-clips from a set created and validated by Kret et al. (2011). Each clip depicted one actor, dressed in black against a green background, moving in a socially meaningful manner (e.g. raising fist as if angry, moving shoulders as if disappointed). Six actors were males and 9 females, with each actor recorded 3 times. The videos were recorded using a digital video camera and were edited to two-seconds (50 frames) long clips. The faces in the body videos were masked with Gaussian filters so that only information of the body was perceived (for full details see Kret et al., 2011).

In addition, various clips of non-human moving objects (e.g. windscreen wipers, windmills, metronomes etc.) were taken from the internet. They were cropped to the same size (960 x 540 pixels, 50 frames, 25 fps) as the human videos using Adobe Premiere Pro and a green border was added.

Stimuli were organized into blocks of five clips (10 seconds). To assess the amount of low-level visual motion in each clip, we computed the average change in luminance between consecutive frames. To do so, for each clip we first estimated change in luminance in the background (corresponding to camera noise level) and for each pairs of frames extracted the number of pixels where the change in intensity was higher than noise. For each clip we computed the average number of pixels with change across the frames. Then we computed the cumulative motion for the five clips in each block. Overall the blocks of non-human clips had slightly more motion than the blocks of body movements clips, although this did not reach statistical significance (t (16)=1.89, CI-[-0.0024:0.0424], p=.076).

3.2.3 Procedure

Data Acquisition: We measured brain activity using a 3T fMRI scanner (Tim Trio, Siemens, Erlangen, Germany) equipped with a 32-channels head coil, using standard EPI sequence for functional scans (TR/TE: 2600ms / 40ms; slice thickness = 3 mm; in plane resolution = 3 x 3 mm). In addition, we acquired a high-resolution T1-weighted structural scan (1 mm3 3D MPRAGE sequence) for anatomical localization.

Parents/guardians were allowed to sit with their children in the scanning room if they or their child wished (This was the case for 3 subjects). Head motion was restricted thanks to appropriate cushioning. Children were familiarized with the environment and we acquired a 3 minutes-dummy scan while they watched a cartoon. This allowed us to give them feedback about their head motion and train them to stay still.

Main Experiment: A MATLAB script using the Psychophysics Toolbox Extensions (Brainard, 1997) was used to present the stimuli. Stimuli were organized into nine blocks of non-human stimuli (10 seconds; 5 clips), nine blocks of human stimuli and six 10-seconds-long blocks of blank screen as a baseline each presented twice in m-sequence (a method of pseudo-randomising the stimuli to avoid correlation effects between blocks of stimuli, see Buracas and Boynton (2002)). An experimental run lasted 480 seconds. Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head-coil. Subjects were instructed to fixate in the centre of the screen and where monitored during the scan to make sure they kept their eyes open. They were then probed verbally post scan to ensure they paid due attention to the stimuli. Subjects also participated in another independent 8-min functional scan (the TVA localiser used in **Chapter** 5) during the same scanning session, before completing the structural scans.

3.2.3.1 Pre-Processing

Pre-processing and statistical analysis of MRI data was performed using SPM 8 (Welcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm). Functional data were corrected for motion by using a two-pass procedure to register the images to the mean of the images after the first realignment. They were then re-sliced with a 4th Degree B-Spline interpolation. Movement correction was allowed up to 2mm translation or 2 degrees rotation; the three participants who had larger head motion were excluded from the analysis. Functional data were co-registered with the individual 3D T1-weighted scans by identifying AC-PC landmarks manually. These anatomical scans were segmented for different tissue types and transformed into MNI-space using non-linear registration. The parameters from this transformation were subsequently applied to the co-registered functional data. For all analyses, the data were spatially smoothed with a Gaussian kernel (8mm FWHM). High-pass temporal filtering was applied at a cut off of 128 seconds to remove slow signal drifts.

By normalising the data from our adults and children into the same stereotactic template, we were able to directly compare the strength and extent of activation across age groups. Several studies examining the feasibility of this approach have found no significant differences in brain foci locations when the brains of children as young as 6 were transformed to an adult template (Burgund et al., 2002;Kang et al., 2003). These findings gave us confidence that there is no confound of brain size in our results.

3.2.3.2 Whole Brain Analysis

A general linear model was created with one predictor for each condition of interest (Body and Non-Body). Head motion parameters were also included as regressors of non-interest. The model was estimated for each participant and individual contrasts (Body vs Non-Body) were taken to second-level random effect analyses to create group-averages separately for children and adults and then to compare children and adults. For the main group analyses, resulting statistical maps are presented at a threshold of $p<0.001$ uncorrected with a cluster extent threshold of 10 voxels. For group comparisons contrasts are masked by the uncorrected $p<0.05$ one-way contrasts maps before being reported at $p<0.001$ uncorrected. Anatomical names for various functional activations were determined using the Harvard-Oxford cortical and sub-cortical structural atlases in FSLview (Jenkinson et al., 2012).

3.2.3.3 ROI Definition and Analysis

We defined six regions of interest (ROIs): bilateral EBA, bilateral FBA and bilateral pSTS. These were derived by taking the set of contiguous voxels within a sphere of radius 8 mm surrounding the voxel in each anatomical region that showed the highest probability of activation in a meta-analysis of 20 studies examining contrasts between moving body and controls in adults (detailed in Grosbras et al., 2012).

To test for differences in activity across ROIs and age group for each participant we extracted the individual peak t values as well as the size (in mm3) of the activated clusters at three statistical thresholds ($p<0.05$ FWE corrected (whole brain contrast) $p<0.001$ uncorrected, $p<0.01$ uncorrected). These parameters summary statistics were then entered into 2x6 mixed design ANOVAs, with Age-Group as between subject factor and ROIs as within subject factor.

3.2.3.4 Multivariate Bayesian Analysis

We investigated the coding activity patterns within the ROIs with an MVB decoding approach (see Friston et al., 2008; Morcom and Friston, 2012). Decoding models that operate on any voxel sets are ill-posed as there are an infinite number of equally likely solutions. MVB gets around this by using constraints (priors) to estimate the voxel weights under different models (Distributed encoding can be described as where individual patterns of activity are expected to contribute sparsely to the decoding; so most voxels make a small contribution, while a few make a large contribution, and a macroscopic region may contain neurons that have different functional properties. Clustered encoding, on the other hand, indicates that the pattern of activity is clustered with smooth local support (defined by a Gaussian with FWHM = $4mm^3$); so the voxels making the most contribution are clustered together).

Then the set of voxel patterns chosen constitutes a hypothesis about the nature of the mapping between the brain activity (in this case voxel-wise activity in each of our ROIs) and the target variable (our Body>Non-Body contrast from the whole-brain analysis). MVB can therefore decode the neuronal activity pattern of the target variable according to the spatial priors afforded by each model. The evidence for each model can then be treated as a summary statistic and compared to other models using analysis of variance (ANOVA) (Friston et al., 2008). The dependent measure used is the difference in log-evidence of free energy for the chosen model and a null model (one in which there are no patterns and no mapping).

This allowed us to evaluate competing coding hypotheses (distributed vs. clustered as in Morcom and Friston, 2012 or contiguous vs. non-contiguous as in Golarai et al., 2010) within each ROI of both groups. Furthermore, it allowed us to look at the difference between different coding hypotheses across groups.

3.2.4 Control for Potential Artefacts

3.2.4.1 Head Motion

Three subjects who showed head motion larger than 2 mm in any translation or 2 degrees in any rotation direction were excluded from the analysis. For the remaining participants, rigid body motion parameters were estimated and used to realign each volume to the averaged image. Those motion parameters were included in the general linear model as parameters of non-interest in order to exclude any potential effect on the activation of interest. In addition, independent t-tests did not reveal any significant differences in the mean displacement across six axis between adults and children (X: t(48)=-1.05, p=.298; Y: t(48)=1.92, p=.061; Z: t(48)=-1.35, p=.185; Pitch: t(48)=.334, p=.739; Roll: t(48)=.412, p=.682; Yaw: t(48)=-.597, p=.553) . We are therefore confident that any potential group differences in fMRI activation are not a by-product of a small group difference in head motion.

3.2.4.2 Variance in BOLD signal and model fit

Further, variance in BOLD signal could also explain any potential difference we observe between children and adults. To account for this confound we compared the standard deviation of the BOLD signal during blank-screen blocks in our six ROIs across age-groups. We found no significant difference between adults and children in any ROI (rEBA: t(48)=1.12, p=.270; lEBA: t(48)=1.89, p=.065; rFBA: t(48)=.70, p=.489; lFBA: t(48)=1.26, p=.215; rpSTS: t(48)=.688, p=.495; lpSTS: t(48)=1.415, p=.163).

In addition, we looked at the residual sum of squares of the full model fit in each of the six ROIs across age. This gave us an estimate of noise in our model for each participant. Again, we found no significant difference between adults and children (rEBA: t(28.21)=1.95, p=.061; lEBA: t(25.49)=1.98, p=.059; rFBA: t(48)=1.50, p=.140; lFBA: t(48)=-.749, p=.457; rpSTS: t(26.52)=.1.35, p=.187; lpSTS: t(28.66)=1.618, p=.117).

These controls give us confidence that any potential differences in fMRI signal change observed between adults and children are due to functional processing of the stimuli, and not simply due to differences in motion, variance in signal, or within subject error in model fit.

3.3 Results

3.3.1 Whole brain contrasts

3.3.1.1 Within groups

In adults, viewing dynamic bodies compared to viewing dynamic objects activated the bilateral fusiform gyri (including FBA), bilateral occipitotemporal cortices (including EBA), bilateral posterior superior temporal sulci (pSTS), right precentral, right inferior frontal gyrus, right superior parietal lobule, and bilateral amygdalae. In children, bilateral activity in the occipitotemporal regions and, only in the right hemisphere, fusiform gyrus, pSTS, amygdala and precentral gyrus reached significance level. (See Figure 3-1 and Table 3-1).

Table 3-1 - Regions activated in a whole-brain group-average random-effects analysis contrasting Bodies>Non-Bodies.
(p<0.001 uncorrected, cluster extent threshold of 10 voxels). Coordinates are in MNI space.

Adults						Children					
Region	x	y	z	t	mm^3		x	y	z	t	mm^3
Right Fusiform Gyrus	45	-46	-17	13.00	1890		42	-49	-17	5.51	918
Left Fusiform Gyrus	-42	-40	-20	5.54	567						
Right Occipitotemporal	45	-76	-8	11.32	1566		48	-73	4	10.16	1890
Left Occipitotemporal	-45	-76	7	7.59	1728		-54	-67	16	7.00	1512
Right P Superior Temproal Sulcus	57	-43	10	10.10	2187		60	-40	13	7.28	2187
Left P Superior Temporal Sulcus	-63	-49	19	7.42	1458		-51	-55	13	4.00	837
Right Superior Parietal Lobe	30	-49	67	4.55	432						
Right Inferior Frontal Gyrus	45	17	28	7.34	2025		36	17	25	4.33	621
Right Precentral Gyrus	48	5	46	8.16	2025		51	2	49	6.18	1323
Right Amygdala	18	-7	-14	7.14	1620		21	-7	-11	6.07	1377
Left Amygdala	-18	-7	-14	6.28	1215						
Right Temporal Pole							36	17	-32	4.43	648
Right Precuneus							3	-58	31	5.08	2295
Left Supramarginal Gyrus							-54	-43	31	4.17	972

3.3.1.2 Between groups

Adults showed more activation than children in the bilateral occipitotemporal areas, right pSTS, right fusiform gyrus, bilateral amygdalae, right thalamus and the right inferior frontal gyrus.

No region showed higher activity in children than in adults. (See Figure 3-1 and Table 3-2).

Table 3-2 - Regions activated by whole-brain group-average random-effects analyses contrasting Adults and Children for Bodies>Non-Bodies. (p<0.001 uncorrected). Coordinates are in MNI space.

	x	*y*	*z*	*t*	*mm*^{3}
Adults>Children					
Right Fusiform Gyrus	45	-52	-17	4.33	1215
Right Occipitotemporal	45	-76	-11	3.91	918
Right P Superior Temporal Sulcus	54	-46	7	3.79	351
Left P Superior Temporal Sulcus	-63	-49	19	3.63	81
Right Anterior Inferior Frontal Gyrus	51	32	10	3.76	81
Right Inferior Frontal Gyrus	54	17	25	3.42	162
Children>Adults					
No regions active at given threshold					

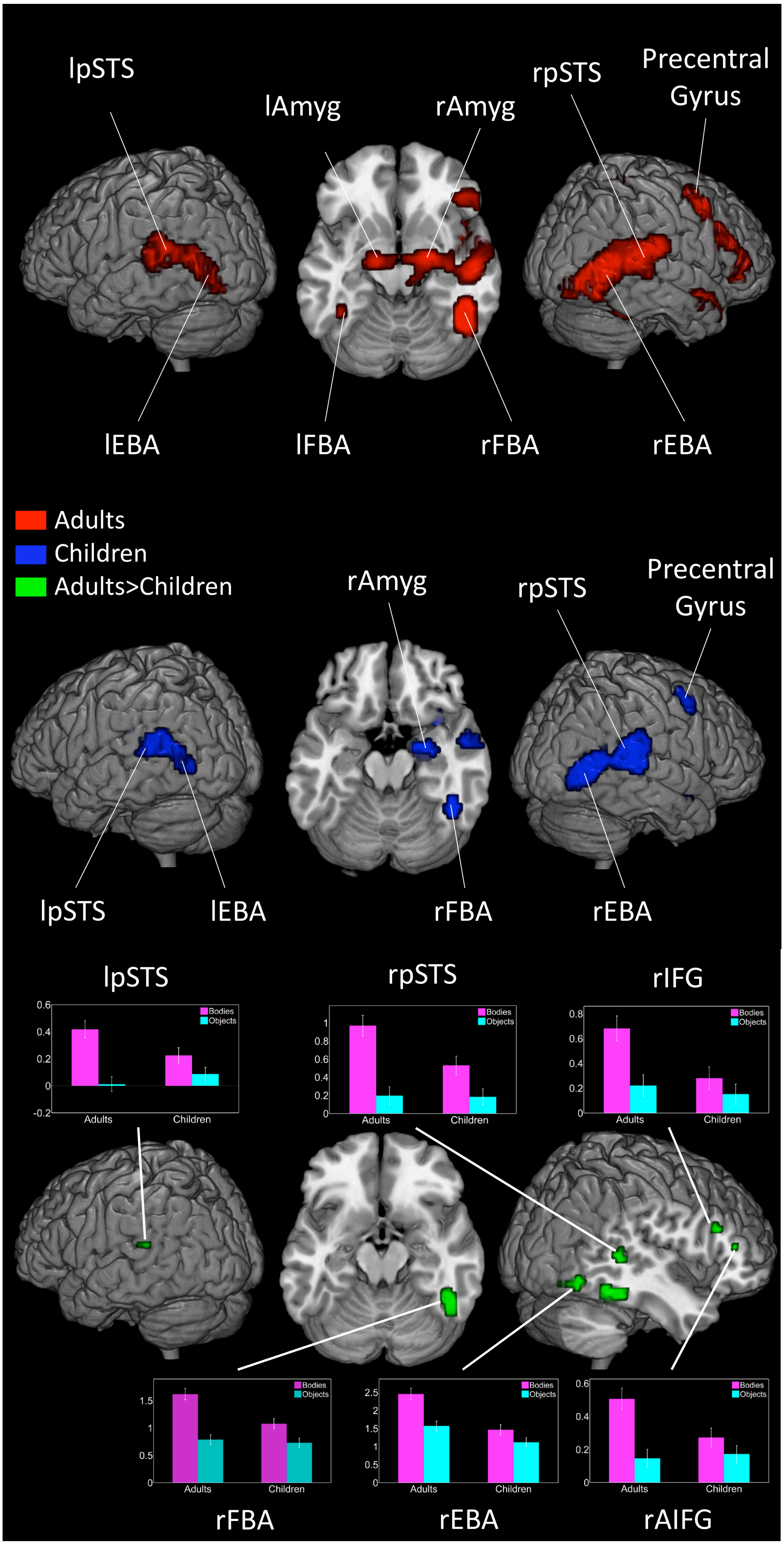


Figure 3-1 - Brain activity when viewing Bodies>Non-Bodies stimuli in adults and children. Graph represents effect size of subject's activity in each area when viewing bodies and objects (threshold at p<0.001 and 10 voxels extent). Error bars represent SEM.

3.3.2 Region of interest analysis

3.3.2.1 Localization

The average MNI coordinates of the highest positive t-value in each of the ROIs were similar in both children and adults, confirming that these regions occupy the same cortical space (See Table 3-3).

Table 3-3 – Average MNI coordinate of peak t-value in all ROIs

ROI		x(SD)	y(SD)	z(SD)	n
rEBA	Children	49(3)	-72(3)	-1(3)	24
	Adults	50(3)	-72(3)	-1(4)	26
lEBA	Children	-49(3)	-77(3)	-1(3)	21
	Adults	-48(3)	-75(3)	-1(1)	26
rFBA	Children	42(2)	-42(4)	-19(4)	24
	Adults	43(2)	-44(3)	-20(3)	26
lFBA	Children	-40(1)	-45(4)	-16(4)	21
	Adults	-41(2)	-44(3)	-19(3)	26
rpSTS	Children	55(4)	-57(5)	11(3)	24
	Adults	56(4)	-56(5)	11(3)	26
lpSTS	Children	-46(4)	-57(5)	14(3)	22
	Adults	-46(4)	-56(5)	14(3)	26

3.3.2.2 Size

For the three statistical thresholds that we considered (p<0.05 corrected for multiple comparison, p<0.001 uncorrected and p<0.01 uncorrected), the number of participants showing at least one voxel above threshold was higher in adults than in children in each of the six regions of interest (See Table 3-4).

Table 3-4 - No. of subjects showing activity in the six ROIs at each statistical threshold. Mean and standard deviation of activity extent in mm3 is also presented.

	rEBA	lEBA	rFBA	lFBA	rpSTS	lpSTS
***p*<0.01**						
Children						
No.	21	14	17	11	17	19
Mean (SD)	1044.9(712.8)	494.1(378)	475.2(540)	291.6(280.8)	1439.1(823.5)	747.9(726.3)
Adults						
No.	26	22	25	18	25	25
Mean (SD)	1539(523.8)	939.6(569.7)	912.6(548)	380.7(353.7)	1458(634.5)	688.5(586)
***p*<0.001**						
Children						
No.	18	12	12	6	17	13
Mean (SD)	918(672.3)	342.9(315.9)	359.1(502.2)	248.4(205.2)	1139.4(820.8)	683(650.7)
Adults						
No.	26	21	24	12	24	23
Mean (SD)	1304.1(612.9)	815.4(548.1)	696.6(494.1)	345.6(251.1)	1247.4(666.9)	459(553.5)
***p*<0.05 corr.**						
Children						
No.	13	4	3	1	8	2
Mean (SD)	432(558.9)	94.5(135)	270(421.2)	81	718.2(577.8)	54(37.8)
Adults						
No.	22	16	14	2	21	8
Mean (SD)	899.1(594)	548.1(442.8)	286.2(210.6)	162(37.8)	731.7(637.2)	286.2(281)

In those participants, the average extent of activity was significantly higher in adults than in children at all three thresholds (Main effect of Age Group: F(1,233)=9.78, p=.002; F(1,201)=6.0, p=.015 and F(1,107)=6.12, p=.015, for threshold p<0.01 uncorrected, p<0.001 uncorrected and p<0.05 corrected respectively). The main effect of ROIs was highly significant at the three thresholds (F(5,233)=18.99, p<.0001; F(5,201)=12.80, p<.0001 and F(5,107)=4.36, p<.0001), and interactions were observed between Age Group and ROIs in all but the most stringent threshold (F(1,233)=14.99, p=.0001; F(1,201)=7.85, p=.006 and F(1,107)=.03, p=.864). These interactions were driven by children showing, relative to other areas, significantly less extent of activation than the adults in the rFBA (t(48)=-3.58, p<.001) and lEBA (t(31)=-2.73, p<.01) for threshold p<0.01 uncorrected and p<0.001 uncorrected respectively.

3.3.2.3 Peak-t value

The peak t-values for adults and children in all six ROIs are presented in Figure 3-2.

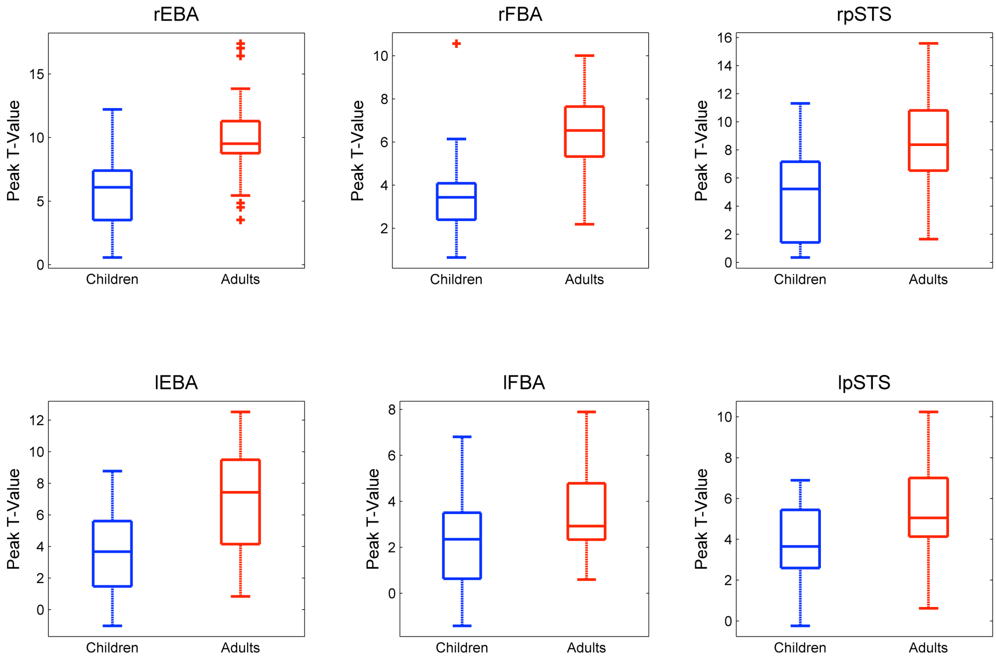


Figure 3-2 - Peak t-values in each ROI for each participant for the Bodies>Non-Bodies contrast.
Children and adults are presented in Blue and Red respectively. It should be noted that the y-axis scales are not homogeneous across ROIs.

An Age Group x ROI ANOVA revealed a main effect of ROI (F(5,240)=29.05, *p*<.0001), a main effect of Age Group (F(1,48)=41.16, *p*<.0001) and an interaction between ROI and Age Group (F(5,240)=3.38, *p*=.006).

Follow-up (post hoc) analyses confirmed that a lack of a significant difference in the lFBA between adults and children was driving this interaction, while all other regions showed significantly higher activity in adults than in children (rEBA: (t(48)=-4.77, p<.001); lEBA: (t(48)=-4.22, p<.001); rFBA: (t(48)=-4.91, p<.001); lFBA: (t(48)=-2.41, p=.095); rpSTS: (t(48)=-3.91, p<.001); lpSTS: (t(48)=-2.97, p<.001)

In addition we verified that this effect was not due to group differences in the processing of moving stimuli: none of the ROIs displayed an age-difference for the contrast Non-Bodies vs. Blank Screen (p<0.001 uncorrected). Furthermore, we found no gender differences in any of our ROIs for either age group.

3.3.2.4 Hemispheric differences

Using the peak-t data, a 3x2x2 mixed design ANOVA with within subject factors ROI (EBA/FBA/pSTS) and Hemisphere (Right/Left), and between subjects factor Age Group (Adults/Children) yielded a main effect of Hemisphere (F(1,48)=83.35, *p*<.0001), reflecting greater activity in the right hemisphere than the left. An interaction between Hemisphere and Age-Group (F(1,48)=7.18, *p*=.01) was driven by a greater increase in activity in right-hemisphere ROIs over age compared with the left. We found no interaction between ROI and hemisphere (F(2,96)=1.17, *p*=.314), and no 3-way interaction (F(2,96)=.74, *p*=.480).

A further 3x2x2 mixed design ANOVA using a count of the contiguous voxels surrounding each peak yielded similar results. A main effect of Hemisphere (F(1,48)=92.36, *p*<.0001) reflected a larger extent of activation in the right hemisphere ROIs. We also observed an interaction between Hemisphere and Age-Group (F(1,48)=7.98, *p*<.01) and Hemisphere and ROI (F(2,48)=11.32, *p*<.001). Post-hoc analyses found this to be caused by a significant increase in activity extent over age in the 3 right lateralised ROIs, but no significant difference in extent activation between children and adults in any of the left lateralised ROIs (rEBA: (t(48)=-2.76, p<.01); rFBA: (t(48)=-2.95, p<.005); rpSTS: (t(48)=-2.66, p<.05); lEBA: (t(48)=-1.61, p=.115); lFBA: (t(48)=-1.68, p=.099); lpSTS: (t(48)=.239, p=.812).

3.3.3 Multivariate Bayesian analysis

As evidence is only relevant within groups (see Section 3.1 Introduction and (Morcom and Friston, 2012)), the main effect of age is meaningless in the following analysis, while the interaction terms allow us to test for differences of models across age groups.

Figure 3-3 shows the group-averaged log-evidence for the competing spatial decoding models in the six ROIs for the children and adults. We performed an ANOVA with within-subject factors spatial prior (Distributed/Clustered) and ROI (rEBA/lEBA/rFBA/lFBA/rpSTS/lpSTS) and between-subject factor Age Group (Children/Adults). We observed a main effect of model (F(1,48)=335.1, p<.0001), reflecting higher log-evidence for a distributed representation. Although still significant, the difference between distributed and clustered models was smaller in the lFBA relative to other areas, which yielded a significant interaction between model and ROI (F(5,240)=12.2, p<.0001). We observed no three-way interaction (F(5,240)=.861, p=.508), indicating that although the difference in log-evidence between distributed and clustered models differs across ROIs, age produces a purely additive effect to these differences.

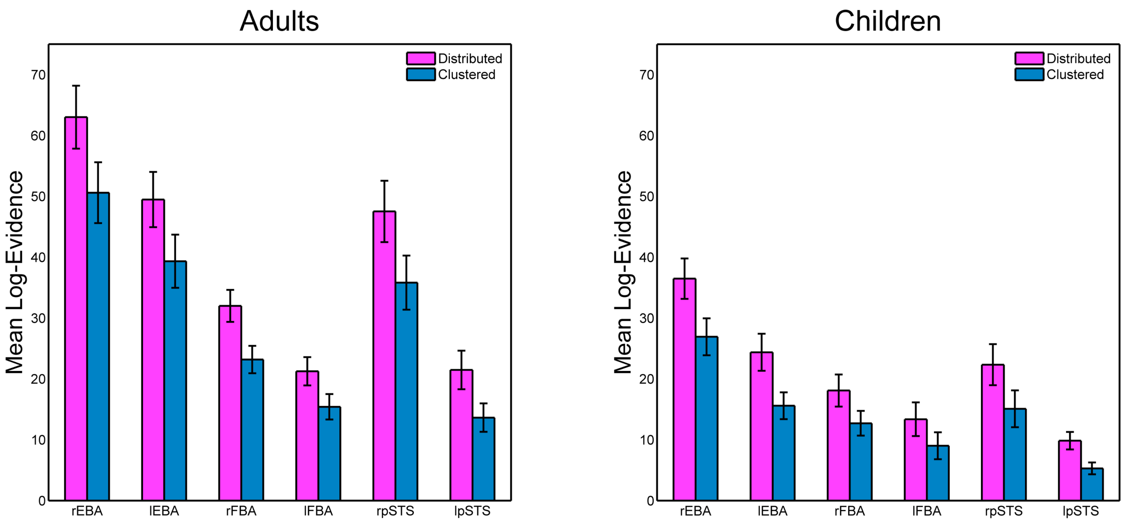


Figure 3-3 - Mean log-evidence for distributed and clustered models of spatial encoding in the six ROIs in adults and children. Error bars represent SEM.

3.4 Discussion

We investigated the development of the body-selective areas by comparing brain activity in primary-school children (age 6-11) and adults during passive viewing of body movements compared to object movements. In both groups we observed activity in similar regions to those reported in previous studies using static (Downing et al., 2001;Astafiev et al., 2004;Peelen and Downing, 2005;Taylor et al., 2007) or dynamic (Carter and Pelphrey, 2006;Blake and Shiffrar, 2007;Kret et al., 2011) body stimuli. We observed a right lateralisation of the body-selective regions, and contrary to our hypothesis, extent of activation became more right lateralised in the adults. Finally, children showed, on average, less activation than adults in terms of strength and extent, but we found no difference in the pattern of spatial encoding between children and adults, with both showing more evidence for a distributed model of neural representation.

3.4.1 Similar ‘Body Circuits’ recruited in children and adults

A number of studies have confirmed that viewing static or dynamic bodies engages specific regions in the occipito-temporal cortex. Here we observe that these regions are also active in children. With regard to the EBA and the FBA, this confirms previous reports that had used static stimuli (Pelphrey et al., 2009; Peelen et al., 2009). The EBA coordinates are in line with previous reports in adults (Downing et al., 2001; Pelphrey et al., 2009) and children (Peelen et al., 2009; Pelphrey et al., 2009). Our FBA coordinates were also similar to those previously reported by Peelen et al. (2009). Like previous studies we also observed higher activity in the right compared to the left hemisphere in both children and adults. This indicates that the advantage of the right hemisphere in processing socially relevant information is present early on in development. Furthermore, while most previous reports of FBA are limited to the right hemisphere, we also observed activity in the left hemisphere. The age effect, however, was only found to be significant in the right hemisphere ROI. It should be noted, however, that the findings of Willems et al. (2010) suggest that lateralisation of EBA depends on participant handedness. As such, without this data we must be careful when drawing conclusions regarding lateralisation from these results.

In addition, we observed activity in the pSTS in both adults and children. As previously stated, the pSTS is implicated in the processing of body related motion (Blake and Shiffar, 2007; Carter and Pelphrey, 2006). Saygin (2007) showed that when pSTS activity is disrupted, either permanently following a stroke, or temporarily following repetitive trans-cranial magnetic stimulation (rTMS), a person’s ability to perceive bodily motion is significantly impaired. In contrast to EBA and FBA activation (which increases towards bodies compared with objects regardless of whether or not the stimuli are moving), activity in the pSTS is thought to be related only to bodies in motion (Saxe et al., 2004;Pitcher et al., 2011). Furthermore, Candidi et al. (2011) demonstrated that event-related rTMS over pSTS increased the accuracy of a subject in detecting changes of threatening human postures. These results support the notion that along with being involved in the processing of bodily motion, the pSTS is crucial to the detection of socially relevant information concerning others’ actions. Interestingly pSTS activity can be identified with fMRI in children and adolescents during more complex social tasks, such as mentalising, but this activity is still reduced compared to adults (Blakemore et al., 2007).

We also observed activity in both groups in the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL). These regions have been reported during both action observation and action execution (Grèzes and Decety, 2001;Hodzic et al., 2009), which led to suggestions that they contain mirror neurons and represent other people's actions in relation to one's own actions (Rizzolatti and Craighero, 2004). It is interesting to observe that this network is already engaged with children when passively viewing body movement (Pfeifer et al., 2007).

Finally, both adults and children showed activity in the amygdala, bilaterally for the adults, while only the right hemisphere cluster reached significance in the children. Amygdala activity is commonly reported in fMRI studies of socially relevant facial expression perception (Grosbras and Paus, 2006;Fusar-Poli et al., 2009). As previously mentioned, it has also been implicated in the processing of body movements and posture in the human (Bonda et al., 1996;Hadjikhani and de Gelder, 2003;de Gelder, 2006;Grosbras and Paus, 2006) and non-human (Brothers et al., 1990) brain. While other developmental studies have reported amygdala activity in children during face perception (Killgore and Yurgelun-Todd, 2007;Passarotti et al., 2009), biological motion in point-light displays (Anderson et al., 2013) and inferring mental state from pictures of eyes and stories (Rice et al., 2014), this is the first evidence of children amygdala involvement in processing of full-light dynamic body stimuli.

3.4.2 Differences in strength and extent of activity in ROIs

Our finding of a significant difference in both peak and extent activity in EBA, FBA and pSTS between children and adults contradicts previous work. Pelphrey et al. (2009) have suggested that the EBA is already as large in children as in adults by the age of 7 years; albeit with a different asymmetry pattern (right dominance in the children but left dominance in adults). This was observed using a very lenient threshold ($p<0.01$ uncorrected), however, yielding regional activity probably beyond the boundaries of the EBA (with clusters of 38,000 mm^3). Here we use a different measure in taking the contiguous voxels surrounding the peak in each of our ROIs and this could explain why our results are contrary to Pelphrey et al. (2009). Instead, using bodies, we replicate the results that Golarai et al., (2010) obtained using faces; we too observed an increase over age in the amount of contiguous voxels in our right hemisphere ROIs, but no significant age difference in the left.

Using a more restricted ROI definition than Pelphrey et al., (2009), Peelen et al., (2009) yielded similar cluster sizes to those we see here. Contrary to the current study, however, they observed no difference between adults and children in the size of FBA and EBA activity (defined by contrast static Body > Tools in the right hemisphere); they even report larger right EBA in children compared to adults when the activity was defined at a threshold $p<0.01$ or $p<0.05$ uncorrected. In addition, although they report a trend for increased activity with age, they don't find any significant difference in peak activity when comparing adults and children. One has to note, however, that the group in their study comprised children and adolescents (age from 7 to 17), with only nine children under the age of 11. Thus differences between children and adults could have been masked by comparatively larger activity in the group of adolescents. Other differences might arise from the use of static photographs as compared to the dynamic stimuli used in our study. A possibility is that the dynamic stimuli engage more of the body-selective areas (Amoruso et al., 2011) and that this difference is stronger in adults than in children. This would then explain the increase over age in strength and extent of activity in the pSTS region and is further supported by reports of a delayed maturation of motion processing compared to static perception in the visual cortex (Bucher et al., 2006; but see Grèzes et al., 2007). Whether the age differences we observe are due to changes in low-level processing or development of higher-level perceptual functions remains to be tested.

Another possibility to be considered is that top-down influences are responsible for the differences observed between children and adults. In other words, although the scans were kept deliberately short in an attempt to minimise a lack of attention in participants, attentional differences could still have arisen from the clips having different significance to adults and children. Sinke et al. (2010) showed a top-down influence on the body-selective areas when viewing socially meaningful stimuli. These areas, however, were found to be most active when subjects were not attending the stimulus. Therefore to attribute the differences we see here to purely top-down modulation, the adults would have had to be paying less attention to the stimuli than the children.

So, although we cannot rule out the possibility of some top-down influence, we can say with confidence that this is not the sole factor in our observed differences between adults and children.

Taken together with the developmental studies of face perception (Golarai et al., 2007;Scherf et al., 2011), our results suggest that the body-selective areas in the visual cortex do not become adult-like in terms of extent and strength of activity until the second decade of life. How this could be related to the development of social perception abilities like recognizing and interpreting others bodily movements should be explored in future studies.

3.4.3 A difference in neural representation?

Previous studies showing increase in specificity of cortical activity over age (Carter and Pelphrey, 2006;Grill-Spector et al., 2008) have led authors to suggest different neural representation strategies are used across ages, possibly reflecting different spatial activity patterns within specialized cortical areas (Golarai et al., 2010). Here, using MVB, we directly tested whether, at a functional level, there could be a difference in the way in which the stimuli are being neurally represented. We found strong evidence that a distributed spatial prior gives the best model of neural representation in all ROIs in both adults and children. This means that most voxels in these ROIs are making a small contribution, with a few making a large contribution. The lack of change in representation model over age indicates that the patterns of activity in these regions do not become any more or less functionally distributed between childhood and adulthood. So, even if the amount and extent of neuronal activity when looking at the human body increases throughout childhood into adulthood, the functional representation of the stimuli does not change in terms of spatial encoding. This is in line with work by Golarai et al., (2010) who found, using a similar measure (size of ROI clusters with contiguous or non-contiguous voxels across age), that a sparse spatial representation best explained the data, and that this spatial pattern did not change over age. This is the only aspect of body perception (aside from the extent of activation in the left hemisphere ROIs) that we found to be ‘adult-like’ in children.

3.5 Conclusions

Previous studies had suggested that the body-selective regions in the visual cortex are ‘adult-like’ by the age of 7 years old. Here, using a larger and more homogenous sample, we present evidence for the first time that 11 year-olds still exhibit reduced extent and strength of activation in these areas compared to adults. We also find a significant increase with age in the extent of activation in the body-selective regions, but only in the right hemisphere. Furthermore, using multivariate Bayesian techniques we find evidence that patterns of neural representation do not differ between adults and children. Therefore we conclude that a significant quantitative, but not qualitative maturation occurs during adolescence for processing signals from the human body.

4 Emotion Modulation of the Body-Selective Areas

4.1 Introduction

A large corpus of literature indicates that the ability to perceive emotions from other people doesn’t reach adult levels until mid-adolescence (Herba et al., 2006). Moreover, the brain circuits engaged while exposed to a stimulus depicting an emotion also undergo functional and structural changes in the period encompassing late childhood and adolescence. There is evidence of structural development in the linear increase in white matter and non-linear decrease in grey matter during adolescence (rev in Blakemore and Choudhury (2006)). Loenneker et al. (2011) used diffusion tensor imaging (DTI) to show that structural reorganisation of fiber pathways from medial to lateral-temporal cortex occurs between childhood and adulthood. Functionally, event-related potentials (ERPs) studies have shown that the signature of emotion processing when viewing faces doesn’t show adult patterns before the age of 14 (Batty and Taylor, 2006). fMRI studies also indicate less activity in children, as compared to adults, in most regions involved in viewing emotional faces (Thomas et al., 2001;Evans et al., 2010). Further studies on emotion processing from faces indicate that amygdala activity is increased in adolescents as compared to younger children when they process the emotion of a face (Pavuluri et al., 2009).

As we have seen in previous chapters, all of the aforementioned research has been conducted in relation to the perception of emotion from faces. Emotion is also strongly conveyed by body posture and movements, especially when interaction takes place from a distance. We reported in **Chapter 2** that the capacity to recognize basic emotions from body movements improves throughout childhood and adolescence (Ross et al., 2012). The question of whether related brain processes also change during this time has not yet been addressed. Various brain areas have been identified as being specialized for the recognition and interpretation of human form and human motion: namely the EBA located bilaterally in the lateral occipitotemporal cortex (LOTC), the FBA and areas in the inferior parietal lobe (IPL) and pSTS (Downing et al., 2001;Peelen and

Downing, 2005;de Gelder, 2006;Weiner and Grill-Spector, 2011;Grosbras et al., 2012b).

In terms of emotion modulation of these body-selective areas, research consistently reports modulation by emotion in both the fusiform gyrus (de Gelder et al., 2004b;Grosbras and Paus, 2006;de Gelder et al., 2010;Kret et al., 2011) and in the LOTC (Grosbras and Paus, 2006;Grèzes et al., 2007). Peelen et al. (2007) demonstrated that the strength of emotion modulation was related, on a voxel by voxel basis, to the degree of body selectivity, but showed no such relationship with the degree of selectivity in faces. In other words, the emotional signals from the body might modulate the complexes of neurons that code for the viewed stimulus (Sugase et al., 1999), rather than providing an overall boost in activation for all visual processing in the extra-striate visual cortex. Furthermore, amygdala response to emotional bodies was shown to positively correlate with the modulation of body-selective areas across participants (Peelen et al., 2007). This does not mean, however, that emotion information is coded into the body areas, but rather the evidence suggests that affective state information is processed elsewhere and fed forward/back to the relevant areas (Vuilleumier et al., 2004;Vuilleumier, 2005;Downing and Peelen, 2011). This emotion modulation network suggests that the amygdala ‘modulates’ cortical pathways in an additive or competitive manner with other higher cortical areas. Any age related changes in this network have yet to be tested, particularly the amygdala response/emotion modulation correlation found by Peelen et al. (2007). A change in this correlation over age would perhaps suggest a maturational change in the emotion modulation network. This would shed light on other behavioural findings, particularly our finding of a bilinear increase in emotion recognition ability described in **Chapter 2**.

As we have seen in **Chapter 3**, only two fMRI studies have explored the structural and functional development of the body-selective regions in children and adults, reporting that body-selective activity within the EBA and FBA was similar (in terms of location, intensity and extent) in children older than 7 and in adults (Peelen et al., 2009;Pelphrey et al., 2009). In contrast it seems that face-selective regions in the ventral stream take more than a decade to become adult-like (Scherf et al., 2007;Grill-Spector et al., 2008). Another study found that activity in EBA and FBA did not differ significantly in adults and children while watching dynamic stimuli, while pSTS activity during biological motion perception contrasted to non-biological motion perception, seemed to increase with age in the small sample tested (Carter and Pelphrey, 2006).

Here, our first goal was to expand upon this research and that of **Chapter 2** and **3** by further investigating the functional development in children, adolescents and adults, of the EBA, pSTS, FBA and amygdala in relation to emotional human body movements. Secondly, we wanted to replicate the results of Peelen et al., (2007) and explore whether amygdala response is correlated with the emotion modulation of the body-selective areas across age. Any age related changes in emotion modulation or amygdala strength/emotion modulation correlations would provide a parallel to our behavioural findings in **Chapter 2**, and our brain imaging findings in **Chapter 3**.

4.2 Materials and Methods

4.2.1 Participants

Forty-six primary and secondary school children were recruited from local schools and after-school clubs in the West End of Glasgow. Three of the younger children were excluded because of excessive head motion in the scanner. Thus data from 43 children (25 young children aged 6-11 years: M = 9.55 years, SD 1.46, 13 females; 18 adolescents aged 12-17: M = 14.82, SD = 1.88, 9 females) were included in this analysis. Permission was obtained from managers of after-school clubs and/or head teachers in order to promote the study. Written consent was then obtained from each child's parent or guardian before testing began (adolescents aged 16 and over were able to provide their own consent). The study was in line with the declaration of Helsinki, was approved by the local ethics board, and all participants understood that participation was voluntary. A sample of 26 adult volunteers recruited from the University of Glasgow also took part (aged 18-27 years: M = 21.28 years; SD = 2.11, 15 females). This gave us 69 subjects in total.

4.2.2 Stimuli and Procedure

The stimuli, procedure and analytical pre-processing were identical to that of **Chapter 3**. A brief summary of which is presented below.

Forty-five short video-clips were taken from a larger set created and validated by (Kret et al., 2011). Each clip depicted one actor, dressed in black against a green background, moving in an angry, happy or neutral manner. Six actors were males and nine females, with each actor recorded three times (for each of the three emotions). The videos were recorded using a digital video camera and were edited to two-seconds (50 frames) long clips. The faces in the body videos were masked with Gaussian filters so that only information of the body was perceived (for full details and validation of stimuli (see Kret et al. (2011), de Gelder and Van den Stock (2011)). In addition, various clips of non-human moving objects (e.g. windscreen wipers, windmills, metronomes etc.) were taken from the internet. They were cropped to the same size (960 x 540 pixels, 50 frames, 25 fps) as the human videos using Adobe Premiere Pro and a green border was added. Stimuli were organized into blocks of five clips (10 seconds).

To assess the amount of low-level visual motion in each clip, we computed the average change in luminance between consecutive frames. To do so, for each clip we first estimated change in luminance in the background (corresponding to noise level) and for each pair of frames extracted the number of pixels where the change in intensity was higher than noise. For each clip we computed the average number of pixels with change across the frames. Then we computed the cumulative motion for the five clips in each block. Overall the blocks of non-human clips had slightly more motion than the blocks of body movements clips, although this did not reach statistical significance ($t(16) = 1.89$, $p = 0.076$). In the emotion clips there was found to only be a significant difference in movement between the angry and neutral body expressions ($t = 3.78$, $p<0.005$). These data were added as parametric modulators in our whole-brain analysis, allowing us to control for this increased motion in the angry body expressions.

Data Acquisition: We measured brain activity using a 3T fMRI scanner (Tim Trio, Siemens, Erlangen, Germany) equipped with a 32-channels head coil, using standard EPI sequence for functional scans (TR/TE: 2600ms / 40ms; slice thickness = 3 mm; in plane resolution = 3 x 3 mm). In addition, we acquired a high-resolution T1-weighted structural scan (1 mm3 3D MPRAGE sequence) for anatomical localization.

Main Experiment: A MATLAB script using the Psychophysics Toolbox Extensions (Brainard, 1997) was used to present the stimuli. Stimuli were organized into nine blocks of non-human stimuli (10 seconds; 5 clips), nine blocks of human stimuli (three blocks of each emotion) and six 10-seconds-long blocks of blank screen as a baseline each presented twice in an m-sequence (a method of pseudo-randomising the stimuli to avoid correlation effects between blocks of stimuli, see Buracas and Boynton (2002)). An experimental run lasted 480 seconds. Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head-coil. Subjects were instructed to fixate in the centre of the screen and where monitored during the scan to make sure they kept their eyes open. Following the scan they were then given a very short forced choice emotion recognition task using the same stimuli to gauge their understanding of the emotional content of the stimuli. There was no difference between age groups in emotion recognition accuracy (F(2,67)=.787, *p*=.46). Some of the subjects also participated in another independent 8-min functional scan (the voice-selective area scan for **Chapter 5**) during the same scanning session, before completing the structural scans.

4.2.2.1 Pre-Processing

Pre-processing and statistical analysis of MRI data was performed using SPM 8 (Welcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm). Functional data were corrected for motion by using a two-pass procedure to register the images to the mean of the images after the first realignment. They were then re-sliced with a 4th Degree B-Spline interpolation. Movement correction was allowed up to 2mm translation or 2 degrees rotation; the three participants who had larger head motion were excluded from the analysis. Functional data were co-registered with the individual 3D T1-weighted scans by identifying AC-PC landmarks manually. These anatomical scans were segmented for different tissue types and transformed into MNI-space using non-linear registration. The parameters from this transformation were subsequently applied to the co-registered functional data. For all analyses, the data were spatially smoothed with a Gaussian kernel (8mm FWHM). High-pass temporal filtering was applied at a cut off of 128 seconds to remove slow signal drifts.

Furthermore, and as noted in **Chapter 3**, by normalising the data from our adults and children into the same stereotactic template, we were able to directly compare the strength and extent of activation across age groups. Several studies examining the feasibility of this approach have found no significant differences in brain foci locations when the brains of children as young as 6 were transformed to an adult template (Burgund et al., 2002;Kang et al., 2003). These findings gave us confidence that there is no confound of brain size in our results.

4.2.2.2 Whole Brain Analysis

A general linear model was created with one predictor of interest for each of the four conditions (Happy, Angry, Neutral, Non-Body). We added our measure of luminance change (video clip motion) as a parametric modulator, allowing us to control for the increased motion in the anger body movements. Six head motion parameters were also added as regressors of non-interest. The model was estimated for each participant and individual contrasts (Angry>Neutral, Happy>Neutral, Body>Non-Body etc.) were taken to second-level random effect analyses to create group-averages separately for children, adolescents and adults. For the main group analyses (ANOVA and independent *t*-tests), resulting statistical maps are presented at a $p<0.001$ uncorrected threshold with a cluster extent of 10 voxels. Anatomical names for various functional activations were determined using the Harvard-Oxford cortical and sub-cortical structural atlases in FSLview (Jenkinson et al., 2012).

4.2.2.3 ROI Definition and Analysis

We tested whether the activity of the six ‘body’ regions used in **Chapter 3** (bilateral EBA, FBA and pSTS) were modulated by the emotional content of the body movement (de Gelder et al., 2004b;Grosbras and Paus, 2006;Grèzes et al., 2007;Peelen et al., 2007;de Gelder et al., 2010;Kret et al., 2011). These ROIs were created by taking the set of contiguous voxels within a sphere of radius

8mm surrounding the voxel in each anatomical region that showed the highest probability of activation in a meta-analysis of 20 studies examining contrasts between moving body and controls in adults (detailed in Grosbras et al., (2012a).

We also included ROIs covering the amygdala (AMY) in the analysis. These were defined using the WFU PickAtlas software within SPM (Maldjian et al., 2003).

To explore differences in the strength of activity in these ROIs across age, we extracted the peak *t*-value from each ROI in each participant for the Angry>Neutral and Happy>Neutral contrasts. These parameters were taken as summary statistics and entered into 3x8 mixed design ANOVAs, with Age Group and ROI as between and within subject factors respectively.

4.2.2.4 Correlation Analysis

For each ROI in each subject we extracted the peak *t*-value under two contrasts, (Angry>Neutral, Happy>Neutral), and the Non-Body condition. Data was averaged across hemispheres, which allowed us to correlate amygdala activity in each subject against activity in the EBA, FBA and pSTS in each of the three age groups. This resulted in one correlation of amygdala vs. the three body-selective ROIs individually, at each age group, and for each contrast.

4.3 Results

4.3.1 Whole brain contrasts

4.3.1.1 Bodies > Non-Bodies

4.3.1.1.1 Within Groups

In adults, viewing dynamic bodies compared with non-bodies elicited activation in the bilateral fusiform gyri (including FBA), bilateral pSTS, bilateral occipitotemporal cortices (including EBA), bilateral amygdalae, right inferior frontal gyrus, right frontal pole, right precuneus, right precentral gyrus and left superior frontal gyrus.

Adolescents displayed activation in the same areas as the adults with the exception of the left fusiform gyrus, left superior frontal gyrus and right frontal pole, where they did not reach significance.

Children also showed similar activation locations as the adults, but showed no activation in the left fusiform gyrus, left posterior superior temporal sulcus, left amygdala and left superior frontal gyrus. (Figure 4-1 and Table 4-1).

Table 4-1 Regions activated in a whole-brain group-average random-effects analysis contrasting Bodies>Non-Bodies.
(*p*<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space. (OTC=Occipitotemporal Cortex; FG=Fusiform Gyrus; pSTS=Posterior Superior Temporal Sulcus; IFG=Inferior Frontal Gyrus; FP=Frontal Pole; AMY=Amygdala; Pre=Precuneous; PCG=Precentral Gyrus; SFG=Superior Frontal Gyrus; OFG=Occipital Frontal Gyrus; OP=Occipital Pole; Hip=Hippocampus; LG=Lingual Gyrus; THA=Thalamus; TP=Temporal Pole).

Region	Adults					Adolescents					Children				
	x	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*
rOTC	51	-73	4	12	11.1	51	-70	4	7.6	7.91	48	-76	1	8.8	6.35
lOTC	-48	-76	7	7.7	6.64	-48	-79	4	6.2	3.48	-48	-79	4	5.6	2.57
rFG	42	-46	-17	10	4.29	42	-43	-17	5.1	0.70	42	-46	-17	6.0	1.49
lFG	-42	-43	-17	5.1	0.38										
rpSTS	51	-40	7	9.5	21.3	60	-43	13	7.5	10.7	60	-40	13	7.3	14.7
lpSTS	-63	-49	19	7.6	10.1	-54	-52	10	6.4	6.62					
rIFG	54	20	22	710	10.1	45	17	25	4.2	1.03	54	29	22	4.0	0.54
rFP	9	47	43	4.7	0.12										
rAMY	18	-7	-14	8.6	5.48	18	-7	-14	4.3	0.57	18	-7	-11	6.3	2.57
lAMY	-18	-10	-14	6.3	2.43	-18	-10	-11	4.6	0.57					
rPre	3	-55	34	5.4	2.6	3	-58	34	4.5	1.27	3	-58	31	5.0	3.00
rPCG	48	5	46	7.8	8.24	48	2	52	4.6	1.03	45	2	46	6.4	5.48
lSFG	-12	-7	67	4.9	1.57										

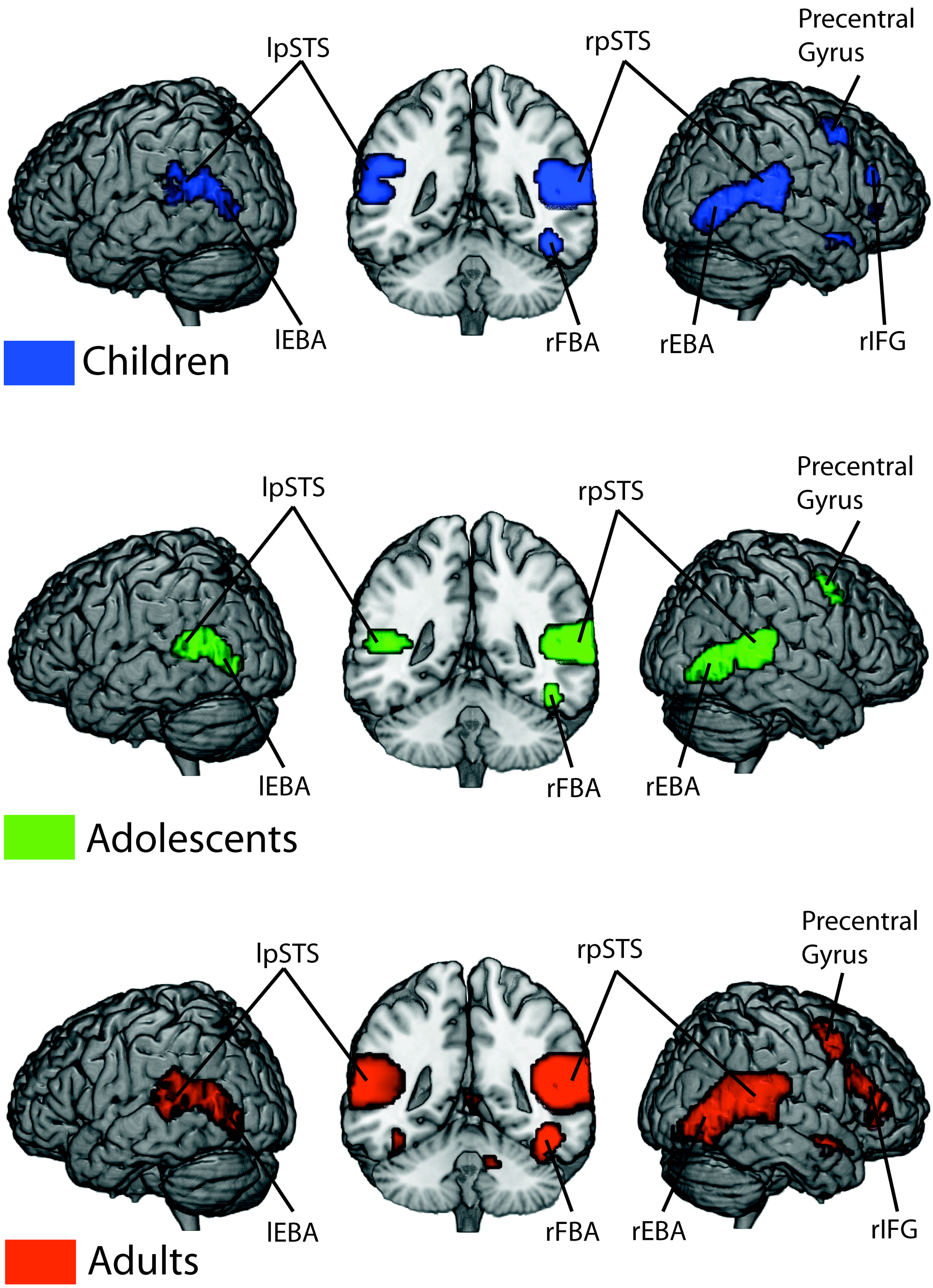


Figure 4-1 Brain activity when contrasting Bodies > Non-Bodies in Children, Adolescents and Adults.
($p<0.001$ uncorrected, cluster extent threshold of 10 voxels)

4.3.1.1.2 Between groups

One-way ANOVA of the brain maps with Age as the between groups factor revealed significant activation differences across age in the bilateral lingual gyrus and the right fusiform gyrus (Table 4-2). We then performed 6 planned comparisons comparing each group individually with each other (Table 4-3).

We found that the adults showed increased activity compared with adolescents and children in the main body-selective areas of the visual cortex; namely the right FG (including the FBA), right pSTS, right LOC (containing EBA), and right IFG.

Conversely, when compared to the adults, both the children and adolescents showed higher bilateral lingual gyrus activation, driving the main effect of the One-Way ANOVA.

Table 4-2 Regions activated by One-Way ANOVA of whole-brain random-effects analysis contrasting Bodies>Non-Bodies with Age as between subject factor.
(p<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space.

Region	Main Effect of Age				
	x	*y*	*z*	t	*cm3*
Left Lingual Gyrus	-9	-73	-2	18.5	11.4
Right Lingual Gyrus	9	-73	-2	16.9	Sub-peak
Right Fusiform Gyrus	45	-52	-17	11.9	0.51

Table 4-3 *t*-tests contrasting Bodies>Non-Bodies across Age contrasts.
(*p*<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space.

Region	Adults>Children				
	x	*y*	*z*	t	*cm3*
Right Inferior Frontal Gyrus	51	32	10	4.37	0.65
Right Fusiform Gyrus	45	-52	-17	4.29	0.95
Right Posterior Superior Temporal Sulcus	51	-46	7	3.87	0.59
Right Lateral Occipital Cortex	42	-76	-11	3.66	0.70
	Adults>Adolescents				
Right Middle Temporal Gyrus	60	-19	-11	3.64	2.43
Right Thalamus	12	-28	4	4.42	0.49
Right Fusiform Gyrus	45	-52	-17	4.25	0.81
Right Occipital Fusiform Cortex	27	-88	-11	4.01	0.43
Left Supramarginal Gyrus	-63	-49	19	3.93	0.70
Right Inferior Frontal Gyrus	51	32	7	3.75	0.54
Right Posterior Superior Temporal Sulcus	48	-43	22	3.60	0.70
	Adolescents>Children				
	No regions active at given threshold				
	Adolescents>Adults				
Left Lingual Gyrus	-9	-76	-2	5.42	14.9
Right Lingual Gyrus	9	-73	-11	4.89	Sub-peak
	Children>Adolescents				
	Children>Adults				
Right Lingual Gyrus	6	-73	-2	5.47	14.6
Left Lingual Gyrus	-9	-73	-2	5.24	Sub-peak
Left Temporal Occipital Fusiform Cortex	-24	-46	-17	4.60	1.05

4.3.1.2 Angry Bodies > Neutral Bodies

4.3.1.2.1 Within Groups

When contrasting Angry bodies and Neutral Bodies, Adults showed activation in the bilateral occipital temporal cortices, bilateral occipital fusiform gyri, right middle STS, left posterior STS, right thalamus and right fusiform cortex.

Adolescents displayed activation in similar areas with the exception of the right thalamus.

Children showed activation in the same regions as adults except for the bilateral occipital fusiform gyri. In addition, they showed activation in the left occipital pole, the left superior fusiform gyrus, right hippocampus, left temporal pole, left amygdala and left thalamus (Figure 4-2 and Table 4-4).

Table 4-4 Regions activated in a whole-brain group-average random-effects analysis contrasting Angry>Neutral.
(*p*<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space.

Region	Adults					Adolescents					Children				
	x	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*
lOTC	-48	-70	10	7.3	9.59	-51	-73	10	6.4	7.48	-48	-76	7	5.1	6.64
lpSTS	-51	-52	10	5.0	Sub-Peak	-51	-52	13	5.5	Sub-Peak	-63	-52	13	5.4	6.15
rmSTS	48	-43	10	6.6	8.67	48	-40	7	5.0	3.86	51	-46	16	5.5	11.7
rOTC	48	-67	7	6.2	8.96	48	-64	7	5.9	8.32	45	-67	7	6.9	12.3
rTha	3	-16	-2	4.52	2.54						18	-31	1	6.5	3.51
rFG	39	-49	-17	4.5	2.19	39	-49	-14	5.2	3.11	39	-49	-17	6.2	7.34
rOFG	27	-76	-8	6.8	9.23	21	-85	-8	7.8	8.91					
lOFG	-30	-76	-8	6.9	9.00	-24	-82	-11	5.8	6.67					
lOP											-9	-100	7	5.6	5.91
lSFG											-12	11	67	4.6	1.13
rHip											21	-13	-14	4.4	1.22
lTP											-54	8	-17	3.9	0.27
lAMY											-18	-10	-11	4.1	0.84
lTha											-18	-31	1	3.9	0.49

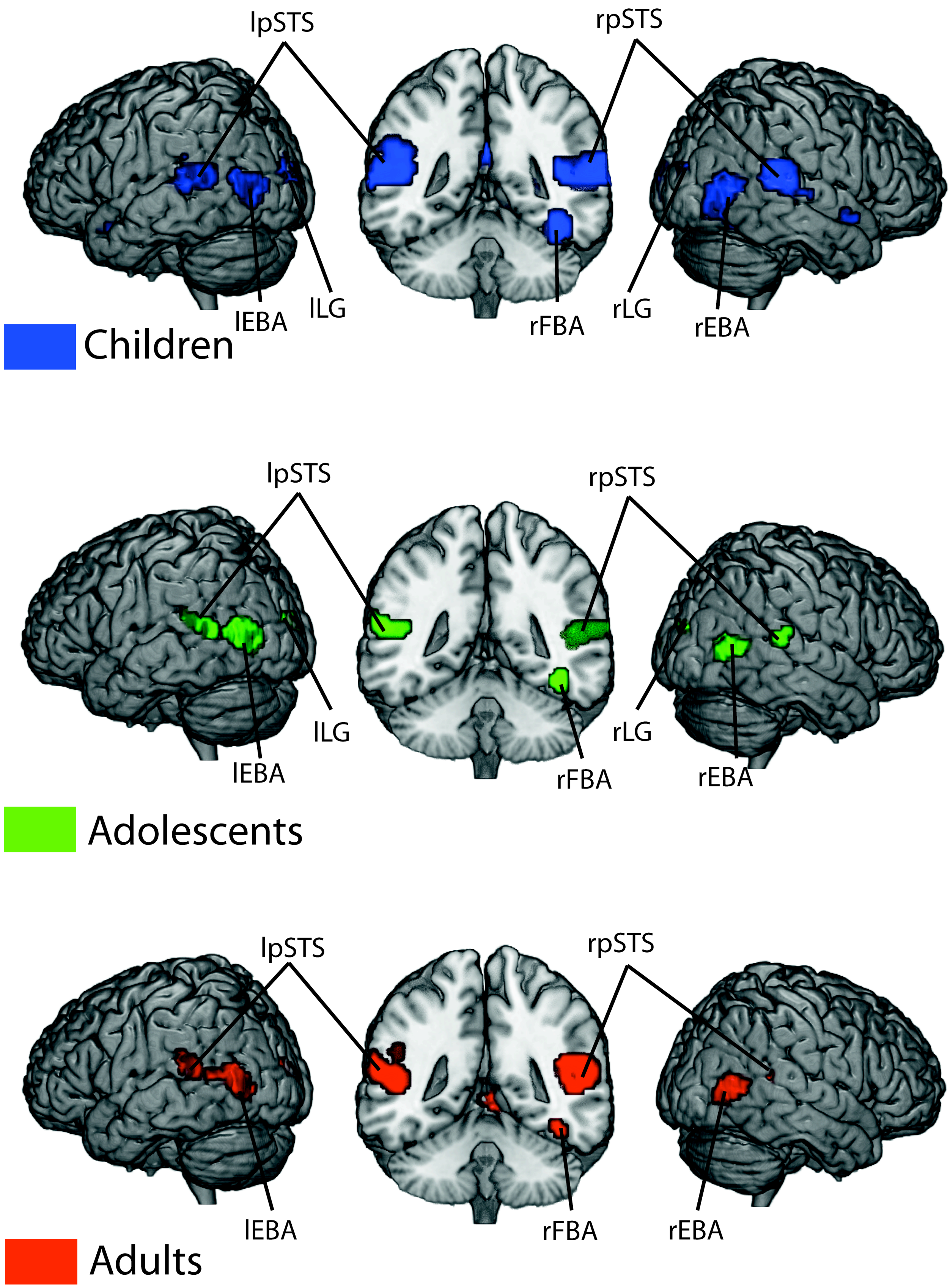


Figure 4-2 Brain activity when contrasting Angry > Neutral Bodies in Children, Adolescents and Adults.
(p<0.001 uncorrected, cluster extent threshold of 10 voxels)

4.3.1.2.2 Between Groups

We observed no main effect of age when performing a One-Way ANOVA of Angry>Neutral brain maps with Age as the between subjects factor. We thus conclude that, at a whole-brain level, no significant difference in activation exists across our age groups when contrasting Angry>Neutral bodies (Table 4-5).

Table 4-5 Regions activated by One-Way ANOVA of whole-brain random-effects analysis contrasting Angry>Neutral with Age as between subject factor.
(*p*<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space

Region	Main Effect of Age				
	x	*y*	*z*	t	*cm3*
	No regions active at given threshold				

4.3.1.3 Happy > Neutral

4.3.1.3.1 Within Groups

The Happy>Neutral contrast in adults revealed activation in the bilateral occipital temporal cortices, left lingual gyrus, right middle STS, bilateral posterior STS, left amygdala and right fusiform gyrus.

Adolescents showed the same pattern of activation with the exception of the left amygdala. In addition to the right, they also showed activation in the right lingual gyrus, as well as the bilateral occipital poles.

Children, while showing activation in the bilateral occipital temporal cortices, bilateral occipital poles, bilateral lingual cortices and right posterior STS, showed no activation in the right middle STS, left posterior STS, left amygdala or right fusiform gyrus (Figure 4-3 and Table 4-6).

Table 4-6 Regions activated in a whole-brain group-average random-effects analysis contrasting Happy>Neutral.
(*p*<0.001 uncorrected, cluster extent threshold of 10 voxels, maximum cluster sphere 20mm radius). Coordinates are in MNI space.

Region	Adults					Adolescents					Children				
	x	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*
rOTC	48	-67	4	6.9	9.48	48	-73	4	4.0	Sub-Peak	45	-76	1	4.6	Sub-Peak
lLG	-9	-88	-8	9.1	10.6	-12	-88	-11	6.1	6.62	-15	-85	-11	4.3	2.32
lOTC	-48	-73	7	7.8	7.97	-51	-73	10	5.9	5.29	-45	-79	4	3.9	1.62
rmSTS	45	-40	10	6.9	5.35	48	-37	7	5.7	6.86					
rpSTS	42	-58	7	5.8	Sub-Peak	45	-64	7	6.5	6.05	45	-64	7	5.5	4.67
lpSTS	-51	-49	10	4.9	2.21	-54	-49	13	5.5	Sub-Peak					
lAMY	-12	-7	-11	4.5	0.43										
rFG	39	-43	-23	3.7	0.41	42	-43	-14	4.2	0.65					
rLG						18	-85	-8	7.3	7.70	15	-82	-11	4.4	2.40
rOP						24	-91	19	6.0	4.46	21	-91	16	4.8	1.86
lOP						-18	-91	16	5.8	5.24	-21	-91	16	4.2	1.84
rAMY											21	-10	-14	3.7	0.46

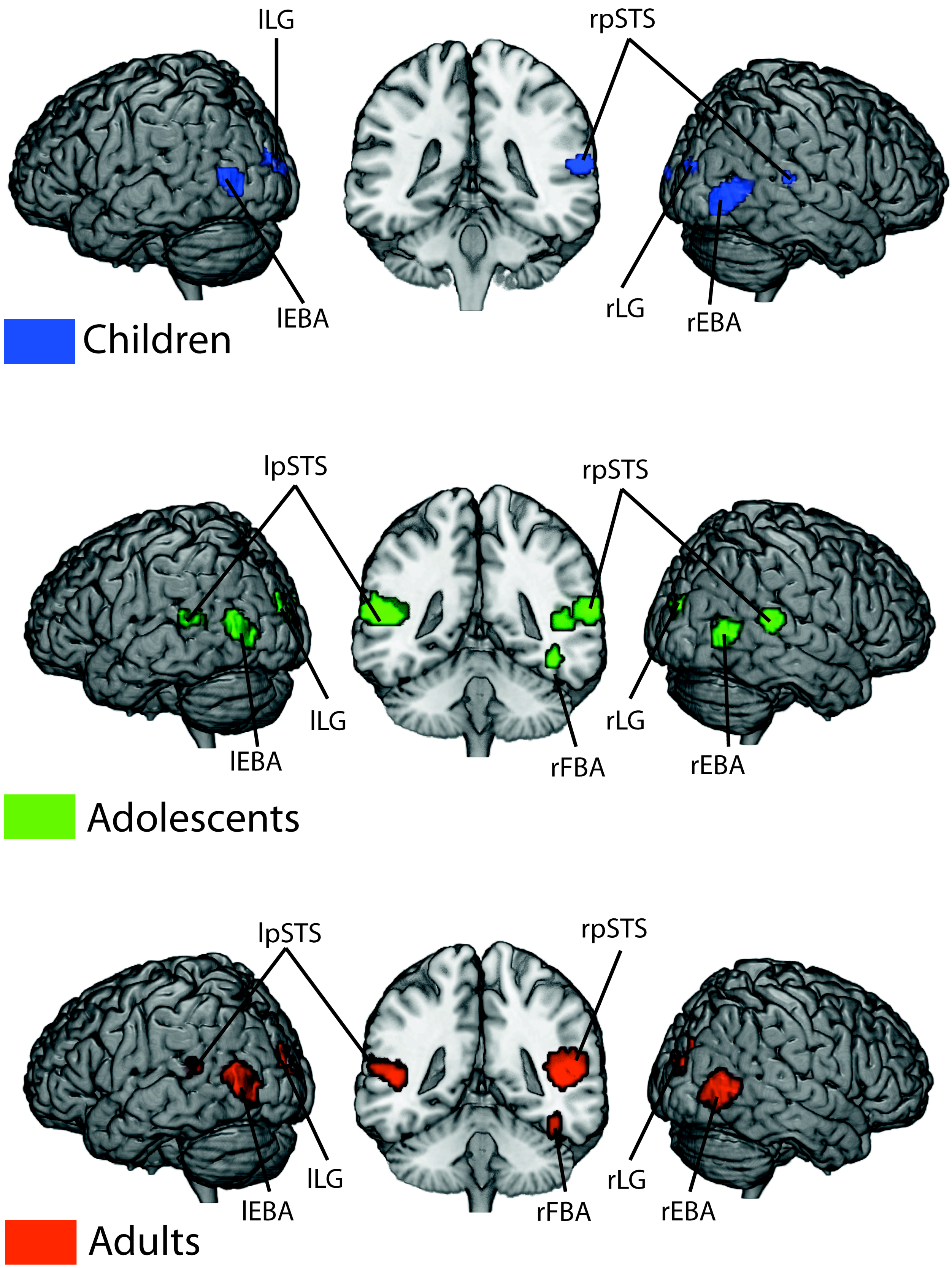


Figure 4-3 Brain activity when contrasting Happy > Neutral Bodies in Children, Adolescents and Adults.
(p<0.001 uncorrected, cluster extent threshold of 10 voxels)

4.3.1.3.2 Between Groups

We observed no main effect of age when performing a One-Way ANOVA of Happy>Neutral brain maps with Age as the between subjects factor. We thus conclude that, at a whole-brain level, no significant difference in activation exists across our age groups when contrasting Happy>Neutral bodies (Table 4-7).

Table 4-7 Regions activated by One-Way ANOVA of whole-brain random-effects analysis contrasting Happy>Neutral with Age as between subject factor.

Region	Main Effect of Age				
	x	*y*	*z*	t	*cm3*
	No regions active at given threshold				

4.3.2 Region of interest analysis

4.3.2.1 Bodies > Non-Bodies

4.3.2.1.1 Peak *t*-value

The peak *t*-values for children, adolescents and adults in all eight ROIs are presented in Figure 4-4.

A 3x8 Age Group x ROI ANOVA revealed a main effect of Age Group (F(2,66)=19.10,*p*<.001), main effect of ROI (F(7,462)=81.99,*p*<.001) and interaction between ROI and Age Group (F(14,462)=4.31,*p*<.001).

Bonferroni corrected follow-up (post-hoc) analysis found there to be a main effect of age in all ROIs with the exception of the lFBA (rEBA: F(2,66)=14.54, *p*<.001; lEBA: F(2,66)=10.47, *p*<.001; rFBA: F(2,66)=12.71, *p*<.001; lFBA: F(2,66)=2.27, *p*=.111; rpSTS: F(2,66)=9.25, *p*<.001; lpSTS: F(2,66)=4.00, *p*<.05; rAMY: F(2,66)=3.28, *p*<.05; lAMY: F(2,66)=7.79, *p*<.001).

These effects were driven by adults having an increased activity when compared to children in all ROIs except the lFBA which showed no main effect (rEBA: *p*<.001; lEBA: *p*<.001; rFBA: *p*<.001; lFBA: *p*=.116; rpSTS: *p*<.001; lpSTS: *p*<.05; rAMY: *p*<.05; lAMY: *p*<.05).

Adults also showed increased activity over adolescents in the rEBA, rFBA and rAMY (rEBA: *p*<.005; rFBA: *p*<.001; rAMY: *p*<.05).

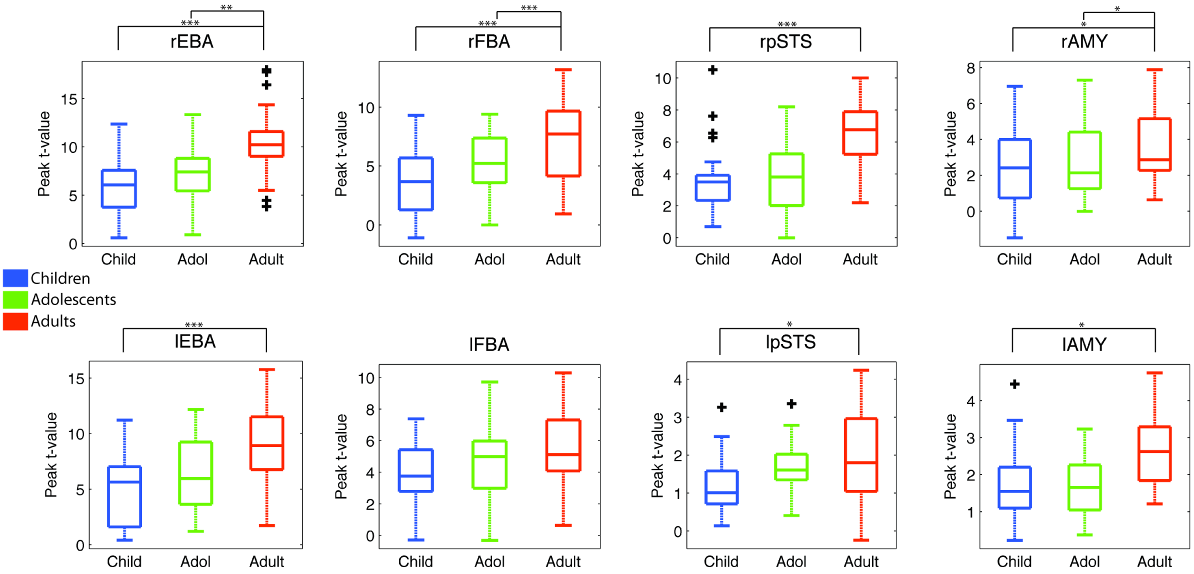


Figure 4-4 Peak *t*-values in each ROI for each Age Group for the Bodies > Non-Bodies contrast.
(It should be noted that the *y*-axis scales are not homogeneous across ROIs). *=*p*<.05; **=*p*<.01; **=*p*<.001.

4.3.2.2 Angry > Neutral

4.3.2.2.1 Peak *t*-value

An Age Group x ROI ANOVA using the peak *t*-values from the Angry>Neutral contrast revealed a main effect of ROI (F(7,462)=20.46, *p*<.001), but no main effect of Age Group (F(2,66)=.081, *p*=.923) and no interaction between Age Group and ROI (F(14,462)=1.37, *p*=.166). The peak *t*-values for children adolescents and adults in each ROI are shown in Figure 4-5.

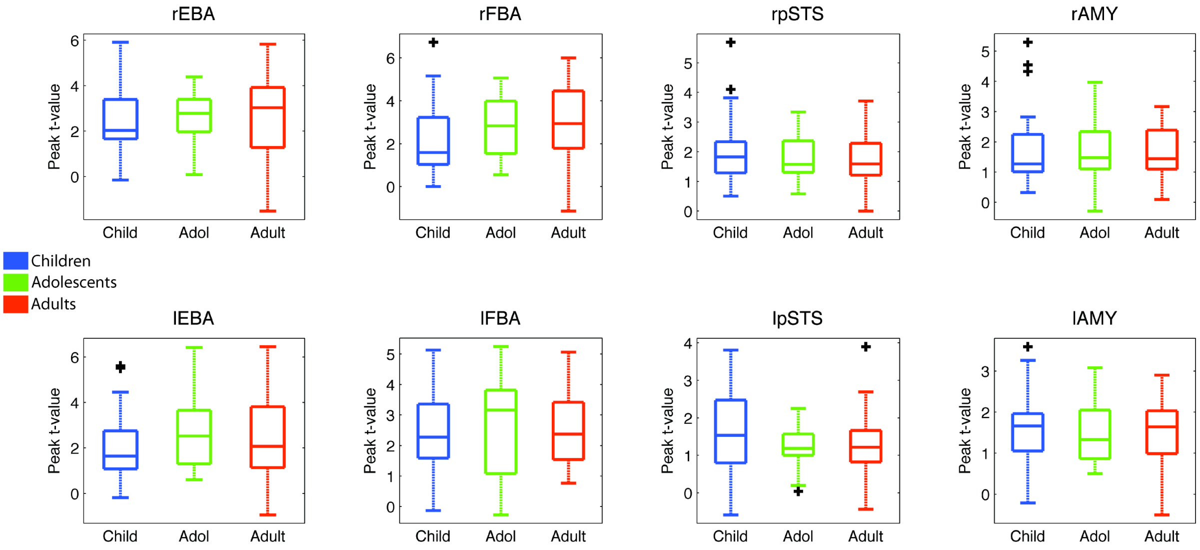


Figure 4-5 Peak *t*-values in each ROI for each Age Group for the Angry > Neutral contrast.
(It should be noted that the *y*-axis scales are not homogeneous across ROIs).

4.3.2.3 Happy > Neutral

4.3.2.3.1 Peak t-value

A final Age Group x ROI ANOVA using peak *t*-values form the Happy>Neutral contrast revealed a main effect of ROI (F(7,462)=18.44, *p*<.001), no main effect of Age Group (F(1,66)=1.07, *p*=.350) and no interaction between the two (F(14,462)=1.18, *p*=.290). The peak *t*-values for children adolescents and adults in each ROI are shown in Figure 4-6.

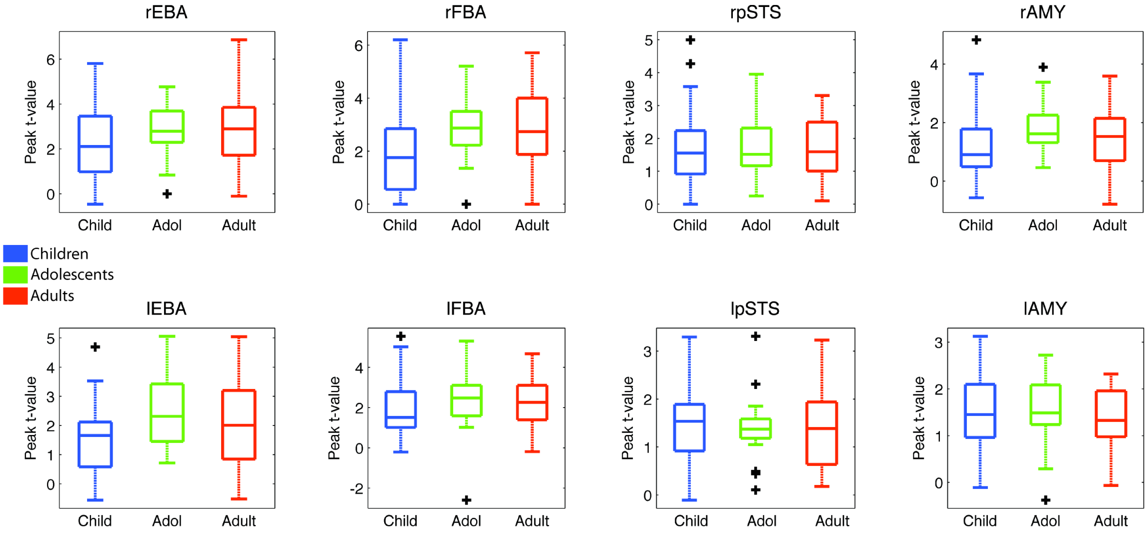


Figure 4-6 Peak *t*-values in each ROI for each Age Group for the Happy > Neutral contrast. (It should be noted that the *y*-axis scales are not homogeneous across ROIs).

4.3.3 Correlations

Finally, we wanted to replicate the Peelen et al., (2007) result that amygdala response to emotional body stimuli in adults is correlated with emotion modulation in the body-selective areas, as well as exploring whether this result holds true in children and adolescents.

We took subject's individual peak *t*-values in the EBA, FBA and pSTS (averaged across hemispheres) for the two emotion contrasts as well as when subjects viewed the Non-Body stimuli, and correlated them against the averaged peak *t*-value across the bilateral amygdala. This analysis revealed that the peak activation in the amygdala to Angry>Neutral body expressions was significantly correlated with the degree of emotional modulation in the FBA (r=0.53, *p*<.01) and pSTS (r=0.51, *p*<.01) in children, no regions in adolescents and the EBA (r=0.56, *p*<.005), FBA (r=0.70, *p*<.001) and pSTS (r=0.53, *p*<.01) in adults (Figure 4-7(A)).

Similarly, for the Happy>Neutral contrast peak amygdala activity was significantly correlated with emotion modulation in the body-selective areas in the FBA (r=0.50, *p*<.05)and pSTS (r=0.67, *p*<.001) in children, no regions in adolescents and the FBA (r=0.44, *p*<.05) in adults (Figure 4-7(B)).

In the Non-Body condition there was no significant correlation between peak amygdala activity and any of the body-selective ROIs in any age group. Thus, children who showed stronger amygdala activation to emotional body stimuli also showed a stronger modulation in the FBA and pSTS, but not when presented with non-human stimuli. Similarly, adults who showed stronger amygdala activation to both angry and happy body stimuli also showed a stronger modulation in the EBA, FBA and pSTS. Again this effect was not found when they were presented with non-human stimuli. Adolescents showed none of these correlations.

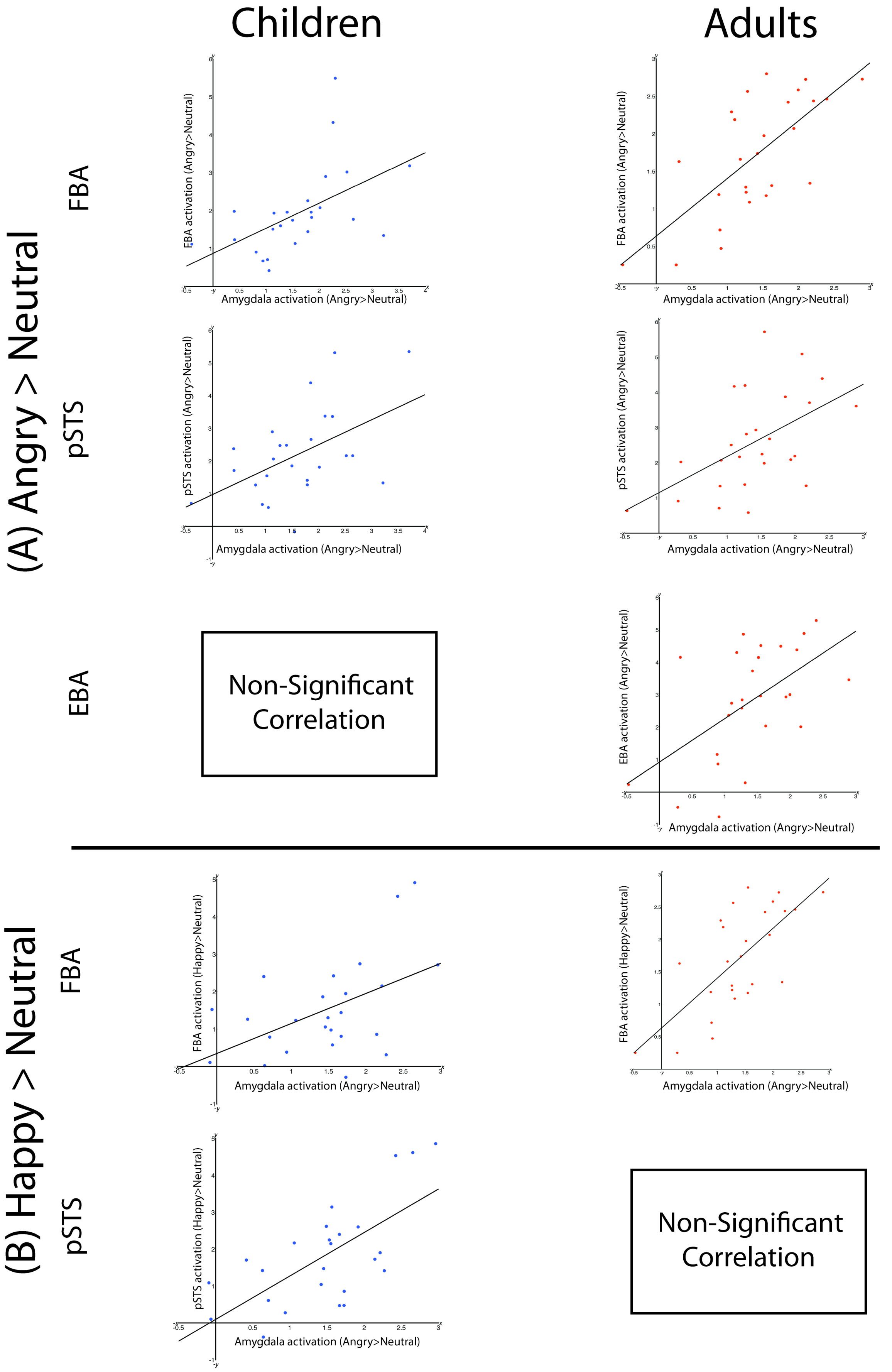


Figure 4-7 Significant correlations between emotional increases in amygdala and emotional modulation of FBA and pSTS in children, and FBA in adults for both (A) the Angry>Neutral contrast and (B) the Happy>Neutral contrast.
ROIs are averaged across hemispheres and each point represents one subject. Adolescents showed no significant correlations and so are not included here.

4.4 Discussion

We investigated the development of the body-selective areas in the visual cortex by comparing brain activity in adults, adolescents and children passively viewing angry, happy and neutral body movements, as well as non-body object movements. The present results show that all three age groups show activity in the main body-selective areas of the visual cortex (EBA, FBA and pSTS) when viewing Bodies>Non-Bodies. Whole-brain analysis revealed a main effect in the bilateral lingual gyrus driven by higher activation in the children and adolescents compared with the adults, and in the rFBA driven by higher activation in the adults compared with the children and adolescents. ROI peak *t*-value extraction showed that when viewing Bodies>Non-Bodies, the adults showed more sensitivity in the body-selective areas than the children (except for the lFBA), and more selectivity than the adolescents in the rEBA, rFBA and rAMY. This is in line with the findings of **Chapter 3** (Ross et al., 2014).

In terms of emotion modulation, at a whole brain level all three age groups showed similar activation in the body-selective areas when viewing Angry>Neutral bodies. Interestingly, only children showed amygdala activity at our $p<0.001$ uncorrected threshold. We observed no main effects at a whole-brain level and the ROI analysis yielded no significant difference across age in the sensitivity of these regions to the emotional stimuli.

Similarly, all three age groups showed modulation of the body-selective areas under the Happy>Neutral bodies contrast. In this instance the adults were the only group to display amygdala activity, and the rFBA could not be identified in the children. There was, however, no main effect of age in the whole brain analysis. As with the Angry>Neutral contrast, the ROI analysis yielded no significant difference in peak *t*-value across age in any ROI.

Finally, by using the peak *t*-values in a correlation analysis, we showed that children who showed stronger amygdala response to Angry or Happy>Neutral bodies also showed stronger emotional modulation of the FBA and pSTS. On the other hand, adults who showed stronger amygdala response to Angry>Neutral bodies showed stronger emotional modulation of the EBA, FBA and pSTS, while adults who showed stronger amygdala response to Happy>Neutral bodies showed stronger emotional modulation only in the FBA. Adolescents showed no correlation between emotion modulation in the body-selective areas and the concomitant response in the amygdala, and no age group showed any correlation between body-selective areas and amygdala activity when viewing the Non-Body stimuli.

4.4.1 Body-Selective Areas in Adolescents and Children

Chapter 3 in this thesis is the 3rd study to explore the functional development of the body-selective areas, with Peelen et al. (2009) and Pelphrey et al. (2009) being the first two (Carter and Pelphrey (2007) also used children in their fMRI study but focussed more on biological motion specifically). We could argue that this study is the first to use adolescents in a developmental fMRI study into the body-selective areas, however, Peelen et al. (2009) defined 'children' as anyone aged 7-17, so technically this is the second study to use adolescents in this way. This is the first study, however, to split its younger participants into clearly defined groups for more precise analysis (Children = Pre-pubescent, Adolescents = Currently Pubescent to Post pubescent), and the first to look at the function development of emotional body movement processing. It also has by far the largest sample of under 18 year-olds in an fMRI study of this kind with 43 children and adolescents, double that of any other study in the body recognition field.

When comparing viewing Bodies to viewing Non-Body movements, as in **Chapter 3**, we found similar body-selective areas in children and adults. As expected we also found these areas to be active in adolescents. Interestingly, both children and adolescents showed higher activation in the bilateral lingual gyrus compared to adults in our whole-brain analysis. The lingual gyrus has been identified as having a role in word processing (Mechelli et al., 2000), complex visual processing (Klaver et al., 2008), and most relevant to this study, the perception of human biological motion (Vaina et al., 2001;Servos et al., 2002;Ptito et al., 2003;Santi et al., 2003). Using diffusion tensor imaging (DTI), Loenneker et al. (2011) found that fiber tracts in the ventral stream differed between adults (aged 20-30) and children (aged 5-7). They found no difference in the fiber tract volume of the ventral pathway, but instead showed that adults had additional connections to posterior lateral areas (OTC), whereas children showed additional connections to posterior medial areas (LG). In other words, the ventral visual system was 'adult-like' in terms of fiber tract volume, but these differences in connection trajectories between children and adults suggests a reorganisation of fiber pathways from medial to lateral-temporal cortex. This reorganisation is also not complete by adolescence, as our adolescent group showed the same effect. Loenneker, Klaver et al. (2011) also show that ventral stream connections to the right fusiform gyrus (containing the FBA) seem to not be completely established in their 5-7 year old children.

They suggest that the fiber bundles to the lingual visual areas of the cortex in children may prune until adulthood due to experience-based plasticity. Unfortunately their study can shed no light on the functionality of this reorganisation, but it remains plausible then that the fiber tracts in children allow for visual stimuli to reach cortex dedicated to visual memory and language centres. As the child gets older and their cerebral architecture is shaped by experience, they show more fiber bundles leading to the OTC, an area specialised in processing visual semantic categories (Grill-Spector, 2003).

The ROI analysis, using nearly the same data as **Chapter 3**, showed similar results in adults and children; with adults showing more sensitivity (represented by higher peak *t*-values) than children in all ROIs except the lFBA. The adolescents, however, only showed significantly lower peak *t*-values than the adults in the rEBA, rFBA and rAMY. Given that these three regions also showed a significant difference between adults and children, but no difference between children and adolescents, one could argue for a developmental trajectory that is either so gradual during childhood and adolescence that it is undetectable here, or is simply flat. This is followed by an obvious jump in peak *t*-value once subjects come out of adolescence into adulthood.

However, all of these results are in the right hemisphere. This may be partially explained by the right lateralisation we observed in children in **Chapter 3**, and those observed in children using other modalities such as face stimuli (Golarai et al., 2010) or voice processing (Bonte et al., 2013;Rice et al., 2014). Again, these results should be examined with the caveat of not taking participant handedness into account (Willems et al., 2010). The literature presents a mixed picture in which the cortex becomes less lateralised over age (Golarai et al., 2010), increases in lateralisation (Ross et al., 2014), or in the case of Pelphrey et al. (2009), a full reversal of lateralisation. Right lateralisation in children could explain the lack of a difference in the rEBA, as children would already show adolescent levels of body-sensitivity in the right but not the left hemisphere.

4.4.2 Emotion Modulation of the Body-Selective Areas

The Angry>Neutral and Happy>Neutral contrasts produced similar activity to the Body>Non-Body contrast across groups in the body-selective areas. Interestingly, there was no main effect of age in either the Angry>Neutral or Happy>Neutral contrasts. So, contrary to the increase over age with the Body>Non-Body contrast, the ROI analysis for both Angry>Neutral and Happy>Neutral revealed no age differences in emotion modulation of the body selective areas, and no age differences in amygdala response. This rules out an attentional explanation for our Body>Non-Body age differences. If the children were showing significantly lower peak t-values due to paying less attention to the stimuli than the adults or adolescents, one would expect that effect to be present in the emotion modulation analysis as well. Furthermore, Sinke et al. (2010) demonstrated that, when presented with socially meaningful stimuli, the body-selective areas were found to be the most active when subjects were not attending the stimulus. Thus, according to this study, a lack of attention in the stimuli would manifest itself in the data as greater activation (in the context of socially meaningful stimuli).

This leads to the question then of why there is no increase in the emotion modulation of the body-selective areas over age, but under the Body>Non-Body contrast there was marked increases in sensitivity over age. One explanation is that even though the body-selective areas are increasing in size and selectivity between childhood and adulthood (Ross et al., 2014), the emotion modulation of these areas is already adult like in children. This seems to present a contradiction with our previous behavioural results in **Chapter 2**. Here, from a behavioural point of view, there was a sharp rise in emotion recognition accuracy from full-light human body movements between the ages of 4 and 8.5 years old. After 8.5 years we found a much slower rate of improvement in recognition accuracy. In this current study our youngest subject was 6 years of age. As our children subjects range from this 6 year old to an 11 year old, it is possible that if the child subjects in this fMRI study took part in our original behavioural study, they would be indistinguishable from the adult group in terms of recognition accuracy. In which case finding no age difference in the amygdala response and emotion modulation of the body-selective areas would come as no surprise. It is also possible that the differences in performance are linked to the differences in other occipital circuits (see Table 4-7), but a better model of the body processing network would first be needed in order to explore this possibility.

This, however, says little about the function of the body-selective system when it is being modulated by emotion. Using PLDs, Atkinson et al. (2012) showed strong evidence that emotionally expressive movements do not modulate precisely the neuronal populations that code the viewed stimulus category. This implies that a body-selective area that is active during emotional modulation may only be so due to top-down influence from some higher cortical area. Pichon et al. (2008) provided evidence in adults of the amygdala combining with activation in the fusiform areas when presented with angry body actions. They attribute this to the brain's natural response to threat, which has been replicated (van de Riet et al., 2009) and mirrored in primate studies (Amaral et al., 2003). But, if the stimuli do not modulate the body-selective areas directly, is there a top-down influence from the amygdala? Or, in other words, do the emotional cues contained in the stimuli produce amygdala activity that in turn activates category-specific populations of neurons in the visual cortex?

4.4.3 Correlation between Body-Selective Areas and Amygdala Activity

Our finding of significant positive correlations between amygdala response to emotional body movements and emotion modulation of the FBA and pSTS in children, EBA, FBA and pSTS under the Angry>Neutral contrast in adults and FBA under the Happy>Neutral contrast in adults partially supports the findings of Peelen et al. (2007). Furthermore, this is the first study to our knowledge to observe this effect in children.

Our results also support the van de Riet et al. (2009) work showing amygdala and fusiform cortex sensitivity to fear signals. We too find supporting evidence for a model of the EBA in which the region is specifically involved in processing the human body. We also provide evidence of a significant correlation between amygdala activity and emotion modulation in the adult EBA under the Angry>Neutral contrast (Grèzes et al., 2007;Pichon et al., 2008;Sinke et al., 2010;Kret et al., 2011). The positive correlation between amygdala activity and the pSTS in children could also shed some light on the findings of Atkinson et al. (2012) (in which they find that emotionally expressive movements modulate precisely those regions that code for the viewed stimulus). If we assume that the amygdala is influencing the activation in the pSTS, then the pSTS isn't just more active and sending more information to the amygdala. The increased exposure to body stimuli generally in childhood could lead to increased amygdala response being responsible for greater emotion modulation of the pSTS, heightening the sensitivity to the motion of the stimulus. This would account for our correlation between amygdala activity and pSTS emotion modulation in children for both Happy>Neutral and Angry>Neutral contrasts. Whichever direction the information is travelling, future work using DTI to explore the fiber tracts in this region at these age groups should answer some of these questions. Work addressing whether children show more sensitivity than adults to angry (or threatening) stimuli would also help support this hypothesis.

Equally intriguing, however, is the lack of any correlation between amygdala response and amount of emotion modulation in the adolescents. Considering the adults (as described by van de Riet et al. (2009)) and children show this correlation with the FBA, it is unusual that we do not observe it in adolescents. In an experiment looking at the development of emotional regulation, McRae et al. (2012) found that adolescents may not normally recruit regions associated with mental state attribution. They found a quadratic pattern of activation over age, with the adolescents responsible for the dip in the model. This quadratic pattern of activation implies an 'adolescent dip' in activation in areas associated with social cognitive processes (McRae et al. (2012) cite the anterior temporal cortex, medial prefrontal cortex and posterior cingulate cortex). If this were the case here we might expect to see the adolescents showing lower peak *t*-value activation in some of the emotion modulation contrasts. Perhaps we may have seen such a result if we had included some kind of online task for subjects to perform while viewing the stimuli. Vink et al. (2014) suggest that an increase of recruitment in medial prefrontal cortices coupled with a decrease in limbic subcortical regions occurs in adolescence. They go on to describe an increase in functional coupling between the limbic subcortical and frontal regions. Forbes et al. (2011) describe more ventrolateral prefrontal cortex (VLPFC) activity in adolescents when presented with Angry>Neutral faces. Perhaps due to the increase in VLPFC activity, which seems to serve a regulatory function for amygdala activity during social threat signals (Monk et al., 2008); this change in coupling pathways from the amygdala might account for the curious lack of an amygdala-FBA correlation during emotion modulation in our adolescent subjects. It is this change in white matter connectivity and a lack of top-down control in this age range which may be masking the effect (Casey et al., 2008).

More adolescent subjects would allow us to perform regression analysis across age and get a better picture of the quadratic relationship in these correlations. It would also allow us to group our subjects by all Tanner stages and not just pre-pubescent and above. Perhaps most useful would be a longitudinal design (see Moore et al. (2012)), as this would eliminate group differences and would allow comparison across all Tanner stages in a relatively short period of time (3-6 years).

4.4.4 Conclusions

To summarise, we found evidence that the body-selective areas of the visual cortex are not adult-like bilaterally in children and not adult-like in the right hemisphere in adolescents. Further, we present evidence, for the first time, of emotion modulation in these areas in children and adolescents. We found that the emotion modulation of the body selective areas were adult-like in children and adolescents for both Angry and Happy body movements. Finally, we showed positive correlation between amygdala activity and emotion modulation of the FBA and pSTS of children under both emotional contrasts, EBA, FBA and pSTS in adults under the Angry>Neutral contrast and FBA in adults under the Happy>Neutral contrast, suggesting that the modulation of the visual areas may originate from higher cortical areas. A lack of any correlation in our adolescent group could be explained by maturational increases in prefrontal cortex activity, serving a regulatory function for amygdala activity when presented with social stimuli. These data provide new directions for developmental studies focussing on emotion processing of the human body, and could have wide clinical applications in both typically and atypically developing populations.

5 Functional Development of the Temporal Voice Areas

5.1 Introduction

Efficient processing of the information carried within the human voice is critical for normal social interaction. Recent studies have explored the neural basis of our ability to interpret a speaker's gender, character traits, emotional state or age (Belin et al., 2008;Bestelmeyer et al., 2010;Belin et al., 2011;McAleer et al., 2014) from both linguistic and non-linguistic information. Functional magnetic resonance imaging (fMRI) studies have identified regions along the anterior, middle and posterior portions of the superior temporal sulcus (aSTS, mSTS and pSTS) that show a selective response to vocal sounds, even when devoid of linguistic content (Bestelmeyer et al., 2010;Latinus and Belin, 2012). The importance of these temporal voice areas (TVA) in voice processing is widely acknowledged, even if the exact functional role is still being investigated.

Generally, social cognition continues to improve during childhood and adolescence. In addition, previous research indicating that face-specific (Batty and Taylor, 2006;Golarai et al., 2010) and body-selective (Ross et al., 2014) cortical activity is lower in children and adolescents than in adults. Much less is known about the functional development of the voice-selective areas, both in terms of extent of activation and sensitivity to vocal sounds.

To date, only three studies have explored the functional development of the TVA, and at quite different age ranges. Using functional near-infrared spectroscopy in infants, Grossmann et al. (2010) found that 7-month-olds, but not 4-month-olds, showed increased responses in the bilateral TVA when listening to human voices compared to non-vocal sounds. Blasi et al. (2011) replicated this result with 3-7 month old infants, and further showed that emotional voices modulated various other regions involved with the processing of affective stimuli. More recently, using fMRI in children, adolescents and young adults, Bonte et al. (2013) looked at the developmental trajectories of both the function and morphology of the superior temporal cortex (STC) region. They found a rightward lateralisation for voice-selective regions in all age groups, but this effect decreased with age. They also show that this rightward asymmetry in the STC's response to voice changes from being less sensitive (lower *t*-values) and more spatially diffuse (larger numbers of voxels) in children toward highly selective and focal activation 'spots' in adults.

Conversely, Belin et al. (Submitted) found, using a random effects analysis of 152 adult subjects, that there was no significant lateralization of the TVA. Instead, they suggest that the previously reported larger maxima in the right hemisphere are likely to be simply an artefact of small sample sizes. Belin and colleagues, however, did not use children in their large study, so it remains to be seen whether the decreasing right lateralisation over age result observed by Bonte et al. (2013) could be replicated.

Belin et al., (Submitted) also identified 3 clusters found bilaterally along the STS that make up the TVA. They found the densest cluster to be located where the STS is the deepest, along the mid/posterior portion of the sulcus. These clusters are highly sensitive to human vocal sounds and are in line with Bonte et al.'s findings of focal spots in adults. However, the spatially diffuse and less selective STC voxels found by Bonte et al. (2013) in children could simply be masking these clusters. Furthermore, if adult clusters are also selective in children, then what is their developmental trajectory?

Here we will address these questions using similar peak *t*-value extraction techniques employed in **Chapters 3** and **4**. We will also use multivariate pattern analysis when looking at TVA differences over age. This will give a more sensitive analysis of the data, as it will essentially eliminate any masking effect of the surrounding activity in the children found by Bonte et al. (2013). This will allow us to look, for the first time, at the classification accuracy of the voice-selective brain areas across age, as well as the developmental trajectory of classification accuracy in the 6 TVA clusters identified in adults.

Therefore, in the present study, we investigated the developmental trajectory of the TVA in children, adolescents and young adults using fMRI. We first set out to replicate Bronte et al.'s findings of a right lateralisation in the voice-selective areas, the effect of which should decrease with age (reflecting the lack of lateralisation effects found by Belin et al. in adults (Submitted). We then focused on exploring the developmental trajectory of the TVA clusters outlined by Belin et al., and hinted at by Bonte et al. (2013). Following this, we used MVPA to give a more sensitive level of analysis and chart the development of voice-selective area selectivity free from any potential masking effects caused by children's diffuse activation, found by Bonte et al. (2013). We hypothesise that the classification accuracy of the TVA in children, as with the sensitivity (measured by peak *t*-values), will be lower in children than adults.

5.2 Materials and Methods

5.2.1 Participants

Sixteen children aged 7-12 (M = 9.25 years, SD = 1.77, 8 females) and 15 adolescents aged 13-17 (M = 15.27 years, SD = 1.44, 10 females) were recruited from Primary and Secondary schools and afterschool clubs in the West End of Glasgow. All of the child participants were at Tanner stage 1, that is, pre-pubertal, as assessed using the Pubertal Developmental Scale (PDS; Petersen et al. (1988)), a sex-specific eight-item self-report measure of physical development (e.g. growth in stature, breast development, pubic hair etc.) filled in by parents. All adolescent participants were Tanner stage 2-5; that is, either currently pubertal, or post-pubertal. All participants understood that participation was voluntary, written consent from the children's parents or guardians were obtained before testing began, and subjects received payment for their time at a rate of £6/hour (or equivalent in book or cinema vouchers for the children). The study was in line with the Declaration of Helsinki and was approved by the local Ethics Committee. A sample of 18 adults from the University of Glasgow also took part in the study (Age 21-27: M = 25.61 years, SD = 1.29, 8 females).

5.2.2 Stimuli

The stimuli set used to localise the TVA is adapted from the contrast of Vocal vs. Non-Vocal sounds used in Belin et al. (2000a). It contains 40 8-second blocks of sound (16 bit, mono, 22050 Hz sampling rate): 20 blocks consist of only vocal sound (baby babbling, syllables, coughing etc.) and 20 consist of only non-vocal sounds (animal vocalisations, environmental sounds etc.). All sounds have been normalised for RMS and a 1 kHz tone of similar energy is provided for calibration. Stimuli are publically available at http://vnl.psy.gla.ac.uk/resources.php.

5.2.3 Procedure

We measured brain activity using a 3T fMRI scanner (Tim Trio, Siemens, Erlangen, Germany) equipped with a 32-channels head coil, using standard EPI sequence for functional scans (TR/TE: 2000ms / 30ms; slice thickness = 3 mm; in plane resolution = 3 x 3 mm). In addition, we acquired a high-resolution T1-

weighted structural scan (1 mm3 3D MPRAGE sequence) for anatomical localization.

Parents/guardians were allowed to sit with their children in the scanning room if they or their child wished (This was the case for 3 subjects). Children were first familiarised with the environment with a 3-minute dummy scan while they watched a cartoon. This allowed us to give them feedback on any movement and thus, along with appropriate cushioning, minimise their head motion.

The blocks of vocal and non-vocal auditory stimuli were presented in a randomized order with 10 seconds of silence in between two blocks. The experiment lasted ten minutes. Stimuli were presented through MRI-compatible insert earphones. Participants were asked to listen passively with their eyes closed.

Some subjects also participated in another 8-minute functional scan (for **Chapter 3** and **4**) from an independent study before completing the structural scan.

5.2.3.1 Pre-processing

Pre-processing and statistical analyses of the data was performed using MATLAB and SPM 8 (Welcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm). Functional data underwent motion correction using a two-pass procedure to register the images to the mean of the images after the first realignment. They were then re-sliced with a 4th Degree B-Spline interpolation. Movement correction was allowed up to 2mm translation or 2 degrees rotation; participants showing larger motion in any direction were excluded from the analysis. Functional data were co-registered with the individual 3D T1-weighted scans by identifying the anterior and posterior commissures manually. The anatomical scans were segmented for different tissue types and transformed into MNI-space using non-linear registration. The parameters from this transformation were subsequently applied to the co-registered functional data. For the whole-brain and region-of-interest analyses, the data were spatially smoothed with a Gaussian kernel (8mm FWHM). Unsmoothed (but still spatially normalised) data was used for the multivoxel pattern analyses. High-pass temporal filtering was also applied at a cut off of 128 seconds to remove slow signal drifts.

As explained in previous chapters (see **Chapters 3** and **4**), by normalising the data from our adults and children into the same stereotactic template, we were able to directly compare the strength and extent of activation across age groups. Several studies examining the feasibility of this approach have found no significant differences in brain foci locations when the brains of children as young as 6 were transformed to an adult template (Burgund et al., 2002;Kang et al., 2003). These findings gave us confidence that there is no confound of brain size in our results.

5.2.3.2 Whole brain analysis

One predictor for each condition of interest (Voice and Non-Voice) was used in a general linear model. The six head-motion parameters were also used as covariate of non-interest. The model was estimated for each participant and individual contrasts (e.g. Voice>Non-Voice) were taken to the second level for random effects analysis. For comparison across age we created group-averages separately for children, adolescents and adults. Group analyses were performed with a random-effect model and the resulting statistical maps presented at a threshold of $p<0.001$ uncorrected with a cluster extent threshold of 10 voxels. Anatomical names for various functional activations were determined using the Harvard-Oxford cortical and sub-cortical structural atlases in FSLview (Jenkinson et al., 2012).

5.2.3.3 ROI Cluster definition and analysis

We defined three bilateral TVA clusters or ‘voice patches’ alongside mid-to anterior STS/STG by considering voxels within a 5-mm radius sphere centred at the MNI coordinates in Belin et al. (Submitted). These clusters are the anterior, middle and posterior voice patches (TVAa, TVAm, TVAp respectively, see Figure 5-1). To test for differences in activity across ROIs and age group for each participant we extracted the individual peak *t*-values of the activated clusters. These parameters were then entered into a 3x6 mixed-design ANOVA, with ‘Age-Group’ as between subject factor, and ‘ROI’ as within subject factor.

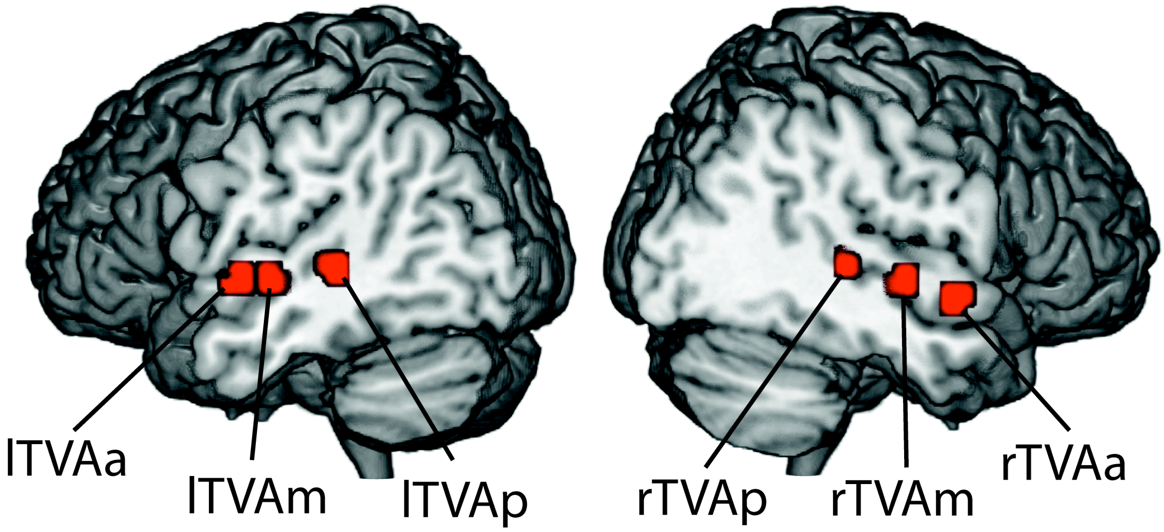


Figure 5-1 The location of the six TVA clusters.

5.2.3.4 Multivariate pattern analysis

Using unsmoothed data, we first estimated the parameters of a linear model modelling the response to each of the 40 blocks (20 vocal and 20 non-vocal). We then used a searchlight approach (Kriegeskorte et al., 2006) in these parameter-estimates brain maps (one map/bloc). At each voxel, we defined a local spherical mask (radius 6mm, 33 voxels) and performed a 'leave-one-out' procedure, training a support vector machine (SVM) (vocal or non-vocal) on 39 of the blocks before being tested on recognizing the category of the 40th. This was then repeated 40 times in each searchlight, using a different bloc for testing in each iteration. If a searchlight area did not include at least 50% grey matter, it was excluded from further analysis.

This procedure resulted in classification maps for each participant, depicting at each voxel the number of times the classification was accurate for the searchlight centred in this voxel. These maps were used to perform both whole-brain and ROI group-level analyses.

5.2.4 Control for potential artefacts

5.2.4.1 Head motion

No subjects reached our criteria to be excluded from analysis for excess head motion (motion larger than 3mm in any translation or 3 degrees in any rotation direction). However, any potential group difference in fMRI activation could still be a by-product of a small group difference in head motion. Thus, each participant's motion parameters (obtained when performing the realignment in the pre-processing stage) were included in the general linear model at the first level analysis as parameters of non-interest in order to exclude any potential effect on the activation of interest. In addition, a 6X3 repeated measure ANOVA with 'Motion Direction' as the within subject factor and 'Age-Group' as the between subjects factor found no main effect of Age-Group (F(2,39)=.343, p=.712).

5.2.4.2 Variance in model noise

Finally, for comparison of within subject error, we looked at the residual sum squares for the whole time-course in each of the 6 ROIs across age. This gave us a noise estimate in our model for each participant. Here we found no main effect of age in the residuals in any of the ROI clusters (rTVAa: F(2,46)=2.69, p=.079; rTVAm: F(2,46)=2.13, p=.131; rTVAp: F(2,46)=1.15, p=1.15; lTVAa: F(2,46)=.118, p=.889; lTVAm: F(2,46)=.180, p=.836; lTVAp: F(2,46)=2.22, p=.120).

5.3 Results

5.3.1 Whole brain contrasts

When contrasting Voice>Non-Voice, all three groups showed activity in the bilateral posterior superior temporal sulcus (pSTS), bilateral mid-to anterior temporal gyri and sulci (aSTS), precentral gyrus in the adults and adolescents and left amygdala in the adults (Figure 5-2 and Table 5-1).

Table 5-1 Regions activated in a whole-brain group-average random-effects analysis contrasting Voice>Non-Voice.
(p<0.001 uncorrected, cluster extent threshold of 10 voxels). Coordinates are in MNI space.

Region	Adults					Adolescents					Children				
	x	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*	*x*	*y*	*z*	t	*cm3*
Left STS	-63	-10	4	15.2	37.4	-57	-1	-11	7.1	19.1	-60	-22	4	7.6	10.4
	-54	-19	-2	12.8	Sub-Peak	-60	-19	1	7.0	Sub-Peak	-57	-13	1	7.2	Sub-Peak
	-69	-25	4	11.7	Sub-Peak	-51	-22	1	6.5	Sub-Peak	-57	8	-17	5.8	Sub-Peak
Right STS	63	-28	1	11.2	38.4	51	-19	4	9.0	23.7	60	-19	-2	6.9	13.3
	57	-34	4	10.9	Sub-Peak	54	11	-14	7.9	Sub-Peak	69	-25	4	6.4	Sub-Peak
	63	-4	-5	8.9	Sub-Peak	45	5	-14	7.6	Sub-Peak	57	-28	7	6.3	Sub-Peak
Right PFG	54	-1	46	5.7	1.22	51	5	43	7.0	0.81					
Left AMY	-18	-10	-14	4.2	0.38										

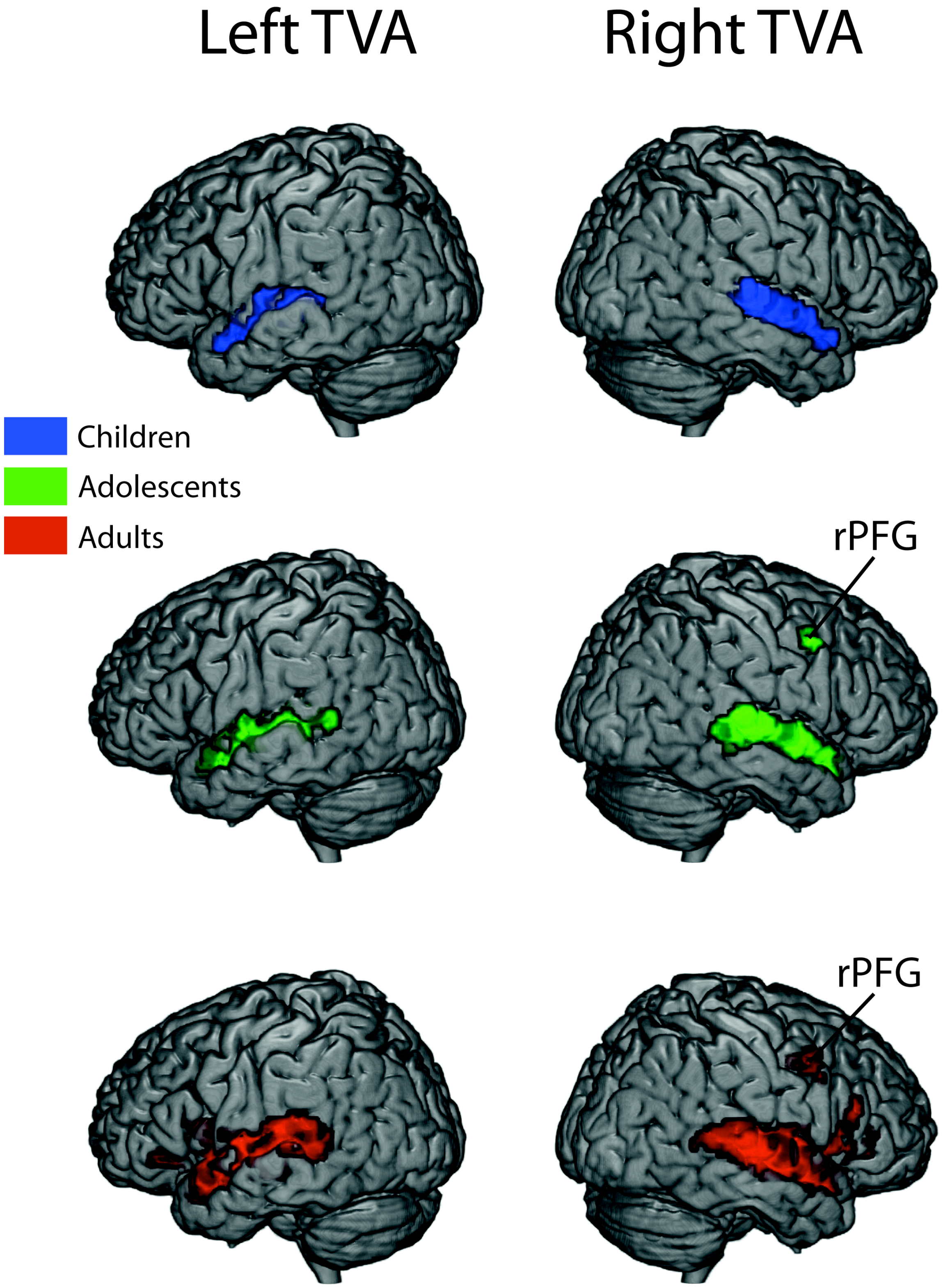


Figure 5-2 Brain activity when listening to Voice>Non-Voice stimuli in children, adolescents and adults.
(Threshold at $p<0.001$ uncorrected and 10 voxels extent).

We found no main effect of age between the three age groups, at our *p*<0.001 uncorrected threshold level.

In terms of activation extent in both the right and left TVA (calculated by taking a count of voxel showing a difference above *p*<0.001 in the STS whole-brain analysis activation in both hemispheres, Table 5-1), ANOVA revealed no main effect of age in either hemisphere. We observed a significant right hemisphere lateralisation in all age groups (Children: *t*(13)=7.16, *p*<.001; Adolescents: *t*(16)=6.17, *p*<.001; Adults: *t*(17)=5.08, *p*<.001).

5.3.2 Region of interest analysis

5.3.2.1 Peak t-value

The peak-t values for children, adolescents and adults in all six ROIs are presented in Figure 5-3. An 'Age-Group' x 'ROI' ANOVA revealed a main effect of age-group (F(2,44)=3.25, p<.05), a main effect of ROI (F(5,220)=12.13, p<.001) but no interaction between the two (F(10,220)=1.55, p=.835). Bonferroni corrected follow up analyses showed that the main effect of age-group was driven by a difference in the rTVAm F(2,44)=5.87,p<.005. Further post-hoc analyses revealed that the adults showed significantly higher activation in this region than the young children (*p*<.005).

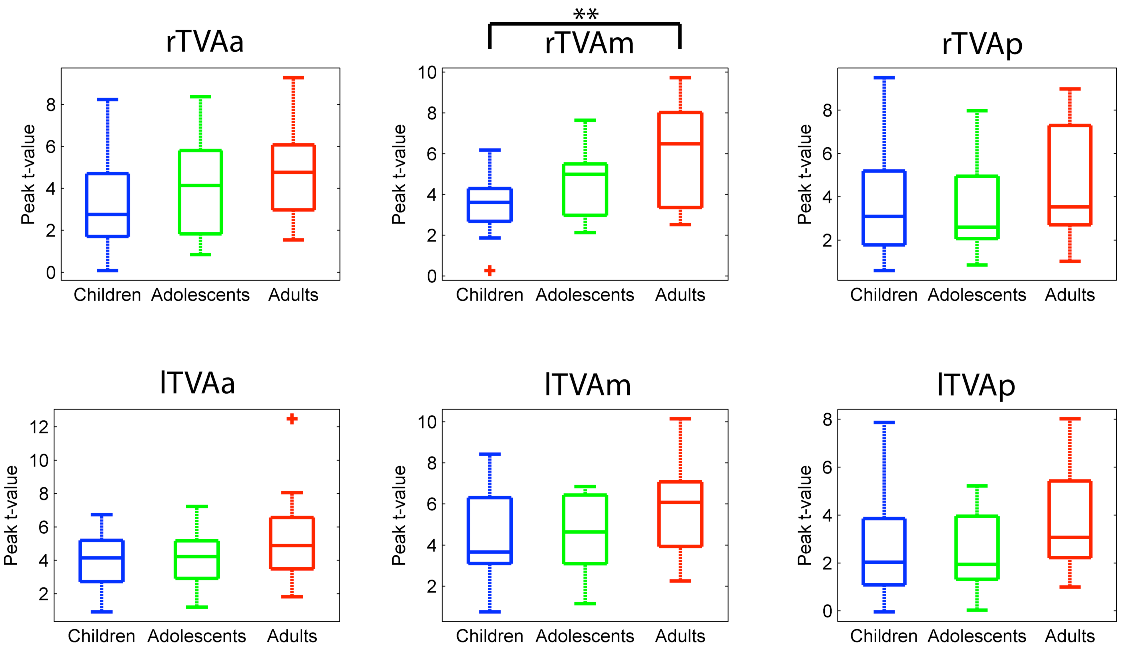


Figure 5-3 Box-plots displaying the peak *t*-value in the six TVA clusters across all subjects. (Note that *y*-axes are not homogeneous)

5.3.2.2 Multivariate pattern analysis

We observed classification accuracy above chance (defined as 50% due to the two types of stimuli, voice and non-voice) along the STS/STG in all three age groups. Using a 2nd level whole brain random-effects analysis, we found no main effect of age on the classification accuracy at a $p<0.001$ uncorrected threshold level.

Averaging the percentage accuracy scores across voxels within each of the six ROI clusters, and using a non-parametric ANOVA, we observed no main effect of age in any cluster whether we were looking at the average classification accuracy per cluster (rTVAa: $X^2(2)=3.50$, $p=.174$; rTVAm: $X^2(2)=2.83$, $p=.243$; rTVAp: $X^2(2)=.727$, $p=.695$; lTVAa: $X^2(2)=3.38$, $p=.184$; lTVAm: $X^2(2)=931$, $p=.628$; lTVAp: $X^2(2)=1.14$, $p=.566$; See Figure 5-4 A), or the maximum classification accuracy per cluster (rTVAa: $X^2(2)=3.07$, $p=.216$; rTVAm: $X^2(2)=3.45$, $p=.179$; rTVAp: $X^2(2)=1.27$, $p=.530$; lTVAa: $X^2(2)=1.72$, $p=.422$; lTVAm: $X^2(2)=780$, $p=.677$; lTVAp: $X^2(2)=1.27$, $p=.531$; See Figure 5-4 B).

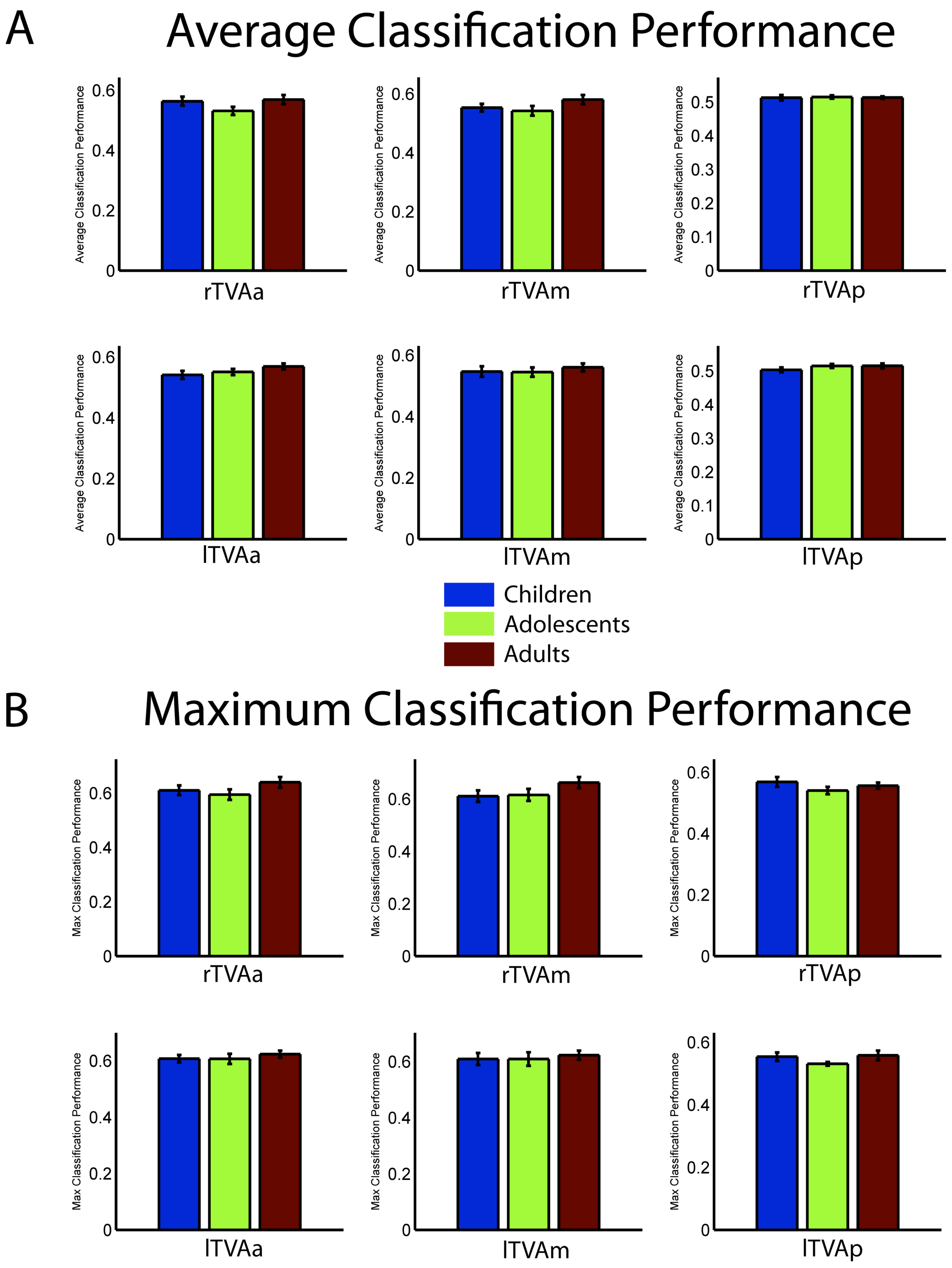


Figure 5-4 (A) Average classification accuracy of each TVA clusters across all participants. (B) Maximum classification accuracy of each TVA clusters across all participants.

5.4 Discussion

Using fMRI we investigated the functional development of the voice-selective areas in the superior temporal cortex of adults, adolescents and children. We found no age related difference in the whole brain analysis, either in terms of strength or extent of activation. When focussing on the 6 TVA clusters, we found no main effects of age in any clusters except the rTVAm. This reflected significantly higher selectivity (measured as peak *t*-value) in adults than in children in this area. MVPA showed no difference across age. In the 6 TVA clusters, we found no main effect of age in the peak classification accuracy, or the cluster average.

Partially contrasting the findings of Bonte et al. (2013) we find a right lateralisation in children, which continues through adolescence into adulthood.

Interestingly, we also find that in terms of selectivity and sensitivity, the TVA is 'adult-like' in children and adolescents. Based on the current literature on face-selective regions and the body-selective regions (results of **Chapters 3** and **4** in this thesis), this would make the voice-selective areas the first major interpreter of social stimuli to functionally mature to an adult level.

5.4.1 Lateralisation

As mentioned above, we found a significant right lateralisation of the TVA in children, but contrary to Bonte et al. (2013) this effect did not decrease with age. There was also no significant age effect in the activation extent of either hemisphere. This commonly reported right lateralisation is addressed in Belin et al., (Submitted), in which they suggest that the lateralisation is caused by an artefact of small sample size. They acknowledge that their large sample size shows slight right lateralisation, but this difference is not statistically reliable. They claim that when a conveniently large sample size is examined using the statistical test of lateralisation that they use (the lateralisation index (Wilke and Schmithorst, 2006)), no significant lateralisation effect is found. However, the articles they cite showing a right-lateralisation are the original study outlining the voice-selective areas (Belin et al., 2000a) that had 14 participants, and a similar experiment using macaque monkeys that used 7 participants (Petkov et al., 2008). Here we had 49 participants (arguably a rather large sample), and found significant right lateralisation of the TVA. Therefore although our sample of adults is relatively modest, and so could adhere to the small sample bias outlined in Belin et al., (Submitted), the same may not be said for the right lateralisation observed in our child or adolescent sample. As the average age in the Belin et al. (2000a) study was 24 years, their results cannot be applied to the right lateralisation in our younger participants, even though ours are relatively small samples. We must, therefore, take these results to be corroboratory evidence with Bonte et al. (2013) and conclude that there is supporting evidence for a right lateralisation of the TVA in children, albeit one that persists over age.

5.4.2 An 'Adult-like' voice area in children

When looking at differences in activation strength, it should be noted that our artefact controls give us strong confidence that any age-group differences in fMRI signal change and peak *t* extraction are not due to differences in head motion, within-subject error in model fit, or variance in signal, but are due to functional processing of the stimuli.

Having said this, the only difference we observed in any age group was between the peak *t*-value of the children and adults in the rTVAm. Interestingly, this location also corresponds to the portion of the sulcus with the largest depth (Belin et al., Submitted). One could argue that this relative increase in grey matter within rTVAm increases statistical power of our comparisons. Future work in this area could focus on voxel-based morphometry (VBM) to explore any potential focal difference in anatomy in this region over age.

A finding of no main effect of age in our whole brain analyses in either extent or strength of activation indicates that the voice-selective areas of children are already adult-like by the age of 7 years old. This contrasts the findings of Bonte et al. (2013) who found the area to be less selective and more spatially diffuse in children compared to adults.

In terms of spatially diffuse activation in children, along with our motion and model variance controls, we also performed an MVPA, which negated any possible noise and diffusion of activation effect in the children. This more sensitive analysis also revealed no age difference in the classification of vocal and non-vocal sounds. This reflects a voice-selective system in the temporal sulci which is selectively mature from a functional point of view in children as young as 7 years old.

This is in line with studies finding voice-selective responses in infants, which correspond to areas observed in adults. Blasi et al. (2011), found that 3 to 7-month-old infants displayed similar activation to adults in the anterior temporal cortex (likely the anterior or middle TVA cluster). Interestingly, they also found that emotionally negative voices modulated the activity in the orbitofrontal cortex and insula in the infants. Children as young as 5 years old have been shown to recognise ten emotions (Achievement, Amusement, Contentment, Relief, Neutral, Surprise, Anger, Fear, Disgust and Sadness) from non-verbal vocalisations with an average accuracy of 78% (Sauter et al., 2013). This was not shown to significantly increase over age. Thus one might assume that the ability to process the emotional content of voice occurs very early in a child's development. Future work could both combine the work of Sauter and colleagues and our fMRI work here to explore the functional development of the TVA throughout childhood, and perhaps try to mirror our results from **Chapter 4** by looking for a correlation between amygdala and the voice-selective areas.

5.5 Conclusion

The voice areas then are among the earliest social signal processing systems to develop to an adult level of activation strength, extent, and specificity. It has already been shown using near-infrared spectroscopy that a voice-sensitive brain system in the bilateral STC has materialised by 7-months of age (Grossmann et al., 2010;Blasi et al., 2011), however, this is the first study to directly explore the development of the strength, extent and specificity of human voice processing. Without any means of direct comparison (due to morphological, practical and methodological issues) between children younger than 7 years of age and adults in terms of functional processing, for now, this is as young as we can speculate that children's neural processing is adult-like on a purely functional level.

6 General Discussion

6.1 Summary of Aims

The main purpose of this thesis was to explore the functional development of social signal processing. In contrast to the abundance of literature on face recognition, research on the perception and recognition of the human body and human voice has been in short supply. There is even less work detailing the development of these processes.

We began with a behavioural study examining the development of the ability to recognise emotions from body movements. To separate form and motion perception we used both full-light and point-light displays (**Chapter 2**). We expected poorer recognition accuracy when subjects viewed point-light displays compared to full-light displays across all participants. Furthermore, the ability to recognise emotions from body movements was expected to continue to improve through childhood and adolescence. Based on the face literature, this may have taken a non-linear trajectory (De Sonneville et al., 2002;Tonks et al., 2007;Lagerlof and Djerf, 2009;Gao and Maurer, 2010).

Any interaction between age and the lighting condition would also indicate a differential use (at a functional level) of different aspects of the stimuli (form or form and motion here). This led to the question: ‘Do children and adults process the human body differently on a functional level?’

Only two studies before that had directly compared the recruitment of the body-selective areas of the visual cortex in children and adults. One study (Peelen et al., 2009) had defined children as anyone 7-17 years old, and the other (Pelphrey et al., 2009) had used low thresholds leading to very large body-area definitions. We set out to replicate the results of these studies, both of which found the body-areas to be ‘adult-like’ by 7 years old, using a larger, more homogenous sample of children (all pre-pubescent). Pelphrey et al. (2009) also showed an initial right lateralisation of the EBA in children, and found a reversal of this effect in adults.

Using the face literature again as a basis, we turned to the spatial pattern of neural representation. Golarai et al. (2010) found that a sparse spatial representation of activation best explained the face perception data in adolescents, and that this pattern did not change over age. Using a multivariate method of Bayesian model comparison, we wanted to determine which spatial pattern of neural representation best described the body-selective regions. Based on previous work, we also hypothesised that along with the strength and extent of activation in these regions, the pattern of neural representation would also not be ‘adult-like’ in pre-pubescent children.

Combining the results of **Chapter 2** and **Chapter 3**, we wanted to find out if the emotion modulation of the body-selective areas was also ‘adult-like’ in children and adolescents. Previous work had shown that these areas show emotion modulation when presented with dynamic (Grèzes et al., 2007;Pichon et al., 2008;Sinke et al., 2010;Kret et al., 2011), but not static (de Gelder et al., 2004b;van de Riet et al., 2009) stimuli. The effect, however, had never been demonstrated in children and adolescents. Therefore, in **Chapter 4** we aimed to expand upon the work of **Chapter 3** by including adolescent data into the developmental trajectory. Then, by using affective stimuli, we could explore the functional development of body-selective area emotion modulation across age.

Finally, and turning away from perception of the body, in **Chapter 5** we focussed on the third (and least studied) social signal, the human voice. Given the work on developmental trajectories of face perception, and our work here on the development of body perception, we wanted to complete the picture with a third social signal modality. The voice has been shown to be a salient communicator of various aspects of social information (Belin et al., 2000a;Belin et al., 2008;Bestelmeyer et al., 2010;McAleer et al., 2014). Despite this, only one study has looked at functional development of voice processing in the brain (Bonte et al., 2013) using children and adolescents. They found a right lateralisation for voice-selective responses that decreased with age. They also found that children showed more diffuse activation, while activation in adults tended to exist in focal ‘spots’. These spots seemed to support the 6 focal regions outlined by Belin et al., (Submitted) in adults. So, first we wanted to replicate the right lateralisation found by Bonte and colleagues, and then find out if these focal regions existed in children. This makes Experiment 4 (**Chapter 5**) only the second study to date to chart the functional developmental trajectory of the bilateral temporal voice areas in children and adolescents. This work combined with the body-selective area developmental studies allowed us to fill a large gap in the social developmental neuroscience literature, a field that has been dominated by face research for over 30 years.

6.2 Overall Findings

We found in our behavioural study that, on average, all subjects showed significantly lower emotional accuracy scores when recognising emotions from point-light displays compared with full-light displays. The improvement of this ability was found to follow a non-linear developmental trajectory. Using piecewise regression, we found that a bilinear model best explained the data. This model had a steep improvement in recognition accuracy until 8.5 years of age, followed by a much slower rate of improvement through last childhood and adolescence. This confirmed that, in line with face literature, child and adolescent recognition of basic emotions from body movements is not fully mature and seems to follow a non-linear developmental trajectory. Interestingly, there was no difference in trajectories between point-light and full-light displays. Form information produced a purely additive effect to recognition scores across age.

So from a behavioural level, children differed from adults in emotional recognition accuracy. But, how did their processing of full-light body movements differ on a neural level? Our first fMRI study showed that, contrary to previous work, the body-selective areas of the visual cortex were not ‘adult-like’ in terms of the strength or extent of activation. We also observed a right lateralisation of the body-selective areas, and contrary to our hypothesis and previous work, extent of activation became more right lateralised in adults. Finally, using MVB analysis, we found that despite the greater strength and extent of activation in adults, there was no difference in the pattern of spatial encoding between children and adults.

We expanded this work in **Chapter 4** to include adolescents and explore the functional development of the body-selective areas across this wider age range, as well as looking at how the emotion modulation of these areas changes over age. We found that the adolescents (like the children) weren’t adult-like in terms of activation strength when viewing body movements compared with non-body movements. However, whereas the children showed this result bilaterally, the adolescents only showed significantly less activation than adults in the right hemisphere. Children and adolescents also both showed more activation in the lingual gyrus than adults. We suggest that this is related to the reorganisation of fiber pathways from medial to lateral-temporal cortex between childhood and adulthood described by (Loenneker et al., 2011).

In terms of the emotion modulation, we found no difference across age in the peak *t*-values of the body-selective regions.

Finally we partially replicated the results of Peelen et al. (2007) by showing that adults who showed stronger amygdala response to angry or happy bodies showed stronger emotional modulation of the FBA (and EBA under the Angry>Neutral contrast). We also, for the first time, showed that children show this same amygdala correlation in both the FBA and pSTS under both emotion contrasts. The adolescents on the other hand did not show any correlation between amygdala activation and amount of emotion modulation in the body-selective areas.

In the final experiment outlining the developmental trajectory of the TVA, we found no difference across age in the six TVA clusters except the rTVAm. Here the adults showed significantly higher sensitivity than children. However, when we performed an MVPA we observed no difference across age. Although we replicated the right lateralisation of the voice-selective areas in children, contrary to Bonte et al. (2013) we found that this lateralisation continues through adolescence into adulthood.

6.3 Developmental Trajectories of Social Signal Processing

Here then we have the first look at a full picture of the development of social signal processing. The voice areas show signs that they are already ‘adult-like’ in children as young as 7 years old, making voice the first major modality to mature in terms of functional processing. The functional processing of the human body on the other hand is still not adult-like in children of 7 years. Indeed, our data suggests that the strength of activation in the rEBA, pSTS and rAMY are all not adult-like even in pubertal and post-pubertal adolescents. This puts it on par with face perception, the development of which is still on going through adolescence (Casey et al., 2008).

Interestingly, our work here suggests that although the body-selective areas are not adult-like in their strength of activation in children, there is no significant difference in their modulation by emotion. It is difficult to directly link this result with our behavioural findings, as we grouped children by pubertal stage in the brain imaging experiments, but used age as a continuous variable in the behavioural. Taken together, it would seem that although there is no functional difference in the emotion modulation of the brain areas, the behavioural responses differ. This could be due to several factors all previously mentioned (deductive reasoning during ambiguous stimuli or using two different sets of dynamic body stimuli for example). The two factors most likely to account for this unusual result are the age of the children in both experiments and the presence of a task.

This has already been touched upon in **Chapter 5**, but the youngest child in our behavioural study was 4 years old, and the knot in our bilinear regression fell at 8.5 years. The pre-pubescent children in our brain imaging studies were approximately 7-12 years old. This leaves only one and a half years of overlap between the two groups. Therefore, without data regarding the functional activation in children between 4 and 7 years of age, it is going to be very hard to square that circle. Unfortunately it would also be very difficult to obtain (and effectively analyse) such fMRI data from children so young. This is part of a wider problem with developmental work of this kind which I expand upon below; namely the various definitions of the word ‘children’.

The other factor of which we cannot account here is the presence of a task. In our brain imaging experiments we deliberately did not include a task for the participants. This was partly to save time and ease the process of scanning children, but mainly it was done to avoid any influence from motor or decision-making regions from interfering or masking the response to the stimuli. If our subjects were given a one-back task or simply given a forced choice emotion recognition task, we would expect the functional activation observed to be quite different. The adolescents in particular may have shown more activation in the prefrontal or anterior temporal cortices and less activation in the limbic subcortical regions (Vink et al., 2014). Not only because the task itself would elicit activation from executive function and motor areas, but also because those two tasks are probing two different types of emotion processing. It is debatable whether a task related to the stimuli, but unrelated to the emotion (implicit emotion processing) or a task involving emotion judgement (explicit emotion processing) is the most useful to explain the underlying emotion processes (review in Gyurak et al. (2011)). Both are necessary forms of emotion regulation, but future studies focussing on explicit (or effortful) emotion processing should perhaps be wary of comparing results with others who have investigated implicit (or automatic) emotion processing and vice versa. This leads into the other intriguing developmental trajectory that we uncovered in this thesis, that of amygdala correlation with body-selective areas during emotion modulation.

The amygdala is widely acknowledged to be involved in emotion processing (Adolphs, 2009), and recently amygdala volume was shown to correlate with the size and complexity of social networks in adult humans (Bickart et al., 2011). Our lack of correlation between amygdala activation and amount of emotion modulation in adolescents supports the notion that some quadratic relationship seems to exist between certain functional aspects of social signal processing across childhood. This effect is not reflected in either the peak *t*-values in the ROIs or the whole-brain analysis. Rather, it points to a change in the pattern of higher cortical processing. Combining the findings of functional reorganisation in Vink et al. (2014) and Loenneker et al. (2011), with the correlations between amygdala response and body-selective area activity in adults described by Peelen et al. (2007), we suggest that rather than showing any difference in the peak activation in the body-selective regions during emotional body processing, or showing any drop in recognition accuracy, adolescents do show some sort of reorganisation in the body-selective network. In children and adults we seem to have a system in which low-level information is fed from the body areas in the visual cortex to limbic subcortical areas, whose influence then in turn modulates activation in the same visual cortex body areas. In adolescents it is possible that an over-recruitment of the prefrontal cortex (Yurgelun-Todd, 2007;Vink et al., 2014) coupled with less recruitment in the limbic subcortical regions are masking this effect. This effect may have been accentuated if an online task was performed in the scanner when viewing the body stimuli, as decision-making would lead to more over-recruitment of the prefrontal cortex in adolescents (summary in Powell (2006)).

In functional emotion processing there seems to be a difference in the developmental trajectory of EBA and pSTS, with adults being the only age group to show a correlation between EBAs emotion modulation and amygdala activity (under the Angry>Neutral contrast). We also observe an ‘adolescent dip’ in amygdala strength and emotion modulation correlation of the pSTS when viewing Angry>Neutral body movements, and FBA when viewing both emotion contrasts. We have provided speculative arguments as to why this may be the case, but using static as well as dynamic body stimuli would shed light on this finding. Previous research suggests a double dissociation between the form and motion pathways (Vangeneugden et al., 2014a), and it may be the case that subjects will not show this pattern of results when viewing static body stimuli.

6.4 Limitations and Future Directions

Some of the limitations with this thesis also form the basis of interesting and necessary directions for future research. Having the same children performing both the behavioural and brain-imaging studies would have been worthwhile, as it would have allowed direct comparison across studies. There are currently no studies exploring the functional developmental trajectories using full and point-light displays, so repeating the brain-imaging studies using the stimuli from the first experiment would have contributed to the literature on the form and motion pathways.

Adding affective voices to a developmental study of TVA development as well would be a novel exercise. Especially, as in **Chapter 5,** it would allow us to explore any correlation between the TVA and the subcortical limbic areas. It would also be interesting to see if adolescents showed a lack of this correlation when presented with affective voice stimuli, as was found with affective body stimuli.

A short face localiser during the scanning would have allowed for direct comparison of functional development across all three social modalities, and future studies are advised to perform this short addition. The pros and cons of using a task or not should also be considered. Here, if we had included a task, we may have more evidence to attribute our lack of adolescent body-selective area and amygdala correlation to an over-recruitment of the prefrontal cortex in making a decision regarding the emotion portrayed. Without one we have avoided unwanted motor or decision-making activation, but also face questions of attention and stimuli understanding. We feel, however, that we have addressed these issues throughout each experiment.

We also faced practical problems regarding recruitment. Primary schools were receptive to our recruitment drives and happy to engage with the Department of Psychology in getting the children involved with brain imaging. Secondary schools proved to be much harder to contact and get involved with. This led us to a potential sample bias, in that the only children who participated in the brain-imaging studies were students who were already interested in science. It would be presumptuous to suggest that these children are likely to be more intelligent than their peers, but we are left with a sampling bias all the same. Much like the problem of most studies performed at universities using undergraduate students as subjects, there is no easy way to avoid such a bias.

Another limitation we found in completing this thesis applies more widely to the literature as a whole. The definition of the word ‘children’ is not consistent across studies. One cannot argue that a group of 5-6 year olds and a group of 7-8 year olds are not both groups of children, but when the definition of children extends through puberty, the teenage years and essentially into young adulthood it makes comparison with other studies that do not adhere to this definition impossible. A more generally accepted meaning is needed, otherwise a study using 13-17 year olds could claim that their ‘children’ show functional, structural or behavioural differences compared with the ‘children’ of another study who all happened to be less than 10 years old.

Of course the same problems arise in the definitions of adolescents and adults. Here, we take anyone over the age of 18 to be an adult, but this is only an arbitrary cultural cut-off point. Developmental research would be better served treating age as a continuous variable, but for obvious reasons of time, money and participant numbers, this isn't always practical.

Treating age in this way touches on another issue with definitions in the literature, that of how to measure developmental maturation. One could use age as stated above and then call any subject under 12 years old a child. Then adolescents could perhaps be the teenagers 13 and above. This chronological age measurement sidesteps the issue of any hormonal and maturational changes that occur during puberty. So then perhaps grouping subjects by pubertal stages is the way to proceed? This, however, requires self-evaluation (or parental evaluation in the younger subjects) of pubertal stage, which may not always be accurate. There is no easy answer to this problem, particularly as it raises more questions of whether it is maturational or hormonal changes that affect behavioural differences. Regardless, future studies should be wary of direct comparison to other studies with different definitions of children or different methods of age grouping.

6.5 General Conclusions

The literature on social signal processing is currently dominated by research focusing on the recognition of the human face. However, despite knowing that the human voice and body are salient communicators of important information, there is surprisingly little research exploring these social stimuli. There is even less work exploring the developmental trajectories of functional response to these stimuli.

Here, we presented evidence that the voice-areas in the temporal cortex are the first to become 'adult-like' in terms of sensitivity and selectivity in children and adolescents. The body-selective areas in the visual cortex on the other hand are still not yet 'adult-like' in children age 11, even though the spatial pattern of the body's neural representation does not change with age. We also present evidence, for the first time, that in the right hemisphere, these areas are still not 'adult-like' in terms of sensitivity through adolescence. We also show, for the first time, that emotion modulation of these regions is ‘adult-like’ in children and adolescents. This is despite also showing that children displayed significantly less emotion recognition accuracy than adults when viewing dynamic full and point-light displays. Finally, we also show, again for the first time, evidence of positive correlations between amygdala activation and emotion modulation of the body-selective areas in children and adults, but this effect was absent in adolescents.

This work all points to a constantly developing social brain, and one in which different social modalities develop at different rates. Much more work will be needed to accurately make sense of these overlapping developmental trajectories; particularly with differences in experience across subjects, the substantial structural overlap in areas selective to both face, voice and body stimuli, the loose definitions of the term ‘children’ in the literature, and the conflicting decisions of whether to measure development by simple chronological means or by hormonal and pubertal stages.

Until quite recently, we thought that much of brain development was complete after early childhood. Progress in neuroimaging has since changed this view. This thesis makes the link between older social psychology studies demonstrating the development of social competences and their importance in successful interaction, and recent models of child and adolescent brain development. It also opens new research avenues in relation to an integrative model of the developing social brain by taking into account a variety of signals (it should be noted that although we look beyond the face here, this is by no means exhaustive).

This research is also not without important clinical applications. Recently, fMRI studies have been providing evidence of possible early diagnostic tools, which could be used in children and adolescents with various social cognitive disorders. Hollocks et al. (2014) showed a significant association between poorer executive functioning and higher levels of anxiety in adolescents with an autism spectrum disorder (ASD). Fladung et al. (2013) found that adolescents with anorexia nervosa (AN) showed increased activity in the ventral striatum when viewing underweight body stimuli relative to healthy controls. Further, the processing of normal-weight body stimuli elicited reduced signalling. This data demonstrates that if a developing dysfunctional signal can be observed at an early stage, then appropriate treatments can be administered to avoid the prevalence of AN through adolescence and into adulthood.

So understanding developmental trajectories is vital to understanding the mechanisms of these deficits, which can have life-long consequences. Effectively, if we can chart the developmental trajectory of typically developing children and adolescents, this trajectory can then be shifted to atypically developing populations. Any deviation from typical functional development would be easily flagged and this process could prove a quick and reliable early predictor of autism, eating disorders and other social cognitive disorders.

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