Spatial representations of touch in infancy and early childhood

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A thesis submitted for the degree of

Doctor of Philosophy (PhD)

University of London

2016

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I, Jannath Begum Ali, declare that the work presented in this thesis is my own work.

Signed on the 11th July 2016

Experiment 1, outlined in Chapter 3, has been published in Developmental Science:

Begum Ali, J., Cowie, D. & Bremner, A.J. (2014). Effects of posture on tactile localization by 4 years of age are modulated by sight of the hands: evidence for an early acquired external spatial frame of reference for touch. *Developmental science, 17*(6), 935-943

Experiment 4b, outlined in Chapter 4 has been published in Current Biology:

Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A. J. (2014). The neural basis of somatosensory remapping develops in human infancy. *Current Biology*, *24*(11), 1222-1226

Dedication

This thesis is dedicated to my dad, Mohammed Kalamdar Ali, whom I know would have been so incredibly proud to see the finished result.

Abstract

The primary aim of this thesis was to examine how infants, and young children, represent touches in space (i.e. with respect to their external environment). Studying infants in the first year of life allows us to map the emergence of the complex processes needed in order to correctly locate touches to the body (and, by extension, the location of the limbs and body parts on which those touches impinge).

In a series of seven experiments, I examined the development of the spatial representation of touch. To do this, I explored the development of an external reference frame in which touches are coded, the modulatory effect of changes in posture on the neural representation of a touch and the relationship between vision and touch when locating a stimulus from these sensory modalities in space.

To investigate the development of an external reference frame for touch, I used a ‘crossed-hands’ task. This task has been used as a marker of the influence of an external frame of reference for localizing touch and is considered to arise out of conflict (when the hands are crossed) between the anatomical and external frames of reference within which touches can be perceived. Previous research with children had found that this reference frame does not develop until after 5.5-years; I extended this finding by determining that children as young as 4-years are able to locate touches in external co-ordinates. Additionally, in a further study, I found that an external reference frame develops between 4 and 6 months of age.

The modulatory role of vision on tactile localization was also investigated. These studies showed that when 4-year-old children are provided with current vision of the hand being touched, this interfered with the benefits of using an external reference frame. However, this interference was limited to when the limbs were in canonical postures. As such, it seems that young children are still refining the ways in which sensory cues to the body help them to locate touches in the world.

Considering that early visual experience was implicated in the development of an external frame of reference I also examined the development of an ability to perceive visual and tactile stimuli in a common spatial location. Here, it was found that 6-month-olds demonstrated this ability, with tentative findings suggesting that it may develop even earlier in life (e.g., at 4 months of age). As such, the ability to co-locate tactile and visual stimuli at 6 months is consistent with a role for visual experience in the development of an external frame of reference for touch at this age.

Further to this, I examined interactions between vision and touch using a crossmodal cueing event-related potential (ERP) paradigm. In this study, it was found that at 7 months of age visual cues to the hand modulate processing of a subsequent tactile stimulus on that same hand. This provides further evidence of early acquired crossmodal links, but this was the first demonstration of crossmodal attentional cuing effects in infancy.

Finally, in a set of two experiments, I investigated how infants (in the first year of life) were able to update the location of a felt touch across changes in arm posture, using an ERP measure. Although these studies demonstrated a null relationship between sensorimotor experience and somatosensory remapping, it was found that only those 8-month-old infants that displayed contralateral reaching behaviours were able to update to the location of a touch across a change in posture. As such, the relationship between sensorimotor experience and somatosensory remapping may not be simple, with other factors (such as brain maturation) also influencing this relationship.

Acknowledgements

This work was funded by a European Research Council grant (no. 241242), awarded to Andrew J. Bremner for a body of work entitled Human Embodied Multisensory Development.

Thank you to my very patient and super supportive supervisors, Dr Dorothy Cowie, Professor Elisabeth Hill and especially Dr Andrew Bremner for dealing with all my ‘quick questions’ that were quick in nature, but the answers were very much not.

To my office mates (both present and former) and InfantLab members: Dan Brady, Luke Mason and Joanne Camp – thank you for all of the invaluable help with both programming and testing; I can foresee that the productivity levels in the office will be significantly greater now that I’m not there! A special thank you to Hana D’Souza, Rhiannon Thomas, Frances Le Cornu Knight and Silvia Rigato for always being there and offering amazing advice and support for my many, many crises (both professional and personal) – my time in the InfantLab was especially enjoyable and successful due to your patience and wisdom. I can’t imagine having gone through this experience with anyone else.

I must also thank ‘The Goats’ (Laura-Lee Kenny, Paige-Ashleigh Cuffe, Hannah Cottell and Alex Martin) and the ‘JAN-DK’ writing group (Katie Rix, Niamh Friel, Alys Griffiths and Dan Jolley) for keeping me sane in the final months of this write up, without whom I imagine there would have been a lot more tears and a lot less laughter. Their words and time will always be remembered and very much appreciated.

Finally, I thank my family and best friend Fatima Zaman for putting up with my last seven years in higher education as I attempted to stave off adult life. It’s okay guys, I’m done now.

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List of abbreviations

EEG = Electroencephalogram

ERP = Event-related potential

IRH = Intersensory Redundancy Hypothesis

MS = milliseconds

RH = Rubber hand

RHI = Rubber hand illusion

SEP = Somatosensory evoked potential

SOA = Stimulus onset asynchrony

TOJ = Temporal order judgement

Chapter 1

Spatial representations of the body

1.1. General introduction

In the first hours, days and even months of life, the newborn infant seems a passive spectator of its environment, bombarded with information from various sensory modalities. With limited motor and sensory abilities, even beyond the newborn stage, how does the human infant go about making sense of this information in order to successfully understand and engage with the world around itself?

A crucial aspect of perception involves representing one's own body and its relation to the world around us. This ability is paramount to action, self perception and self concept and an embodied perception of the external world (e.g., Merleau-Ponty, 1962; Slaughter & Brownell, 2011; Shapiro, 2011; de Preester & Knockaert, 2005). However, there is still very little known about how body representations emerge and develop in early life. Indeed, body representations may be extremely different (to those of adults') for the young infant.

In terms of action, for example, an infant's interactions (in early life) with the environment are restricted as a result of his/her limited repertoire of movements. In the first few months of life, without the ability to crawl or walk (or even to sit upright) the infant has limited interactions with its immediate environment. Certain authors have argued that it is only when these motoric abilities are learnt and mastered that the infant becomes able to actively explore and learn about their environment (Piaget, 1952, 1954; Campos, Anderson, Barbu-Roth, Hubbard, Hertenstein & Wiltherington, 2000). But of course, in order to acquire these new motor abilities, infants must have some knowledge of their bodies/body layout and where their limbs lie in space, relative to not only other limbs, but also to objects and people. For example, when attempting to crawl, the infant must be aware of the placement of their hands and feet in space to accurately guide them to the required positions to initiate movement. This may seem a simple task and one that adults take for granted, but the same principle applies when one is playing a new sport or learning a new musical instrument. Thus, how one represents one's body in space is a necessity for navigating around our immediate environments, and more broadly, the world around oneself.

Although there now exists a substantial literature addressing how individuals represent their limbs and bodies in space (e.g., Berlucci & Aglioti, 1997; Graziano, 1999; Yamamoto & Kitazawa, 2001a; Graziano & Botvinick, 2002), this is still dwarfed by the body of research which addresses representations of the external world (e.g., object representation) in human adults (e.g., Tarr & Bülthoff, 1998; Biederman, 1987; Marr, 1976; Regan, 2000; Enns, 2004). This imbalance seems striking when we consider that an ability to perceive and represent one's body is of paramount importance in the pursuit of perceiving and exploring the environment. The body is the means by which we grasp and haptically explore objects within reach. It is also the means by which we are able to get close enough to people and objects in the first place for multisensory exploration (e.g., Piaget, 1952; Bruner, 1966; Rizzolatti, Fadiga, Fogassi & Gallesse, 1997; Trevarthan, 1984; von Hofsten, 1982; Adolph, Eppler & Gibson, 1993a, 1993b; van der Kamp & Savelsbergh; 2000). To complete these actions, the brain must not only compute the location of the object to be explored, but also the relative layouts of the limbs to be used in reaching it.

In terms of an embodied perception of the external world (in which the mind is shaped by the experience of the body), some have argued that, as well as enabling us to explore our multisensory environments adequately, our bodies provide the context for our perceptual experiences and even our thought processes. Proponents of embodied cognition (e.g., Lakoff & Johnson, 1980, 1999; Gibbs, 2006; Borghi & Cimatti, 2010; Barsalou, 2008; Wilson, 2002) argue that the mind is shaped through our body and the bodily experiences – a plausible theory when one considers that all sensory information about the world is first experienced through the body and the different senses (see Wilson, 2002 for a review).

For the developing infant, there are periods of rapid physical growth and development. So how do infants keep an up to date representation of the limits of their body, in terms of both physicality and also action repertoire? Infants (and adults alike) must build body representations, which must be continually updated to take account of limb growth and also the spatial distances between our bodies and objects/people in the environment (Gori, Giuliana, Sandini & Burr, 2012; Burr, Binda & Gori, 2011; Bremner, Mareschal, Lloyd-Fox & Spence, 2008; Bremner, Holmes & Spence, 2008), especially when one considers that the body is in constant motion during waking hours and, to a degree, even whilst sleeping.

In addition to this, body representations are also important for self perception and the self concept. How does the developing infant recognise a limb as their own and take ownership of that limb? Of course, visual and proprioceptive cues to the limb may be of importance; not only in terms of locating the limb in space but also regarding it as one’s own. But we do not locate our limbs in space in isolation, relying simply on perceptual information concerning the limb itself; for example touches between an external object and a limb can also be informative in locating it (e.g., Botvinick & Cohen, 1998; Tsakiris, 2010; Ehrsson, 2012). But how does this lend itself to a sense of ownership over the limb and/or the body itself?

A variety of methods have investigated the subjective sense of the self in developing populations. For example, using measures of self mirror recognition (Amsterdam, 1972; Gallup, 1970), the emergence of pretend play (e.g., Perner, 1991; Lillard, 2002), synchronic (e.g., Asendorpf, 2002) and deferred imitation (Meltzoff & Gopnik, 1993), Nielson and Dissanayake (2004) found that all but one of these abilities (deferred imitation) emerged between 18 and 21 months, with deferred imitation emerging slightly earlier. Other researchers are also in agreement with these findings, proposing that the subjective sense of the self develops within the first two years of life (e.g., Lewis & Brooks-Gun, 1979; Lewis, 2011; Rochat, 2010) and perhaps is still developing well into early childhood when the self concept is related to more complex processes such as autobiographical memory (e.g., Povinelli, Landry, Theall, Clark, & Castille, 1999; Welch-Ross, 2001).

So how is the human infant able to understand its place in the world? The bodily self, which will be the main focus of this thesis, feeds into the emergence of the subjective sense of the self in the world. But before we get to the central questions of this thesis, of how infants and children develop an ability to perceive and represent their own body, we first look at what is known about the nature of body representations in the mature adult.

1.2 Body representations

1.2.1 Body image vs. body schema

Broadly speaking, body representations have been defined as any type of stored information regarding one's own or others' bodies (Mandler, 1988). Early concepts of body representations have included the body schema (Head & Holmes, 1911-12) and the body image (e.g., Paillard, 1999; Gallagher, 1986, 2005; O'Shaughnessy, 1995) although it has been argued that there are potentially many more body representations (Berlucci & Aglioti, 2010; Dijkerman & de Haan, 2007; for a review, see de Vignemont, 2007), or at least several sub-categories of the two mentioned above (e.g., Gallagher, 2005; O'Shaughnessy, 1995).

The body image is regarded as a fairly controversial concept due to the fact that it resists fine-grained definition; however researchers within the field of spatial and body representations are in agreement that the body image refers to a conscious "perceptual identification and recognition" of both one's own, and others', body" (de Vignemont, 2010, p. 671; Gallagher, 2005). It has been suggested that when the body image concerns one's own body, we are able to consciously represent the experience of visual, tactile and motor information that is either impinging upon our bodies (e.g., tactile information) or that which is being produced (such as motor information; Paillard, 1999).

The definition of the 'body schema' (Head & Holmes, 1911-12), in contrast, has a greater consensus within the psychological community and is defined as a representation of the body that unconsciously guides actions using sensorimotor representations. Researchers contend that it is an automatic process and is imperative in informing individuals about their current posture and without which acting upon one's immediate environment would be entirely impossible.

I have outlined above early definitions of the body image and body schema, however these concepts have prompted further research and thought and have thus, undergone many changes in their definitions. For example, based on research with patients with brain and spinal injuries exhibiting dissociations in body sensibility, Head and Holmes (1911-1912) further subdivided the body schema, arguing that the ‘postural schema’ slightly differed from the body schema. The authors argued that the postural schema is a flexible construct that refers to the position of the body and body parts in space. As individuals are in constant motion, the postural schema continually updates itself, taking into consideration the proprioceptive information about the movement of the limbs to then represent their position in space; so, according to this account, rather than informing us about the specific posture our bodies have adopted, the postural schema provides information about *changes* in, and between, the postures our bodies are capable of adopting. A key differentiation between the body schema and the postural schema is that the postural schema is restricted to proprioceptive and somatosensory signals, whereas the body schema is not (incorporating proprioception, somatosensation, vision and even audition; Holmes & Spence, 2004).

The concept of the body image has also undergone further development. For example, in recent times, rather than limiting the definition of the body image as a conscious representation of the self, it could be viewed as a representation of the usual layout of the body. However, researchers use different terminology for this, specifically describing this as a ‘canonical body representation’ (e.g., Bremner, Homes & Spence, 2012; Longo, Cardozo & Haggard, 2008; Azañón, Longo, Soto-Faraco & Haggard, 2010) and can also refer to the typical layout of the human body more generally (e.g., Slaughter & Heron, 2004; Christie & Slaughter, 2010; Brownell, Zerwas & Ramani, 2007).

The theoretical body representations I have discussed above have involve more than one sensory modality (e.g., the body schema incorporates information from proprioception, somatosensation and vision). These accounts emphasise a multisensory nature of body representations, which I will examine and provide supporting evidence for in the following section.

1.2.2 Multisensory body representations

One does not process, and indeed navigate, one's environment using a unitary sensory modality, but instead several senses are combined to build a rich tapestry of information about the body and the world. For example, in order to locate a hand, we can do this via the sense of objects the hand is touching, the sight of the hand itself and any form of sound it makes.

Within the cognitive neuroscience literature, findings from several studies (for reviews see Heed & Röder, 2012; Maravita, Spence & Driver, 2003; Holmes & Spence, 2004) have demonstrated the means by which the brain integrates information from multiple sensory modalities to represent the body and the space around the body (peripersonal space) in a unified and coherent way.

1.2.2.1 Findings from animal studies

To investigate the neural circuitry underlying the integration of visual and tactile information, many researchers have used the single neuron approach. Here, a microelectrode is inserted into the brain region of interest and is able to monitor the current of the action potential as it moves through the cell. As we shall see, using this method, several brain areas in the monkey brain have been identified as having a particularly important role in visual-tactile representations of the space around the body.

Findings show that the brain regions of the pre-motor cortex (F5) and the posterior parietal cortex (VIP and 7b) play a role in the way monkeys represent peripersonal space. In terms of the pre-motor area of the brain, this houses a network of connected regions, which respond to both visual and somatosensory information, thereby indicating the multisensory nature of these neurons.

Neurons within the pre-motor cortex (which have tactile receptive fields on an area of the body, for example a right hand), are especially reactive to visual stimuli that occurs in the region of space where the hand lies. When the hand moves in the visual field, for example if it moves from the right side of the body to the midline, the visual location which activates the visual tactile neurons changes by moving with the hand. This is also the case when the positioning of the monkey's hand has moved to the contralateral side of space (Fitzgerald, Lane, Thakur & Hsiao, 2004) or when the head was turned, but the fixation point remained the same (Graziano, Hu & Gross, 1997b). Therefore, it seems that as the body (and the tactile receptive field on a limb) moves in external (visual) space, visual receptive fields also shift towards the position of the tactile receptive fields (i.e. where the limb lies in space; Graziano, 1999).

A similar pattern of neural activation has been found in the posterior parietal cortex under similar conditions (Graziano & Gross, 1995). Research investigating Area 5 in the posterior parietal lobe has found that neurons in this area react to somatosensory information, encoding posture and movement of the body and visual information regarding posture of the limbs (Graziano, Cooke & Taylor, 2000), with researchers also finding this area is involved in the planning and execution of actions (Chapman, Spidalieri & Lamarre, 1984; Kalaska, Cohen, Prud'homme & Hyde, 1990). Other areas of interest, within the posterior parietal lobe in monkeys, include the medial bank which has been found to respond to visual, moving stimuli around the hand and arm (Iriki, Tanaka & Iwamura, 1996).

Once again, the above research is demonstrative of the multisensory nature of how animals perceive their bodies in space (in that certain areas of the brain respond to both visual and tactile information within receptive fields that are anchored in terms of limb centred co-ordinates; Graziano & Gross, 1993; 1995; Graziano et al., 1994, 1997).

1.2.2.2 Findings from human studies

Of course, it is not possible to use single neuron experimental procedures in a population of human adults. Therefore in order to discern if there is similar visuotactile integration of peripersonal space in humans, much of the research into multisensory body representations has come from either healthy adults or individuals suffering from some type of trauma (either to the brain or the body) that has resulted in disrupted body representations.

Brain trauma can result in disruptions to the way different sensory inputs are combined to form a representation of the body. Làdavas and colleagues (Làdavas, 2002 for a review) conducted a series of studies with patients suffering from damage to the right hemisphere, resulting in tactile extinction on the left side. These patients are able to detect touches to the left and right hands perfectly well when the tactile stimulus is presented one at a time, however if the stimuli are presented concurrently to both hands, the patients are only able to consciously detect the touch to the right hand (di Pellegrino, Làdavas & Farnè, 1997; Mattingley, Driver, Beschin & Robertson, 1997)

Researchers have attempted to explain this pattern of findings as competing information regarding the hands between the left and right hemispheres of the brain. As a touch on the hand activates the hemisphere contralateral to that hand (e.g. a touch on the left hand would activate somatosensory areas in the right hemisphere and vice versa), there is some disparity in the 'strength' of hemispheric activation due to cerebral damage to the right hemisphere. During instances of tactile stimuli being presented to both hands, this sensory information competes for limited attentional resources, with ultimately the ‘stronger’ and undamaged left hemisphere ‘winning out’ (Mattingley et al., 1997).

This type of extinction has also been investigated using both visual and tactile stimuli (i.e. a visual stimulus was presented in the right hemifield and the tactile stimulus presented to the left hand) and a similar pattern of results was found; individuals were still unable to consciously detect the touch applied to the left hand. This cross-modal extinction persisted even if the hands were crossed over (and placed in the contralateral side of space to their usual placement; di Pellegrino et al., 1997b).

Ultimately, these studies have shown that (hemispherically unequal) visual-tactile integration occurs, with this presenting as tactile extinction in patients who have suffered cerebral trauma. But what does this tell us about body representations?

In Section 1.2.2.1, I discussed research detailing tactile receptive fields in the monkey brain (e.g., Graziano, 1999; Graziano & Gross, 1993; 1995; Graziano et al., 1994, 1997; Iriki et al., 1996). These receptive fields have been shown to respond to both visual and tactile information either on the body or approaching the body (Graziano, 1999; Graziano & Gross, 1993; 1995; Graziano et al., 1994, 1997). Keeping this concept in mind, it may be that the human brain behaves in a similar way. For example, certain neural circuits respond to both visual and tactile information that impinges upon the body. It may be that if the space around the body is coded in terms of a multisensory, visual-tactile representation, disruptions to this representation (via brain injury) could result in some type of interference between visual and tactile information applied to, or near, the body.

di Pellegrino et al. (1997) investigated this question in a group of left hemisphere lesion patients. It was found that when a touch was applied to the left hand at the same time a visual stimulus was presented close to the patient's right hand, this resulted in complete extinction of the left tactile stimulus. Even if the right hand was placed in a different position (such as crossed over the midline), a visual stimulus close to this hand still induced extinction. However, detection of the tactile stimulus to the left hand improved when the right hand was held behind the back.

From these findings, it has been shown that visual-tactile interactions seem to be anchored to, in this case, the hand. Additionally, this finding has been shown for other body parts (e.g., there have also been studies demonstrating tactile extinction to the left cheek, when a visual stimulus was presented close to the right cheek; Làdavas, Zeloni & Farnè, 1998).

Ultimately, from these results (and similarly to what we have learnt about visual-tactile integration and receptive fields in the monkey brain), some have argued that we use body part centred visuotactile representations to construct an accurate layout of not only our own bodies, but also the space around our bodies (see Holmes & Spence, 2004 for a review).

As discussed in this section, body representations are multisensory in nature; with neurons in body part centred receptive fields responding to both visual and tactile information regarding the body. Thus, as this thesis is addressing the development of body representation, it is my contention that it is crucial to consider how the development of multisensory processes impacts on this. In the next section I discuss what is known about body representations and their development in early life, focusing in particular on multisensory aspects.

1.3 Development of body representations

So far I have described various aspects of mature body representations that have emerged from work with adults (both primate and human), either typically developed adults or those with some form of brain damage. From the literature described above, we are able to understand the mature state of the different ways of representing the body. But the fundamental question of how these body representations emerge and develop in early life, or indeed if they are already established upon birth, still remains to be answered. In order to attempt to explore this question, one must investigate body representations in developing individuals (i.e. in infants and children).

Indeed, from research conducted with phantom limb patients, researchers have argued that developmental factors may be particularly important in building representations of the of the body layout as the incidence of phantom limb (when patients 'feel' that an amputated limb remains attached to the body; for a review see Ramachandran & Hirstein, 1998) is much higher in individuals who lost limbs later in life, compared to in childhood (Simmel, 1962), therefore suggesting that it is within late childhood that the body schema undergoes crucial development.

However, this developmental explanation for phantom limb syndrome has been challenged. For example, Melzack and colleagues have described the incidence of the syndrome in individuals with congenital limb deficiencies or with a limb amputated in early childhood, with a prevalence rate of 20% and 50% respectively (Melzack, Israel, Lacroix & Schultz, 1997; Saadah & Melzack, 1994). Given that adults who had lost limbs in early childhood (e.g., before the age of 6 years) have also experienced the phenomenon, this would suggest that body representations undergo crucial development in *early* childhood (as opposed to late childhood), as the body schema is already in place at this stage of development.

In order to understand the development of body representations, in the following section, I will discuss various developing behaviours which are particularly relevant to emerging body representations, such as sensorimotor representations, imitation and the lexical-semantic representations. Following this, I will then discuss the development of the multisensory interactions which underlie emerging body representations.

1.3.1 Visuospatial representations of others' bodies

Visual-spatial representations of the body have been shown to emerge in very early infancy. For example, 2-month-old infants show a preference for schematic drawings of faces with the features in the typical configuration compared to schematic drawings with scrambled features suggesting that infants at this young are not only able to distinguish between typical and scrambled faces, but may also be aware of how facial features should be arranged on a typical face (Maurer & Barrera, 1981). Infants' knowledge of faces may emerge even earlier and perhaps even from birth. Johnson, Dziurawiec, Ellis & Morton (1991) found that newborn infants of only 30 minutes of age or less will track schematic drawings of faces for longer (in comparison to schematic scrambled faces or a blank stimulus), replicating the findings of Goren, Sarty & Wu (1975).

Studies conducted by other researchers have shown similar effects in that infants aged between 1 and 3 days old possess the ability to distinguish the spatial relationships between facial features (Leo & Simion, 2009). The study was similar in design to Maurer and Barrera (1981), newborn infants were habituated to an image of a typical face in the upright position. Infants were presented with an image of a face in which the eyes and mouth had been rotated by 180°. The infants dishabituated to this second image, suggesting they were able to distinguish between the two faces.

Pascalis and Kelly (2009) have reviewed the various developmental models of face processing in infancy that could possibly account for very young infants' preference to view faces. Considering research from developmental, evolutionary and comparative psychology, the authors concluded that face perception and processing relies on specialist, and dedicated, neural circuits (also see Cohen Kadosh & Johnson, 2007 for a review of cortical specialization for face perception in the first ten years of life). From this, Cohen Kadosh and Johnson (2007) proposed that whilst, initially neural circuitry may be biased to perceive faces over other stimuli, it may be through prolonged exposure to faces that this specialized face processing occurs.

Infant research into body perception has not been limited to the face. Slaughter, Heron and Sim (2002) presented infants aged 12, 18 and 24 months with line drawings and photographic images of bodies in either a typical or scrambled form. The authors found that it was only at 18 months that infants were able to distinguish reliably between the two body forms. Further studies conducted by Slaughter and colleagues found that younger infants could discriminate between scrambled and typical bodies if the stimuli were presented in different forms. For example, 15-month-olds were able to achieve this if the stimulus were photographs of bodies, 12-month-olds were sensitive to this difference if the stimuli consisted of three-dimensional dolls and even 9-month-olds could differentiate between body configurations if they were presented with real people in scrambled and typical forms (Heron & Slaughter, 2010).

Using an alternative method to infants' preferential looking to scrambled vs typical body forms, Zieber, Bhatt, Hayden, Kangas, Collins and Bada (2010) presented infants aged 5 and 9 months with photos of the typical body form and photos in which some areas of the body had been elongated (such as the neck and the torso), whilst others were shortened (e.g. the legs) in both the upright and inverted position. The authors investigated whether infants, like adults are able to differentiate between bodies using body proportions (e.g., Johnson & Tassinary, 2005, 2007; Tassinary & Hansen, 1998).

Zieber et al. (2010) found that infants of 5 months of age did not differentiate between the two types of bodies, regardless of their upright or inverted position. However, infants aged 9 months demonstrated preferential looking at the typical body, as opposed to the distorted one, but only in the upright position. As the differentiation between body forms was limited to the upright position, this would indicate that by the age of 9 months, infants have some specialist expertise in visual processing body forms (see Valentine, 1988; Taylor, Batty & Itier, 2004; Rossion & Gauthier, 2002 for reviews on how differentiation of upright faces implies expertise).

Other research has demonstrated that infants as young as 6.5-months are able to derive information regarding emotions from bodies and match them to corresponding emotional vocalisations (Zieber, Kangas, Hock & Bhatt, 2014a, 2014b) and by 9 months of age, they are able to integrate body form and biological movement (of the body form) as means of differentiating between body configurations (Christie & Slaughter, 2010).

So, from this research it appears that, by the first half year of life (and beyond), infants have some specialist knowledge when it comes to body perception, specifically regarding the typical form that a body should take. It also appears that young infants are able to use this knowledge to perceive relationships between body movement (Christie & Slaughter, 2010) and emotional states (Zieber et al*.,* 2014a, 2014b). However, taking the earliest point at which infants demonstrate some specialist knowledge of the body (6.5 months of age), this is still considerably later in development than the earliest ability to represent facial configurations, suggesting that perhaps learning about the human body and its form and configuration follows a different developmental trajectory to learning about faces.

The above research has shown that infants are able to discriminate facial configurations (from birth; Johnson et al*.,* 1999; Leo & Simion, 2009) and body configurations (from 9-months) of other humans (Heron & Slaughter, 2010; Zieber et al., 2010). These findings are certainly pertinent to the emergence of an ability to perceive and understand the human body in a general way. However, we know much less about how human infants develop an ability to perceive and understand their *own* bodies.

Additionally, whilst infants are able to distinguish what "typical" faces and bodies should look like, are we to infer that by extrapolation the infant is aware that their own face and body have this configuration? Research into imitation has argued that given that they are able to mimic seen facial gestures of another, the infant is aware of the features of their own face in order to produce an action. However, as discussed later in this chapter, claims of imitation in early infancy remain contentious (e.g., Anisfeld, 1991; Jones, 1996).

So what body representation research is available that can inform us about what the infant knows about his or her own body? Christie and Slaughter (2009) have investigated this by looking at the relationship between infants' sensorimotor and visuospatial body discrimination abilities. During a human body visual discrimination task in which infants were presented with images of bodies, infants' motor activity was recorded. In addition to this, infant's overall motor and imitation skills were also assessed to compute an index of sensorimotor ability. The relationship between these variables was then investigated. However, due to the null finding between these two factors, this would suggest that the relationship between the perception of one's own body and that of other's is not straightforward.

1.3.2 Sensorimotor behaviours

Researchers have been able to examine sensorimotor behaviour in very early infancy. Von Hofsten (1982) investigated eye hand coordination behaviours in sixteen newborns (aged between 4 and 9 days old) and found that when newborns fixated on a moving object that was dangled in front of them, they extended their arm outwards in an attempt to grasp the moving object. However, the infants were unsuccessful in touching or grasping the dangled object. This lack of success may be due to immature visual-motor integration abilities – after all, considering the age of infants tested in this study, producing an accurate grasp towards a moving target may be a particularly difficult task. Nonetheless, Von Hofsten argued that infants' attempts at reaching for the toy demonstrated newborns' rudimentary ability to integrate visual and motor information to some extent.

Von Hofsten and Fazel-Zandy (1984) have further investigated visually guided hand movements in infancy. This particular study involved a longitudinal design in which a group of 15 infants were assessed at monthly intervals between the ages of 18 and 34 weeks. Infants in this study were presented with horizontal or vertical rods and the infant's hand orientation was measured as it approached the object. The researchers found that even at 18 weeks, there appeared to be some adjustment of hand orientation in order to successfully grasp the object. It appears that infants within the first four months of life are able to coordinate, to some extent, visual information about objects and their own body in order to successfully take hold of the object.

The research described above has been conducted with infants having visual information of their limbs and/or the objects to be grasped, however there is a body of research that has examined reaching ability in infants when vision of their hand was not available (e.g., in the dark, but with the target object luminesced) and has found that at approximately 4 months of age, infants were able to successfully guide their hands to an object to grasp. This was comparable to when the first successful reaches in conditions where visual information of the limbs were available (Clifton, Muir, Ashmead & Clarkson, 1993). Research from this lab has also shown that infants are able to contact luminescent objects that are moving in the dark, although the occurrence of grasping the moving object was much more pronounced in infants that were 7.5 months of age (Robin, Berthier & Clifton, 1996).

Further to this, regardless of the visual information concerning the arm and/or object (a vertically or horizontally placed rod) that were available, 8-month-old infants' positioning of their hands differed to the same extent when producing a reach to contact an object that was positioned either vertically or horizontally (McCarty, Clifton, Ashmead, Lee & Goubet, 2001). Therefore, it appears that infants within the first year of life are able to make use of proprioceptive cues to their limb position to produce an accurate reach, and this can be in combination with visual information of the hand and/or toy, but visual information of either the hand or the toy is not a necessity for this. Although, it has been suggested that rather than relying on current proprioceptive information of the limb alone, perhaps the infant is also making use of a multisensory representation of the arm regarding the usual position and location of this arm (Bremner, Holmes & Spence, 2008a).

Of the research discussed above, infant's co-ordination of vision and proprioception for action has been addressed, demonstrating that infants as young as 4 months of age possess some rudimentary skills concerning multisensory representations of the body in which to guide reaching. Specifically, these studies illustrate that proprioceptive guidance of movement is related to a representation of external space.

Further to this, the above research has shown differing levels of ability (of sensorimotor representations at differing complexities) emerge at different ages; from the newborn stage (Von Hofsten, 1982; Von Hoften & Fazel-Zandy, 1984) to the second half-year of life (Robin et al., 1996; McCarty et al., 2001). Therefore, it is possible that whilst sensorimotor representations may emerge within the first few weeks life, they continue to develop and become more precise and mature throughout the first year of life.

1.3.3 Imitation

Imitation describes the act of copying an observed gesture. In terms of this thesis and the questions to be asked, imitation is particularly related to the ability of infants to perceive and act upon their bodies. By imitating an observed gesture, this could suggest that the infant is able to understand the spatial relations of others' bodies and then map these onto their own. Piaget (1952) believed that imitation was a result of learning (either conditioning or learning associations between the observed action and producing it) through everyday interactions with caregivers. However, this account of imitation fails to explain observations that very young infants are able to imitate actions they have never seen before.

In a particularly influential study, Meltzoff and Moore (1983) investigated imitation of facial gestures in typical newborn infants who were less than 72 hours old (ranging from 42 minutes to 71 hours in age). The infant observed a researcher producing a facial gesture (mouth opening or tongue protrusion) and was then seen producing the gesture themselves. Due to the age of the participants in this study, it is difficult to attribute these results to a learnt association between gesture observation and production. The most interesting aspect of this study, in terms of body representations, is that the newborn infant was able to translate knowledge of an other's body to then produce an action using their corresponding body part, specifically different actions using the same region of the body (i.e. using the mouth to produce an opening and a tongue protrusion gesture). The results of the described study would suggest that we have an innate ability to map observed actions by others to corresponding co-ordinates on our own bodies to mimic the action. From these assertions, researchers have argued that this ability may well be explained by the mirror neuron system (Marshall & Meltzoff, 2011). This could mean that, from birth and possibly even prenatally, the human infant has some way of representing different features of their bodies and how these features (e.g. limbs) can be used to produce an action.

However, other researchers (e.g., Anisfeld, Turkewitz, Rose, Rosenberg, Sheiber, Counterier-Fagan & Ger, 2001) have been more sceptical of the conclusions drawn from newborn imitation research. For example, rather than attributing infant's facial responses to imitation, tongue protrusion has been attributed to general arousal (Anisfeld, 1991, 1996, see Anisfeld, 2005 for a review of infant imitation) or general oral exploration behaviours in response to interesting distal stimuli (Jones, 1996, 2006); with the aforementioned researchers arguing that if tongue protrusion is the only behaviour to be mimicked by infants, this behaviour is too specific to constitute imitation (Heyes, 2001; also see Jones, 2009 for critique of other 'imitated' behaviours by newborn infants such as mouth opening and finger tapping). In addition, other researchers using the same experimental procedures as Meltzoff & Moore (1983) have failed to replicate the finding that newborns are able to imitate a range of facial gestures (e.g., McKenzie & Over, 1983; Hayes & Watson, 1981; Koepke, Hamm, Legerstee & Russell, 1983a, 1983b).

Furthermore, studies have found that imitation of actions seems to develop much later in infancy than first proposed by Meltzoff and Moore (1983). For example, Jones (2007) did not find evidence of imitation before 8 months of age, with 'traditional' acts of imitation (such as tongue protrusion) not mimicked until well into the second year of life, at 20 months. This sits uneasily in relation to other research which has shown that tongue protrusion can be produced by infants as young as 6 months of age during imitative behaviour (Fontaine, 1984). Ultimately, due to the later onset of these imitative behaviours in recent studies many have argued that imitation is a behaviour learnt through sensorimotor learning (Ray & Heyes, 2011 provide a detailed review of this account of imitation).

Considering the large number of studies, from across different labs, that contradict prior observations of newborn imitation and the fact that the earlier body of research on newborn and infant imitation has been criticised (e.g., Anisfeld, 1996, 2005; Jones, 1996; Abravanel & DeYong, 1997), it is difficult to conclude that very young infants possess the capability to map a seen action from another and produce the felt action themselves. So what does this mean in terms of infants' body representations? If we accept that action imitation has been demonstrated in infants no younger than 8 months, this would give rise to the view that, rather than infants possessing an innate understanding of the map of the body, body representation develop (perhaps through sensorimotor experience; Heyes, 2001) in the first few years of life.

1.3.4 Lexical-semantic representations

Language acquisition occurs from the first months of life (and even prior to birth), with evidence that infants can learn the words for body parts as early as 6 months of age (Tincoff & Jusczyk, 2012). However, it may be that the impact of lexical-semantic inputs occurs once the infant is producing words themselves. As such, the research that follows has focused primarily on toddlers.

Witt, Cermak and Coster (1990) examined lexical-semantic acquisition in children aged between 11 and 25-months by asking participants to identify twenty body parts on both a doll figure and themselves. The researchers found a positive correlation between age and the number of correctly identified body parts, with children at 2 years able to correctly categorize at least eleven parts of the body.

Brownell, Nichols, Svetlova, Zerwa and Ramani (2010) also investigated lexical-semantic acquisition, however rather than toddlers identifying body parts on either their own body, or a doll's, participants located body parts on another person. In this particular study, toddlers aged 20 or 30 months watched an experimenter place a sticker on either their own, or another researcher's, body parts. The participants were then given the stickers and asked to place the stickers on their own corresponding body parts. Twenty-month-olds were only able to locate 2-3 body parts (out of 12), whereas this increased to 4-5 in 30-month-olds, suggesting that body part localization is still relatively immature at this age. Although the task was non-verbal, in that researchers did not name the body part to which the sticker was applied, the study provides insight into toddler's abilities to differentiate between the distinct parts of their bodies, whilst also translating these body parts from a seen other to themselves. This may well be related to language acquisition; for example, language provides labels for the parts *within* a limb (arm, wrist, hand, fingers) and may be the driving force in the ability to name these distinct, continguous body parts (see Enfield, Majid & Van Straden, 2006).

1.3.5 Multisensory body representations

An important note to consider when investigating body representations is the fact that bodily sensations are not just restricted to visual inputs (as has been the primary modality of body representations investigation in infancy). Indeed, body perception is multisensory in adults; there are multiple modalities of input (such as the visual, proprioceptive and tactile domains; see Section 1.2.2).

The tactile modality arguably provides the most direct access to body representations given the nature of the distribution of receptors across the body. It is through the perception of touch that we are able to perceive our own bodies. Therefore, one way to learn more about one's own body perception is to investigate the way in which tactile sensations on the skin surface are perceived and coded.

The development in early life of the multisensory processes underlying body representations has been researched in a number of studies investigating visual-tactile and visual-proprioceptive links which I will now detail.

1.4 Touch and the body

1.4.1 The development of visual-tactile and visual-proprioceptive body representations

Everyday behaviour is comprised of processes involving interactions between visual and tactile localizations. One way in which researchers have tackled the question of whether children, infants and indeed newborns can make links between vision and touch is via crossmodal transfer tasks (Gottfried, Rose & Bridger, 1977; Maurer, Stager & Mondloch, 1999; Streri, 2003; reviewed in Bremner, Holmes & Spence, 2012; and Streri, 2012). In crossmodal transfer paradigms, infants haptically explore an object until habituation occurs. Following habituation, the infant is visually presented with the familiar and a novel object, with researchers investigating the infant's reaction to the novel object (infants tend to look longer at the novel object which is indicative that they were already familiar with the visually presented object they had previously haptically explored). Researchers have argued that the ability to transfer a perceptual representation of an object from one modality to another (usually visual to touch and vice versa) is present from approximately 6 months of age (Rose, Gottfried & Bridger, 1981a) and develops throughout the first year of life (Gottfried et al., 1977; 1978), whilst others have claimed that this ability may even be present at birth (Sann & Streri, 2008; although there is some controversy surrounding this and some evidence of early crossmodal transfer abilities; see Maurer, Stager & Mondloch, 1999 and Meltzoff & Borton, 1979).

Other researchers have also investigated visual-tactile correspondences in infants. Ruff (1976) examined the co-ordination of haptic exploration of an object (a set of wooden blocks attached to a panel) whilst infants also fixated on the object (visual motor integration). At 6 months, infants are able to reliably integrate visual and motor information (with infants fixating on, and manipulating, the objects simultaneously).

Crossmodal matching paradigms have also been used to investigate visual-proprioceptive abilities in infancy. One such study was conducted by Bahrick and Watson (1985). Here, 5-month-old infants' legs were hidden from view and they were presented with visual displays of where the seen movement of the leg on the display corresponded with the actual movement of the infant's leg at that point in time or where the seen movement on the video display was incongruent with the infant's current leg movement. The researchers found that infant's looking duration at the two video displays differed, with the infants looking longer at the incongruent display, prompting the authors to interpret this as evidence of 5-month-olds sensitivity to visual-proprioceptive contingencies.

Subsequent studies have also supported the findings of Bahrick and Watson (1985). For example, Rochat and Morgan (1995) presented 3 and 4-5 month old infants with a visual display of their leg moving in space, under several different conditions (e.g., in one video presentation, either the spatial orientation of the seen leg was incongruent to the position of the infant's own leg or the directionality of leg movement differed in the video or the perspective of the leg in the video was manipulated from the infant's point of view to an observer's point of view). Across all of these experimental manipulations, the authors found that by 5 months of age, infants are sensitive to changes in spatial and temporal contingencies, with even 3-month-olds being able to detect discrepancies in spatial orientation of the limbs.

Other studies investigating visual-proprioceptive correspondences (with a self versus 'other' distinction in which infants were presented with visual displays of another infant's moving leg) have demonstrated similar findings of infants' sensitivity to spatiotemporal contingencies (Schmuckler and Jewell, 2007; Schmuckler & Fairhall, 2001).

The above studies have provided support for the view that young infants, within the first half year of life, are sensitive to some of the multisensory correspondences (visual-tactile and visual-proprioceptive spatiotemporal correspondences) which might be useful in perceiving the human body. A point of contention here concerns whether these abilities to perceive visual-tactile and visual-proprioceptive correspondences are crucial components of the representations which we form of our own bodies.

Let's take the visual-tactile crossmodal transfer tasks first. Because the spatial matches in crossmodal transfer tasks are "field independent" (i.e., they do not require an ability to co-locate features within a common spatial frame of reference, but simply register pattern correlations between frames) such findings do not inform us about the development of an ability to register co-location in an external (or at least peripersonal) spatial environment (Bremner & Cowie, 1993; Eilan, 1993).

We might think that the visual proprioceptive matching tasks undertaken by Bahrick & Watson (1976), and Rochat (1998) and described above, get over this by presenting infants with concurrent visual and proprioceptive information about their limbs (rather than a crossmodal transfer scenario). However, given the fact that an image of the limb (usually the legs) is visually displayed on a screen, in external space (typically over a metre away from the infant), it is difficult to argue that these correspondences are processed with respect to the common framework of the body. It may be that infants are matching the movement that is felt in the body with the visual movement which is seen in extrapersonal space (Parise, Spence & Ernst, 2012), but without locating both of these cues in a common body representation.

Other studies have found that the relationships between visual and proprioceptive contributions to body representations continue to change significantly in early and middle childhood. For example, Bremner, Hill, Pratt, Rigato and Spence (2013), studied children's responses to the mirror box illusion task (Holmes, Crozier, & Spence, 2007). It was found that, children between the ages of 5 and 7, made errors in reaching when visual and proprioceptive information of the hand was thrown into conflict. Significantly, this study also revealed developmental increases in how children weighted visual information; it was between the ages of 4.75 and 6 years that children came to rely more heavily on visual information regarding limb position.

The role of visual cues to limb position in giving rise to the felt location of a limb has been considered in depth in studies of the Rubber Hand Illusion (RHI; Botvinick & Cohen, 1998). The RHI is the phenomenon by which, if individuals see a fake hand being stroked in front of them (placed where their own hand would usually sit), whilst their real hand is hidden out of view and is also being stroked in synchrony, individuals can be induced to adopt the fake hand within their body schema and accept it as their own. Cowie, Makin and Bremner (2013) investigated the RHI in children aged between 4 and 9 years, demonstrating that the ways in which children use visual cues to hand position and ownership is still not adultlike by 9 years of age.

In a similar paradigm to that used in the RHI, Zmyj, Jank, Schütz-Bosbach & Daum (2011) investigated visual-tactile matching in a group of infants. In this study, the researchers presented 7 and 10-month-old infants with two video recordings of a life-like doll's leg being stroked in either a synchronous or asynchronous manner to the stroking the infants' received to their occluded legs. The authors found it was only the 10-month-olds that were reliably differentiating between the two video displays, once again demonstrating a preference for the video display that depicted stroking that was synchronous with the stroking they felt on their own leg. From this, the authors concluded that it is by 10 months of age that infants develop a perception of their bodies. However, a critique of note is that the visual stimuli of the infant's legs were presented at some distance from the body (one metre). Considering that adults no longer perceive ownership of a fake hand (in RHI paradigms) when it is placed 60 cm from their body (Lloyd, 2007), it is difficult to conclusively assert that, from the paradigms employed by the above studies, infants perceive the visual body as their own.

Other work with infants using a similar paradigm in which infants were presented with visual information of a body part receiving a tactile input has been conducted by Filippetti, Johnson, Lloyd-Fox, Dragovic and Farroni (2013). Here, newborn infants were presented with a visual stimulus detailing an infant's cheek being stroked with a paintbrush, in an upright or inverted position. At the same time as infants viewed this video, their own cheek was also stroked with a paintbrush. This stroking occurred in either a synchronous or asynchronous manner to that which appeared in the video. The researchers found that the infants showed preferential looking behaviours in the synchronous condition (i.e. when the touches they felt on their cheek temporally matched the touches they saw on the screen). However, this preferential looking was specific to a condition in which the infant's face in the video was upright rather than inverted. From this, Filippetti et al. (2013) argued that newborns are able to detect intersensory synchronies (between vision and touch), however this only occurred when visual information was related to their bodies.

Overall, the research discussed in this section has illustrated the development of visual-proprioceptive and visual-tactile body representations. Additionally, the research has highlighted the key role that tactile information can play in the development of body representations, a point that is discussed in more depth below. However, there is a crucial point of critique to run through all of the studies described above demonstrating visual-tactile and visual-proprioceptive crossmodal interactions in young infants. This is that it is unclear from this evidence whether and at what stage infants are able to locate multisensory cues to the body within the single common spatial reference frame of the body.

1.4.2 Using touch to locate the body in space

Touch can inform individuals about the environment that impinges upon their body through the sensations of texture, movement, pressure and temperature. Locating a touch on the body is a computationally complex task and is made all the more difficult through the constant movement of the limbs in space (Azañón & Soto-Faraco, 2008; Kitazawa, 2002; Overvliet, Azañón & Soto-Faraco, 2011; Graziano et al., 2004). Locating a touch is a multisensory task; individuals do not process tactile information in a vacuum, but use various sources of sensory information (such as proprioception, vision and even audition) to accurately locate a touch on the body and in external space (Macaluso, Frith & Driver, 2002; Kennett, Spence & Driver, 2002; Spencer & Driver, 1994, 1996, 1997; Bruns, Spence & Röder, 2011; Zampini, Torresan, Spence & Murray, 2006; Kitagawa, Zampini & Spence, 2005; see Kitagawa & Spence, 2006 for a review of auditory-somatosensory interactions). Touches can be perceived both relative to the body, and in a location in external space (see Martin, 1993). However, the ways in which bodily and external spatial reference frames are related are not straightforward, and this causes problems for locating tactile stimuli. When limb posture changes, this puts into conflict the anatomical (the location of the felt touch on the skin) and the external reference frames within which touches are perceived. Thus, to locate touches in external space, we are constantly required to update the relations between tactile and visual coordinates across changes in limb posture.

My thesis concerns two primary questions: how infants and children map touches in space and on the body and how they keep track of touches across changes in the posture of their limbs. The question of how infants and children are able to map touches to the body in space is one I have investigated. I will discuss the theoretical rationale and literature in relation to the emergence of this ability below.

1.5 Frames of reference

In general, a frame of reference simply refers to a co-ordinate system in which features, objects, people and even our own limbs and bodies are represented. Within the body representation and tactile localization literature, several terms have emerged, some of which are synonymous and interchangeable, whilst others encompass subtle differences. Throughout this thesis, I will refer to an 'anatomical' and an 'external' frame of reference. I mean anatomical reference frame to refer to a somatotopic reference frame, i.e., a coordinate system defined by position on the skin surface, whereas an external reference frame refers to locating a touch in a coordinate system in the external environment which is independent of the positions of the limbs in space (e.g., a visual frame of reference). Note that this definition of external space does not differentiate between frames of reference related to an egocentric representation of the world (e.g., left right coordinates), and an allocentric representation of the world which is viewpoint independent.

1.5.1 Frames of reference for touch: The "crossed hands effect"

Several techniques that involve manipulating the posture of the limbs can be used to investigate how touches to the body are perceived with regard to anatomical and external frames of reference (i.e. by crossing over the hands so they are in the contralateral side of space to their usual placement). This helps us to disentangle the roles of different kinds of spatial reference in tactile spatial representation.

The "crossed hands effect" (Shore, Spry & Spence, 2002) refers to a deficit in tactile temporal order judgements when participants' hands are placed in less familiar postures, i.e. when they are crossed at the forearm and are in the opposite side of space to their usual placement (Overvliet, Azañón & Soto-Faraco, 2011; Azañón & Soto-Faraco, 2008; Yamamoto & Kitazawa, 2001a). It has been proposed that this deficit arises as a consequence of the conflict between the anatomical and external frames of reference within which touches can be perceived. In the crossed hands posture, the right hand is now placed in the contralateral side of space (i.e. on the left side of the body) and vice versa for the left hand. Therefore, there is a conflict between the location of the touch in its usual location with respect to the body (i.e. the anatomical location of the touch) and its location in external space.

1.5.2 Adult studies investigating the "crossed hands effect"

Yamamoto and Kitazawa (2001a) examined the effect of crossing the hands on tactile localization using a tactile temporal order judgment (TOJ) task. This involved presenting participants' with two tactile stimuli (one to each hand) in very quick succession (stimulus onset asynchronies between 5 and 1500 ms). Participants were then required to indicate the location of the initial vibrotactile stimulus by lifting the index finger of the corresponding hand. This was carried out with participants' arms in the more familiar, uncrossed posture and also in a less familiar posture, with their hands crossed at the forearm. With arms uncrossed, participants were able to correctly judge the temporal order of tactile stimuli when the interval) between the two tactile stimuli was at least 70 ms in 80% of the trials (yielding a "just noticeable difference" or JND of 70 ms). However, with arms crossed, the JND increased to approximately 1500 ms, with intervals of 100-200 ms between the two stimuli resulting in an inverted response from participants (i.e. they attributed the initial tactile stimulus to the opposite, incorrect hand).

Shore *et al.* (2002) conducted a series of experiments that also used a TOJ task and the study yielded similar findings; participants were able to correctly identify the temporal order of tactile stimuli in the uncrossed hands with a JND of 34 ms, however when their hands were crossed, participants' tactile localization accuracy decreased significantly, with the JND increasing to 124 ms.

The "crossed hands" deficit is not limited to tasks where participants are asked to produce a motor response to indicate the location of the initial touch. When participants are asked to produce a visual response to indicate the location of the first felt touch, the early stages of participants' saccades are occasionally made towards the wrong hand when hands are crossed (Overvliet, Azañón & Soto-Faraco, 2011; Groh & Sparks, 1996).

Crucially for this thesis, it is clear that crossed-hands effects can provide an index of an ability to localize touches in both anatomical and external frames of reference. I will report on several studies which have used this manipulation to trace the emergence of such reference frames for touch in Chapter 3.

1.5.3 The role of vision in the development of an external reference frame for touch

It has been argued that visual experience in early life may well influence the emergence of an external frame of reference (Röder, 2012). This account was investigated by Röder, Rössler and Spence (2004). In a tactile TOJ study like those described above (Yamamoto and Kitazawa, 2001; Shore et al, 2002), the authors found that congenitally blind participants' accuracy (and JNDs) in determining the location of the initial tactile stimulus did not differ across crossed- and uncrossed-hands postures. In contrast, sighted and blindfolded sighted individuals performed poorly with crossed hands (in comparison to when their hands were in the uncrossed posture). Crucially, 'late blind' participants (individuals who had some early experience of vision and had acquired a visual impairment) behaved in a similar way to sighted individuals and demonstrated the "crossed hands effect".

The fact that the congenitally blind participants did not show a crossed hands deficit and performed to the same degree of accuracy across postures suggests that they do not employ an external frame of reference when coding touches to the body (if they are not employing an external reference frame to code touches, there cannot be a conflict between the anatomical and the external frames of reference). It may be that in order for individuals to use the external reference frame, as the authors postulated, there needs to be some visual experience in order to learn to map touches in the external world.

It is somewhat surprising that the late blind individuals performed in a similar manner to the sighted controls, especially when considering that these individuals had spent the majority of their lives without vision (and on average, only twelve years in early life without a visual impairment). As suggested by Röder et al. (2004) (in that visual experience is necessary to develop an external frame of reference), it may be that as the late blind individuals had *some* experience of vision in early life, this experience was sufficient for the external reference frame to develop and be available for use. Thus, regardless of the availability of visual information about current hand posture, the use of the external reference frame to map touches in space persists if this frame of reference was available for use for any period of time in early childhood.

However, Röder et al.'s data indicate that individuals without any experience of vision (in the case of the congenitally blind participants) are limited to using only the anatomical reference frame (as the external reference frame did not emerge) when locating somatosensory stimuli, eliminating the conflict between the anatomical and external reference frames and thus, the “crossed hands effect”.

Other research with congenitally blind individuals appears to qualify this conclusion, suggesting that developmental vision is not necessary for the emergence (and use) of an external frame of reference when locating touches on the body. Eardley and Van Velzen (2011) conducted an event related potential (ERP) tactile TOJ study with congenitally and early blind participants and sighted, blindfolded participants. It was found that the neural activity elicited in this task (a reversal and delayed onset of the attention directed anterior negativity component) did not differ between the groups of participants, with the early and congenitally blind participants performing in a similar manner to the sighted matched controls when their hands were in the uncrossed, and the crossed, posture. A possible explanation for the difference in findings to that of Röder et al. (2004) could be due to the fact that Eardley and Van Velzen (2011) allowed all participants to explore the testing room and experimental set up haptically prior to the beginning of the experiment.

Other studies with congenitally blind populations have asserted that, if necessary, they are able to locate their limbs in external co-ordinates. For example, Röder, Kusmierek, Spence and Schicke (2007) presented an auditory tone in external space, either on the left or right side. Participants were asked to move the hand that was nearest to the auditory tone. It was found that congenitally blind adults are able to respond correctly in both uncrossed-hands and crossed-hands postures. The experimental procedure used in this study required participants to compute the location of their hands in external co-ordinates, therefore Röder and colleagues have argued that when an external representation of space is task relevant, congenitally blind individuals appear to make use of an external reference frame. Further to this, Röder, Heed and Badde have argued that whilst congenitally blind individuals do not *automatically* make use of an external reference frame (as evidenced by their performance in the tactile TOJ task; Röder et al., 2004), this reference frame may still be available for use, but at additional processing costs (Röder, Heed and Badde, 2014).

1.5.4 Developmental studies of crossed hands effect

Studies investigating "crossed hands" effect have also used developing populations to map the emergence of the external reference frame in which touches to the body are coded. The developmental literature investigating the "crossed hands" effect has found evidence of young children using an external frame of reference. Pagel, Röder and Heed (2009) used a tactile TOJ task with children aged from 4 to 10 years. The methodology employed was very similar to the adult TOJ tasks described above, however rather than participants' manually responding to the initial stimulus, the children were required to indicate the location of the tactile stimulus by saying which hand they had felt the vibration on. As young children are notorious for confusing the 'left' and 'right' hand labels, animal stickers ('dog' and 'cat') were put on the backs of their hands, substituting the hand labels. It was found that only children aged 5.5 years and above that exhibited the "crossed hands effect", with the researchers highlighting that this was a result of developmentally increasing tactile localization accuracy in the uncrossed posture in particular. Thus, according to Pagel et al. (2009), children begin to map touches on their body in external co-ordinates at the age of 5.5 years, with this external reference frame possibly enhancing tactile localization performance when children adopt usual body postures (when arms are uncrossed).

However, there is evidence that an external reference frame for touch may emerge much earlier in life. Bremner, Mareschal, Lloyd-Fox and Spence (2008) used a different kind of tactile localization task where only a single tactile stimulus was presented to the hands and they investigated infants' manual orienting responses (i.e. movements of the stimulated and non-stimulated hands) comparing 6.5- and 10-month-olds. It was found that 6.5-month-old infants were less able to manually orient correctly towards the hand that received the tactile stimulus when in the crossed hands position compared to the uncrossed posture; often in the crossed hands posture, infants would move the opposite hand to the one which had received the vibrotactile stimulation, indicating that they are unable to update their body representations to take into account the change in posture, and thus the changes in the side of space their limbs now occupy.

Infants in this youngest age group demonstrated poorer tactile localization accuracy in the crossed hands posture, which is indicative of anatomical and external reference frames conflicting. Thus, this is suggestive of infants in the first half year of life using an external reference frame to code touches on the hands.

In comparison, 10-month-olds were able to accurately orient to the same degree of accuracy regardless of hand posture, suggesting that the ability to integrate sensory information from various modalities (visual, proprioception and tactile) concerning both stimulus location in various frames of reference (and body postures) develops at 10 months. As the 10-month-old infants were performing accurately regardless of posture, it can be argued that here they are resolving the conflict between locating touches in the anatomical and the external frame of reference, by updating the location of the touch across changes in posture. As the 6.5-month-old infants were unable to do this, thus resulting in errors in the crossed posture, Bremner et al. (2008) argued that there is a period of development between the ages of 6 and 10 months during which infants acquire the ability to update the site of a tactile stimulus across changes in limb posture.

The above studies highlight the inconsistencies in the developmental literature (cf. Pagel et al., 2009, and Bremner et al., 2008), suggesting that more research needs to be conducted to discover at what age infants/children begin to use an external frame of reference to localize touches to their hands.

The literatures I have discussed thus far covers one aspect of my thesis; that of how touches to the body are coded in external co-ordinates and when this ability emerges in infancy and childhood. Another topic of interest that my thesis covers relates to somatosensory remapping. In order to accurately locate touches in external space, we also need to be able to track any postural changes that are made and update representations of the locations of tactile in external space accordingly (e.g., Eimer & Driver, 2000; Eimer, 2001; Eimer & Forster, 2003; Yamamoto & Kitazawa, 2001a, 2001b; Shore et al., 2002; Shore, Gray, Spry & Spence, 2005; Schicke & Röder, 2006; Kitzawa, 2002; Bremner et al., 2008a; Bremner, Holmes & Spence, 2008; Azañón and Soto-Faraco, 2008, 2011; Badde, Röder & Heed, 2011; Heed & Azañón, 2014).

1.6. What is somatosensory remapping?

Somatosensory remapping refers to the processes by which we update representations of tactile location across changes in body posture (for example, when the hand is placed in a less usual location to that which we are used to i.e. crossed over the midline and in the contralateral side of space). Azañón and Soto-Faraco (2008) developed a crossmodal spatial cueing paradigm to investigate the time course of somatosensory remapping. With hands crossed, participants were presented with a tactile stimulus to one hand, followed by a visual stimulus (a flash of light) presented on the top or bottom of either the same, or opposite, hand. The two stimuli were presented at varying temporal distances (between 30 ms and 360 ms) and participants were required to indicate the location of the visual stimuli (e.g. either top or bottom), irrespective of hand.

The researchers found that when the visual stimulus was presented between 30-60 ms to the hand that did not receive the tactile stimulus (the opposite hand), participants' reaction times for localizing the visual stimulus was faster when (i.e. when the location of the stimuli were anatomically congruent, but spatially incongruent). However, if after 60 ms, the visual stimulus was presented to the same hand (that which received the tactile stimulus), participants' reaction times to the visual stimulus were faster as the location of the stimuli (both visual and tactile) were now spatially congruent. From these results, Azañón and Soto-Faraco (2008) argued that initially participants' locate touch within an anatomical reference frame, before the remapping process begins after 60 ms following stimulus onset.

In a further study, Overvliet, Azañón and Soto-Faraco (2011) investigated participants' saccadic trajectories to tactile stimuli administered to the hands in both the crossed, and uncrossed, postures. When hands were in the crossed posture, the early stages of saccades were made towards an erroneous location (i.e. participants initially looked towards the incorrect hand). From these results, the authors suggested that in order to execute a saccade to the location of the initial touch, the tactile remapping process must be complete, with the timings of the remapping process supporting the findings of Azañón and Soto-Faraco (2008).

The studies described above point to a dynamic process in the brain that remaps the relationship between tactile information and external space across different postures of the limbs. The timeline of this process has been measured by Azañón and Soto-Faraco (2008) and found to occur after 60 ms following a touch being applied to the hands. As reported above, initially individuals code touch within a somatotopic reference frame, but 60 ms after a tactile stimulus has been applied, the process by which individuals map touches with respect to external co-ordinates begins.

The above studies have been useful in determining at what point the somatosensory remapping process begins. Neuroimaging studies have also been informative in this respect, as well as illustrating the different areas of the brain that may be recruited during the somatosensory remapping process. One such study was conducted by Lloyd, Shore, Spence & Calvert (2003). In this particular study, sighted adults' hands were crossed over their midline and a vibrotactile stimulus was applied to this hand when participants either did, or did not have, visual information concerning current hand posture. With eyes open (and visual information about hand posture available), neuronal activity associated with somatosensory remapping was observed in the hemisphere contralateral to the stimulated hand. Conversely, with hands covered so that participants were unable to see the posture of their hands, this activity then shifted entirely to the ipsilateral hemisphere (Lloyd et al., 2003; Rigato, Bremner, Mason, Pickering, Davis & Van Velzen, 2013) when the hand was crossed over into the contralateral side of space (i.e. the opposite side of space to its usual placement). Rigato et al. (2013) suggest that when only proprioceptive information regarding limb posture is available, individuals may localize touch within an external frame of reference, whereas when individuals are able to see their hands, an anatomical frame of reference may be employed. It has been postulated that this may be due to the greater relevance of anatomical coordinates when we have more information about the body (i.e. when we can see it). An important conclusion from this study is that touch can be remapped whether information regarding posture is purely proprioceptive or involves both visual *and* proprioceptive cues (this has also been found in non-human primates; Graziano, 1999).

As mentioned previously, neuroimaging techniques can be useful in determining the time course of the somatosensory remapping process. Whilst this is not a forte of fMRI research, EEG can be informative on this matter. As such, Rigato et al. (2013) found that, with hands visible, the somatosensory remapping process begins at 128 ms. When the hands were covered and vision of arm posture was occluded, not only did the neural activity shift to the ipsilateral hemisphere, the latency of the beginning of the remapping process increased to 150 ms.

Soto-Faraco and Azañón (2013) also conducted an EEG study investigating somatosensory remapping in a group of adults and the findings were similar to that of their behavioural study (Azañón & Soto-Faraco, 2008). That is, neural activity when hands were crossed over the midline showed a greater negativity (compared to when hands were uncrossed), with the greatest difference occurring at 70 ms after stimulus onset.

The latency of the difference in neural activity across postures differs from that found by Rigato et al. (2013), occurring somewhat earlier than the 128 ms reported in that study. A potential explanation could be the methodologies employed in the studies; for example, Azañón and Soto-Faraco (2013) used a 9 ms mechanical tap to the finger, whereas Rigato et al. (2013) used a 200 ms vibrotactile stimulus that was presented to the palms of the hands.

Currently, of the research that is available, the majority of the studies have used only adult populations and thus, very little is known about how the ability to remap touches across changes in body posture develops in infancy. However, Bremner et al. (2008) have conducted behavioural studies with infants in the first year of life in order to understand the developmental origins of somatosensory remapping. As previously mentioned (in Section 1.5.4), single touches were applied to the palms of infants, aged 6.5 and 10 months, in either the uncrossed-hands or the crossed-hands posture. It was found that whilst 6.5-month-olds made manual orienting errors in the crossed-hands posture (relative to the uncrossed-hands posture), the 10-month-olds did not demonstrate this. In fact, this group of infants was able to manually orient to the site of the tactile stimulus in an accurate fashion across both arm postures. From this, the authors argued that by the age of 10 months, infants are able to update the locations of felt touches by keeping track of changes in limb posture.

1.7 Specific questions for this thesis

As already mentioned, there are two principal avenues of investigation followed in my thesis, both of which concern the development of an ability to localize tactile stimuli in early life. The first is about the spatial frames of reference used to locate tactile stimuli on the body and our body in space, and specifically the development of an ability to perceive touches in external space (in infancy and early childhood). Of the developmental literature on this topic (crossed-hands studies conducted by Bremner et al., 2008, and Pagel et al., 2009, discussed in Section 1.5.4), the findings either indicate the origins of external coding of touch in infancy (Bremner et al., 2008) or in early childhood (Pagel et al., 2009). One purpose of this thesis is to attempt to resolve this conflict of findings.

Following this, I will then address the second aspect of my thesis, which considers the development in infancy of the processes by which we update representations of tactile location across changes in body posture (somatosensory remapping). Very little is known thus far about how this ability develops and changes in infancy and currently there is no experimental research examining the developmental origins of somatosensory remapping. As such, we are unaware of the mechanisms used in order for this ability to develop. One candidate of this developmental process is that somatosensory remapping is driven by sensorimotor experience; as the infant becomes able to adopt a wider variation of bodily postures this process may provide the experiences which prompt the development of an ability to remap the location of touch across changes in body posture. Alternatively, it may be that somatosensory remapping occurs as a consequence of maturation of the brain, so that an infant's age is particularly important for the development of this ability.

1.8 Thesis overview

This thesis will discuss my investigations into the development of body representations; specifically investigations of how infants and children locate and code touches to the body and how they update locations of touch across different postures.

The thesis is divided into seven chapters. **Chapter 1** (the current chapter) has provided an overview of the literature concerning both mature and developing body representations and the multisensory nature of these. Chapter 1 also included the relevant literature concerning how adults, children and infants locate touches to their body with respect to external co-ordinates and also reviewed the current literature on somatosensory remapping in both adults and infants.

Chapter 2 details an overview of the various methodologies I used throughout my investigations, both EEG (ERP techniques) and behavioural (visual preference and orienting behaviours) methods. I discuss how the methods were applied to the experiments in this thesis, with specific emphasis on the application of ERP and behavioural techniques to developing populations (i.e. infants in the first year of life).

Chapter 3 presents three behavioural experiments that investigate how children and infants map touches on the body in space and the various reference frames that are employed in this process. In Experiment 1, I investigated the modulatory effect of vision of the limbs on tactile localization in a group of young children (aged 4 to 6 years).

Experiment 2 reported in Chapter 3 investigated further the developing role of vision of the limbs in localizing touch by presenting children (aged 4-years) with fake rubber hands in a posture that was congruent or incongruent to that of their own hands. Experiment 3 reported in Chapter 3 examined when an external reference frame for touch emerges in the first half year of life.

Chapter 4 details three experiments investigating somatosensory remapping in the first year of life. Experiment 4a (a pilot study) and 4b investigated the relationship between midline crossing reaching and somatosensory remapping abilities in 6- and 8-month-old infants via a correlational design.

Experiment 5 reported in Chapter 4, comprised a motor training study that further investigated the findings from Experiment 4b. In this study, a group of 6-month-old infants took part in a contralateral reaching training program for a period of two weeks, in order to determine whether the experience of such sensorimotor behaviours could drive the emergence of somatosensory remapping in the brain.

Chapter 5 addresses, in two experiments, whether infants aged 4- and 6-months perceive visual and tactile information arriving at the body within a common spatial framework. Experiment 6a attempted to address potential explanations of pilot work conducted regarding this question by Freier, Mason & Bremner (in prep.). Experiment 6b investigated the emergence of an ability to perceive visual-tactile co-location in early infancy, across two age groups; 4- and 6-month-olds.

Chapter 6 introduces crossmodal attentional cuing effects as a means of addressing multisensory spatial integration of vision and touch in human infants. Research in this phenomenon in adults has shown that if attention is shifted to a region of space, the neural response to a stimulus in that area is greater than if individuals are not attending to that location. Experiment 7 involved presenting a tactile stimulus to the hands, of 7-month-old infants, preceded by a visual stimulus (a flash of light). Somatosensory evoked potentials were recorded and analysed to determine any crossmodal cuing effects.

Finally, **Chapter 7** is a discussion chapter, providing a summary of the key findings from the seven experiments conducted in my PhD and presented in this thesis, set in the context of the wider literatures on body representation and perceptual development. In this chapter I also discuss potential avenues of future research concerning the development of body representations in early life.

Chapter 2

2.1 General methods

In the following chapter, I will describe and discuss the various methods I have employed to investigate infant and child behaviour over the course of this thesis, as well as the way in which findings using such methodologies can be analysed and interpreted.

For the studies conducted in this thesis, I decided to use both behavioural and physiological methods to investigate the experimental questions under examination. These two research methods provide complementary information. For example, whilst physiological measures can inform us of the underlying neural mechanisms of a cognitive process, this method is often less informative about the behavioural context in which sensory processing occurs.

There are advantages and disadvantages that are unique to physiological and behavioural methods. For example, for physiological measures such as EEG, there usually requires a high number of experimental trials. Further to this, participants are required to keep relatively still throughout the testing session so as not to contaminate the recorded data with movement artifacts. In terms of behavioural paradigms, data is not compromised if participants shift position or blink (as it would be with physiological measures). Further to this, behavioural paradigms often include fewer trials than that used in EEG studies. However, a disadvantage of behavioural measures is the fact that they may be less sensitive to cognitive processes. Ultimately, using both behavioural and physiological measures allows us to examine the relationship between brain development and behaviour (cognitive development). I discuss the advantages and challenges of these methods below.

I will first begin with the behavioural measures I used, specifically visual preference (Experiment 6, Chapter 5) and orienting measures (Experiment 3, Chapter 3) with infants. I will describe these methods, both generally and in terms of the specific ways in which they were employed in the studies described in this thesis.

I will then go on to briefly introduce EEG and ERP in general, before discussing the more specific techniques I used for infant studies investigating somatosensory remapping (Experiments 4a, 4b and 5 in Chapter 4) and cross-modal attention (Experiment 7 in Chapter 6). I will outline the advantages and disadvantages of using EEG, with special regard to its use with infants. I also detail the data acquisition techniques that are typically used in infant EEG and have been employed in the studies reported here. This is an important point of focus given that these techniques typically (and here) differ from those used for EEG obtained from adult participants. Finally, I discuss the ERP data analysis process (deciding the spatial and temporal regions of interest) and the rationale for using certain statistical analyses with such data.

2.2 Behavioural methods

2.2.1 Visual behavioural techniques

There are a number of ways in which infant behaviour can be investigated. One such method involved using infant’s eye movements (saccades) to determine what they knew about their world. Infant looking behaviour and visual fixation has now long been established as a reliable method in indicating infants' visual discrimination abilities (Fantz, 1958), and relies on the principle that infants will prefer to look at a more interesting stimulus and will spend less time looking at a stimulus that they no longer view as new or interesting (e.g. they essentially become bored of this stimulus and are no longer engaged by it, so they will not look at this stimulus very much). Although, it is also possible to observe familiarity preferences in infancy, where the infant spends more time looking at a familiar stimulus (Aslin, 2007). We can establish a novelty preference typically through habituation procedures in which the infant first demonstrates a decline in interest for the familiar stimulus.

An advantage of using visual behavioural techniques is the fact that this method does not require a vocal or physical (e.g. motor) response. As such, it can be used with very young infants in which these behaviours may have not developed and cannot be elicited on demand. Researchers have also employed visual preferences to identify what infants know and understand about the world (e.g., Spelke, 1979; Quinn, 1994). With its popularity not diminishing over the past fifty years, it remains a viable and unique method to garner insight into the ontogeny of perception (e.g., Fantz, 1963, 1975; Slater, Morison, Somers, Mattock, Brown & Taylor, 1990; Cohen, 1972; Baillargeon, 1986, 1987; Leo & Simion, 2009; Lewkowicz & Turkewitz, 1981; Lewkowicz, 2010; Spelke, 1979, Spelke, Kestenbaum, Simons & Wein, 1995; Fillipetti et al., 2013, for a review see Colombo & Mitchell, 2009).

But how does looking behaviour specifically inform us about what the infant perceives? It has been accepted that a look directed to a stimulus is a correlate of the underlying neural activity that mediates detection, discrimination or categorisation of the presented visual stimulus (Aslin, 2007).

A challenge of using visual preference methods as an index of perceptual ability is that infants, despite being able to distinguish between stimuli, may not necessarily attend to one stimulus over the other and may have equal looking durations for both stimuli (Aslin, 2007). Further to this, it must be asserted that if infants have the same total duration of looking time for different stimuli, this does not necessarily mean that this is the result of the same underlying neural activity (Aslin, 2007). For example, Cohen (1972) argued that the same duration of looking at different stimuli may be the result of a long initial look to one stimulus and several short looks to another stimulus, with the total duration being equal. Thus, there are two distinct processes that can be observed; with the initial looking time at the stimulus reflecting an attention-holding process and the latter type of looking reflecting an attention-getting process. Therefore, it is important there is a degree of caution used when interpreting infant looking time data in terms of what they inform us about the underlying processes.

However, even with the potential problems with visual preference paradigms, the method has been employed in a large number of studies and has yielded great advances in our knowledge of infant perception and cognition. This is especially in terms of object discrimination (e.g., Fantz, 1958; Horowitz, Paden, Bhana & Self, 1972), number perception (e.g., Starkey, Spelke & Gelman, 1990) and face perception (e.g., Johnson & Morton, 1991). In fact, one way to combat the problem above (i.e. that of infants looking equally at different visual stimuli) is to present infants with several competing pairs of stimuli in order to establish systematic preferences. This way, at least, conclusions concerning infant's discrimination of preferred and non-preferred stimuli can be drawn (Colombo & Mitchell, 2009).

In Chapter 5, I report two experiments (Experiments 6a and 6b) in which I used a visual preference paradigm to investigate whether infants expect visual and tactile information on the body to occur in the same region of space (i.e., whether they have the ability to co-locate vision and touch within a common spatial framework). However, a methodological challenge with these studies was the fact that it would have been impossible to present stimuli in a simultaneous test procedure. Instead, I used sequential stimulus presentation (see Experiments 6a and 6b, Chapter 5 for further details).

A further challenge related to whether we could actually observe infants' visual preference for tactile stimuli occurring on the body. Whilst there has been much research concerning infants' preference to the display of visual stimuli, as yet, there has been no research conducted that examined visual preference to touch. Thus, we had to establish that visual preference for stimuli presented across the hands was a viable measure of preference. This was a feasible method for use with older infants (of at least 6 months of age; as in Experiment 6a), however considering that infants' hands tend to be within peripheral vision up to approximately 5 to 6 months of age, it was decided that for younger infants, the feet would be used instead as these limbs do not tend to lie in peripheral vision at this age (Experiment 6b).

In terms of the visual preference method (and variations of it), preferences in general are not informative about the extent to which perceptual experiences are referenced to the body. This is because visual preference methods do not typically require the infant to coordinate the internal (body centred) frame of reference with the external (often a visual display of stimuli on a screen) frame of reference (Bremner et al., 2008a).

This may explain the disparity in findings concerning infant's spatial knowledge when using the two different behavioural methods (visual preferences and orienting measures). Visual preference studies, where looking time measures are employed, have shown that within the first few months of life, infants already possess a complex understanding of their environment. For example, studies have found that by approximately 4 months of age, infants have some understanding of ‘above’ and ‘below’ (Quinn, 1994). In a series of studies, infants were presented with a visual display depicting a dot above or below a horizontal line, to which they were familiarized. Following this, the infants were presented simultaneously with two visual displays; the familiar display, with the dot in a novel position but still in the same region of space as during familiarization (either above or below the horizontal line) and a novel display (in which the dot was now in a different position in a different region of space to that in the familiarisation period). It was found that, after familiarisation, infants showed a preference for the novel visual display. From this, it was concluded that by 3 months of age, infants are able to represent spatial categories.

Other research using visual preference methods has also shown understanding of spatial representations in young infants. For example, Kaufman and Needham (1999) habituated 6.5-month-old infants to the spatial location of an object, before either the object or the location of the infant was changed. It was found that dishabituation only occurred when the location of the object was changed, rather than the location of the infant themselves. From this, the authors argued that infants of this age are able to consider the allocentric environment when representing space.

However, if an orienting task (as opposed to a visual preference task) is used to measure infants’ abilities to represent space a differing developmental trajectory is demonstrated. For example, Bremner (1978) presented 9-month-olds with an object that was hidden in one of two locations. Before infants were allowed to search for the object, the spatial relationship between the infant and the object was altered. When the location of the infant was changed, typically their searches were inaccurate. From this, it was argued that 9-month-olds seemed to code space within an egocentric reference frame, seemingly ignoring the allocentric environment. Furthermore, it seems that it is not until the second year of life that they are able to consider both the egocentric and allocentric reference frames and update their orienting responses accordingly (Acredelo, 1978).

So how might these differences in findings concerning infants' spatial representations be resolved? Bremner et al. (2008a) have argued that visual preference methods do not require the infant to use an internal, body-centred reference frame, whereas orienting measures require a co-ordination of the body-centred reference frame with the external frame of reference. Indeed, it seems that particularly useful tools for investigating the spatial frames of reference which infants use when inspecting and exploring the world are body/limb orienting measures.

2.2.2 Introduction to orienting paradigms

There are a number of variations of orienting behaviour that have been measured successfully with infant populations. For example, visual orienting paradigms which involve motoric behaviours such as turning of the head towards a visual or an auditory stimulus (e.g., Acredolo, 1978; Neil, Chee-Ruiter, Scheier, Lewkowicz & Shimojo, 2006; Muir & Field, 1979; Butterworth & Castillo, 1976). Using visual orienting measures has allowed researchers to make conclusions regarding infants' abilities to detect and discriminate between different speech sounds (e.g., Swain, Zelazo & Clifton, 1993), the spatial frames of reference which infants use for locating objects in the world (Acredolo, 1978), and their ability to locate audio-visual stimuli in their environment (Muir & Field, 1979; Clifton, Morrongiello, Kulig & Dowd, 1981) for which they expect such stimuli to occur in a common region of space (e.g., Morrongiello, 1988).

In terms of the questions asked in this thesis (particularly those regarding when an external frame of reference for touch emerges in infancy), orienting behaviours in general are of interest. This is due to the fact that any type of orienting (visual, manual, foot movements, head turning movements and so on) involve co-ordinating an internal frame of reference (the body) with what is being inspected/perceived.

Spatial orienting has been demonstrated in a variety of reflexes in the newborn infant. Fényes, Gergely and Tóth (1960) demonstrated a crossed-extension reflex in newborns. In this study, when infants were presented with a touch close to the inguinal canal at the top of one of their legs, the other leg (which did not receive a touch) extended. Other orienting reflexes have also been demonstrated in newborn infants. For example, if infants are touched on the ulnar part of the hand, they close their thumb and fingers over the object and grip it tightly; the grasp reflex (e.g., Lorenz, 1937; Dietrich, 1957; Twitchell, 1965; Tan & Tan, 1999). The palmar grasp reflex develops at the foetal stage of development (at approximately 11 weeks gestation) and has been proposed to be an instinctive action, which allows infants to practice holding and releasing objects (Lorenz, 1937).

Other demonstrations of spatial orienting to tactile stimuli include head turning or manual orienting behaviours. For example, Moreau, Helfgott, Weinstein and Milner (1978) investigated differences in newborn head turning behaviour to touches on the body using a habituation paradigm. In this study, newborn infants lying in a supine position (with the head restricted in a midline position) received a tactile stimulus on either their left or right side of the mouth. Infants head turning behaviour (in attempts to orient to the touch) was observed.

Bremner et al. (2008b) conducted a study in which infants oriented to a single touch that was applied to the palm of a hand. Here, a tactile stimulus delivered to the hands elicited manual orienting behaviours (such as clenching of the fingers around the stimulus or a pulling away of the arm). Manual orienting, as well as visual orienting (looking to the site of the touch) was taken as a measure of tactile localisation accuracy.

The above studies have demonstrated that it is possible to use orienting behaviours to measure tactile localisation in infants. In terms of the questions posed in this thesis, particularly when examining the emergence of an external reference frame in which touches to the body are coded, a measure of orienting is sufficient in gauging tactile localisation accuracy. For Experiment 3 in this thesis (Chapter 3, Section 3.9), I used an extremely similar orienting paradigm (to that used in Bremner et al., 2008b) in which I measured infants' orienting responses following vibrotactile stimuli on the soles of their feet.

Although Bremner et al. (2008b) also examined visual orienting (in addition to manual orienting) responses to the hands, the researchers found little evidence of visual orienting to touches in the 6.5-month-old sample. Therefore, it was decided that Experiment 3 (which included 4- and 6-month-old infants) would not examine visual orienting and focus solely on foot orienting behaviours.

2.3 Physiological methods

In several of the studies reported in this thesis, I used ERPs to investigate infant brain activity in response to tactile stimuli on the body. Below I describe the equipment and procedures employed and the rationale for using these measures. As previously stated, I do this due to the fact that the methods and equipment differ from those, which are typically used with adults.

2.3.1 Why use EEG?

The EEG method is of invaluable use in infant research. This is due to the fact that the method, potentially, has a greater sensitivity to cognitive/perceptual processes, which may not be obvious in behaviour. Additionally, event related potentials (ERPs) can inform us of the neural processes which can, in turn, illustrate how the brain develops. Furthermore, considering the excellent temporal resolution of the ERP method, it can also demonstrate the ways in which different kinds of information (e.g., posture; particularly relevant to this thesis) interact during sensory processing.

In ideal situations, the ERP method is used in conjunction with behavioural methods (e,g., de Haan, 2007) as this enables us to understand specifically how brain responses are related to behavioural responses. However given certain participant characteristics this is not always possible. For example, using both behavioural and ERP methods necessarily increases the length of testing session, especially with young infants who typically take somewhat longer than adults to respond. The longer time is given for an infant to respond, the fewer stimulus presentations (and thus ERPs) can be made within an already short experimental session. Therefore, in practice, with infant populations it is better to conduct separate experiments to investigate neural activity and infant behavioural responses, although some studies have successfully conducted the two methodologies concurrently (e.g., Karrer & Monti, 1995; Snyder, 2002, Karver, Baurer & Nelson, 2000).

Whilst, EEG is a good method for working with infants and studying the cortical processing of touch (as has been done with adults; Rigato et al., 2013), there are some disadvantages to the method that must be taken into consideration. The EEG method has a poor spatial resolution, which makes locating the source of neural activity problematic. Other limitations of the method include the fact that it is extremely susceptible to 'artefacts' (specific types of electrical signals that are not neural in nature). There are a number of sources of these artefacts. For example, biological artefacts, which occur from activity originating from the eyes such as saccades and blinks. In addition to this, EEG can detect (and often be obscured by) heart rate (ECG) and muscle activity (EMG) in the form of movement artefacts. Movement artefacts are an extremely relevant challenge in acquiring ERP data with infants, as these particular participants cannot be directed to remain still throughout a testing session. As such, in order to reduce the occurrence of movement artefacts, infants are usually held on their parent's lap and take part in an engaging, 'distractor' task which limits their limb movements (e.g., for studies in this thesis, the researcher would hold infant's arms still whilst playing a visually engaging game such as 'peek-a-boo').

Further limitations of the EEG method is that ERPs tend to be quite small in amplitude and given their susceptibility to task irrelevant noise (including background EEG) and artefacts, a large number of trials are required in order to measure ERPs accurately. In adult EEG paradigms, this is not a problem, with such studies often employing upwards of hundreds of trials per condition. However, this would be a particularly difficult challenge with infant samples. There are a number of ways in which it is possible to resolve this difficulty. For one, a between-subjects design can be used to investigate the experimental question. Infants are randomly assigned to a specific condition and group data (each condition) are then compared. However, this is not ideal given the large individual differences between the participants (de Haan, 2007). However, considering that infant ERPs tend to be greater in amplitude to that of adults (due to thinner skulls and less dense cell packing; de Boer et al., 2007), this ultimately means that fewer trials can be administered to achieve an acceptable signal to noise ratio. Therefore, solution to this disadvantage is in perfecting the design and procedure of the study.

Finally, the most challenging aspect of the EEG method is the fact that researchers are not able to explicitly conclude the functional meaning of an ERP component (Luck, 2005). Whilst one can infer what differences in ERP amplitude may possibly mean, this is difficult to do so without making a number of assumptions. However, if this factor is considered when carefully interpreting findings from EEG (and situating such findings within the wider literature concerning the subject under investigating), EEG can be a useful tool when examining the neural correlates underlying behaviour.

2.3.2 Neural origins of EEG and ERPs

The basic principle that the electroencephalography (EEG) method relies upon is that electrical activity within the brain can be measured at the scalp. This electrical activity can come from two neural processes: action potentials and post-synaptic potentials. Action potentials are the electrical charges that travel from the axon to the terminal buttons, whereas post-synaptic potentials refer to the by-product of the process of neurotransmitters binding to post-synaptic cells (and thus comprise activity which is confined to the dendrites and cell body of the neuron). As the charge travels from the dendrite to the cell body, this creates a dipole (a difference in the electrical charge separated by a small distance; Luck, 2005).

Action potentials are extremely short, lasting approximately 1 millisecond in duration, and rarely fire in unison. Additionally, action potentials in different axons usually have opposing charges and tend to cancel each other out. In comparison, post-synaptic potentials are much more long lasting and when thousands and millions of cells fire in unison (in response to a stimulus), the summated voltage is large enough to be measured at the scalp. Thus, due to the reasons outline above, EEG typically record post-synaptic potentials.

EEG records continuous electrical activity that is present in the brain and can be picked up at the level of the scalp. These recordings contain fluctuations in neural activity that may or may not be related to a specific experimental event. Therefore, in order to examine the exact effect of an experimental task on neural activity, it is typical to look at short segments (epochs) of EEG data that are time-locked to, and follow, a particular stimulus: event related potentials (or ERPs). In this thesis, I will report on experiments that measured somatosensory evoked potentials (SEPs). SEPs provide much of the data which was used in this thesis to consider the neural basis of somatosensory (tactile) processing in infancy.

Like EEG, ERPs can contain both task relevant and task irrelevant neural activity. However, whilst task irrelevant noise may occur randomly throughout the entire trial, task relevant neural activity is time-locked to the beginning of each epoch. A general principle of ERPs generally holds that once this activity is averaged across many trials, the random task irrelevant noise will no longer be apparent, whereas the task relevant ERP waveform will remain (e.g., Luck, 2005).

In several of the studies reported in this thesis, I used ERPs (SEPs in particular) to investigate infant brain activity in response to tactile stimuli applied to the hands. The methods and equipment employed for use with infants differs from that which is typically used with adults, therefore I will detail the equipment and procedures employed in this PhD along with the rationale for these choices.

2.4 EEG data acquisition

2.4.1 Hydrocel Geodesic Sensor Net

In EEG research, in order to record neural activity, electrode arrays need to be placed on the head in contact with the scalp. For the ERP studies I conducted (Experiments 4a, 4b and 5), I used the Hydrocel Geodesic Sensor Net (Electrical Geodesics Inc., Oregon, US), which consists of an array of 128 silver-silver chloride electrodes. In this kind of sensor array each electrode is encased in a sponge and a soft plastic pedestal and pre-mounted onto elasticated webbing. The electrode array is organized to ensure the correct distribution of electrodes across the scalp. Due to the large number of sensors and small intersensor distances, the net allows almost complete head coverage. The crucial design aspects of the EGI system which make it good for working with infant participants are the quick preparation (10 minutes) and application times (less than 1 minute). In addition to this, the system does not require gels or scalp abrasion.

Figure 2.1: Infant wearing the Hydrocel Geodesic Sensor Net with electrodes in the correct placement on the head

2.4.2 EGI amplifier and analogue-digital conversion

For all experiments reported in this thesis using EEG, data was acquired using the EGI NetAmps 300 EEG Amplifier. This amplifier is a differential amplifier; it measures and amplifies the difference between the voltage at each individual electrode site and a reference sensor (this can be any sensor on the net array, however on these particular nets, this is the vertex electrode, CZ). As a result of this measurement of amplitude different, voltage differences are relative rather than absolute, which is then amplified. Following amplification, the signal is then digitized by an analogue/digital (A/D) converter which allows offline storage and analysis.

For the EEG studies described in this thesis, a 0.1-100 Hz band pass filter was used, with a sampling rate of 500 Hz. The rule of thumb for sampling rates (the rate of conversion used to convert signals from analogue to digital) is that it must be at least twice as fast as the highest frequency in the signal of interest. So, with a sampling rate of 500 Hz, any signals with a frequency above 250 Hz are filtered out online during data recording.

As mentioned above the NetAmps EEG Amplifier is a differential amplifier, which requires a reference sensor. The EGI system employed in this thesis used the vertex channel as the reference sensor. Due to the fact that this sensor is in a central location on the scalp, it is not subject to hemispheric asymmetry (i.e. it is not biased to one hemisphere over the other and is not biased towards frontal or posterior sites). Additionally, due to its central location, the difficulties associated with hemispheric asymmetry are kept to a minimum.

During the data analysis phase, recorded signals were re-referenced to the average reference. The average reference is the average of the neural activity in all 129 sensors (128 channels plus the vertex) and thus introduced the constraint that the sum of all neural activity should equal to zero (as all electrical potentials are dipoles with a positive and negative potential; Ohm's Law). As the Hydrocel Geodesic Sensor Net has a high density channel array (and an even distribution of electrodes over the scalp) with small inter electrode distances, average referencing is a viable and accurate method of offline data referencing (Tucker, 1993).

2.4.3 Electrode impedance

In order to obtain data recordings that are relatively free from environmental noise, the electrodes need to have a good electrical contact with the scalp. It is common practice to pass low currents through the electrodes in order to gather a measure of impedance (resistance) to the flow of the current and thus the quality of the electrode to scalp contact (Picton et al., 2000). This can be extremely useful in the detection of electrodes with high impedances (as these are subject to greater interference from electromagnetic fields and more noisy data recording). So, if these electrodes are identified before the start of the experiment, they can be adjusted so that they are in better contact with the scalp.

The down-side of impedance checking is that this process usually takes some time and requires the participant's co-operation. These factors make such a process problematic with infant participants. However, as the EEG system used allows for high-input impedances, this is not a particularly necessary step when recording EEG (Picton et al., 2000). Additionally, as infants do not have much hair, ensuring that electrodes were in touch with the scalp was sufficient in having low impedances; this is a precedence that has been adopted by others within infant EEG (e.g., Johnson, de Haan, Oliver, Smith, Hatzakis, Tucker & Csibra, 2001).

High impedance was only judged to be a problem for two infant participants who had a lot of hair (1 participant in Experiment 4b and 1 participant in Experiment 5). As these participants were particularly relaxed, impedances were checked before testing whilst electrode sponges were rehydrated and placed through partings in the hair to ensure direct contact with the scalp. These infants, as with all others, were distracted with toys and bubbles throughout the net application process.

2.5 ERP data analysis

Data was analysed offline using Netstation 4.5.1 analysis software (Electrical Geodesic Inc.). The steps involved in these analyses are described in detail below.

2.5.1 Filtering

The EEG net not only records brain activity, but also records participants' skin and movement potentials. Additionally, the recording apparatus also picks up line noise from electrical equipment in the testing area. As the frequencies of this noise (e.g., line noise is 50 Hz, slow waves with a frequency of less than 0.1 Hz are likely to be skin or movement potentials) in the recording differs from the frequencies of interest in ERPs (less than 30 Hz), it is possible to filter out frequencies that are above below 0.1 Hz and above 30 Hz to get a relatively noise free EEG recording.

During data acquisition, the EGI amplifier used in the ERP studies reported in this thesis employed a band pass filter of 0.1-100 Hz (online filtering). After the data recording stage, the data was then offline filtered with a 0.1 Hz high pass filter and a 30 Hz low pass filter. Any activity that fell beyond these parameters was not considered to be brain activity.

2.5.2 Segmentation

Following filtering, the data was segmented into short epochs time-locked to the onset of the stimuli which were presented. This allowed us to examine the exact neural activity (specifically somatosensory evoked potentials) that immediately followed the presentation of a tactile stimulus. Each segment started 100 ms before, and ended 700 ms after, stimulus onset.

2.5.3 Baseline correction

The epochs of data all were baseline corrected. This is necessary in order to assess neural activity that is the result of a stimulus versus general neural activity (as this can fluctuate over time and brain region). Baseline correction does not alter the waveform in any way, other than shifting the waveform up or down so that the pre-stimulus neural activity is as close to a voltage of zero as possible.

For the physiological studies conducted in this thesis, baseline correction was carried out by taking an average of neural activity that occurs very close to, but precedes, the onset of the stimulus. This average is then subtracted from the entire length of the waveform that follows stimulus onset. Generally, a 100 ms baseline interval is deemed acceptable for this role (Luck, 2005, Picton et al., 2000). All ERP studies reported in this thesis have a 100 ms pre-stimulus baseline (these details are also reiterated in the respective chapters for the experiments; Chapters 3 and 6).

2.5.4 Artefact rejection

After the data had been offline filtered, segmented and baseline corrected, each trial from each participant was visually inspected for noise and artefacts. This process is required because the EEG net not only records electrical activity from the brain, but also picks up electrical activity from other sources (such as the skin and muscles). There are four main artefacts of concern: blinks, eye movements (saccades), alpha activity and movement potentials. Although, it must be stated that it takes a considerably larger number of these artifacts to contaminate infant ERP data than it does adult ERP data (Nelson, 1994).

2.5.4.1 Blinks

Participants' eye blinks can greatly contaminate ERP recordings (particularly at the frontal regions). This contamination can have an experimentally confounding effect especially if participants blink systematically in response to a specific stimulus and/or experimental condition. Eye blink artifact contamination of EEG occurs due to the fact that the eyeball itself acts as a dipole, with the positive pole at the front of the eye and the negative pole at the back of the eye. When individuals blink, as the eyelid passes over the eyeball, this results in a sharp negative-going deflection in voltage, which can be observed across frontal electrodes.

The Hydrocel Geodesic Net allows blinking to be monitored as it has electrodes that are placed around the ocular socket. Whilst the adult EEG nets contain electrodes that are fixed both above and below the eye regions, due to issues of comfort and irritation the infant EEG nets only contain electrodes that sit around the top half of the eye region. Using recordings from these electrodes, it is still possible to inspect the data for eye blink contamination and to then discard contaminated channels and/or trials. A reprieve to the problem of eye blink contaminations is granted to infancy researchers, given that not only do infants tend to blink much less than adults, but infant ERPs tend to be much greater in voltage amplitude (in comparison to adult ERP recordings, contributing to a higher signal to noise ratio). Additionally, researchers have shown that a considerably greater amount of eye activity is needed to contaminate the neural activity of interest in infant ERPs (Nelson, 1994).

2.5.4.2 Eye movements

One of the crucial constraints of infant EEG is that researchers cannot instruct participants to behave in a certain way. Specifically, we cannot instruct infants to fixate on a stimulus in their visual field, so as to minimise eye movement artifacts in the data. Additionally, infants (compared to adults) may be more inclined to visually explore the novel environment of a testing room. As such, saccadic activity is more prominent in infant ERP data than in adult data.

We undertook a number of measures to minimize the occurrence of eye movements. Firstly, the testing room was dimly lit so as to reduce the extent to which features in the room attracted the infants' attention. Also, throughout testing an experimenter was facing the infant in all of the trials. This researcher adopted a direct eye gaze so to capture the infant's gaze and employed engaging facial expressions and speech to sustain their attention. The implementation of this procedural consideration differed slightly across experiments, for reasons that are discussed in more detail in the respective experimental chapters (see Chapters 4 and 6).

Nonetheless, even with these measures in place, it was not possible to eliminate eye movements entirely. Therefore, upon visual inspection of trials, if saccadic activity was present in neural recordings, any electrode channel that contained this activity was marked as 'bad'. Again, due to the physiological differences between adults and infants (thinner skulls and less dense cell packing in the brain), it takes much more saccadic activity to contaminate infant ERPs as infant ERPs give rise to a higher signal to noise ratio (see Nelson, 1994).

2.5.4.3 Alpha waves

Alpha waves are characterized in the EEG by their sine wave morphology with a frequency of approximately 10 Hz (for infants in the first year of life it is around 7 Hz; Smith, 1941) and usually occur when participants are tired. Whilst investigating the continuous alpha rhythm (in the form of oscillatory activity) has been of interest, especially in infants (for a review see Marshall, Bar-Haim & Fox, 2002), the alpha waveform can be problematic if it is present in ERP data. This is due to the fact that the alpha rhythm can become entrained to the stimulus onset and thus averaging across trials in a specific condition does not reduce alpha contamination.

A simple way to minimise alpha contamination is to ensure that participants are well rested. This is not straightforward with infant participants as tiredness can occur quite suddenly and without warning. Nonetheless, I scheduled testing sessions around infant's natural schedule of nap times in order to reduce the incidence of alpha.

However, in some participants, alpha rhythm may not be related to tiredness and these participants tend to have substantial alpha activity even when alert. Due to the low frequency of alpha waves (between 7 and 10 Hz), it is difficult to eliminate alpha activity using filters alone. However, a further simple consideration that can greatly reduce alpha activity relates to the design of the study. In order for the alpha rhythm to become entrained to stimulus onset, the stimulus needs to occur at a constant rate. If, however, a jitter (inter-stimulus interval) is introduced so that there is a random time difference between stimulus presentations, this reduces the likelihood of alpha waves becoming stimulus locked (Luck, 2005). As such, I used a temporal jitter in all ERP experiments (for specific details of this, see Chapter 4, Sections 4.2.1.3, 4.3.1.5 and 4.4.1.4 and Chapter 6, Section 6.2.2).

2.5.4.4 Movement potentials

These artefacts arise from any type of muscle activity and are particularly common and problematic in infant ERP research. In order to reduce the occurrence of movement artefacts, parents were instructed to securely hold their child around the waist and not to bounce their legs. Additionally, the researcher took hold of the infant's arms and gently held them in place, discouraging any arm movements.

Of course, even with these procedures in place, infants would still engage in head turning or body movement behaviours. Upon visual inspection of the data, trial-by-trial, it was particularly obvious when infants had shifted their body posture as this would result in recorded activity with disproportionally large amplitudes (usually below -100 or above 100 microvolts) and thus did not reflect true neural activity. Typically in these situations entire trials were marked as 'bad' and eliminated from further analyses. Whilst entire trials could be contaminated by, for example, movement artifacts and then rejected, there were certain instances in which only a few electrodes in a trial were noisy and had to be removed. I discuss below how I dealt with this situation.

2.5.5 Bad channel replacement

At this stage of data cleaning, I inspected individual trials for electrodes with neural activity which appeared be extremely large (either positive going or negative going) or 'noisy' – a morphology that was not comparable with the electrodes around it. I marked these channels as 'bad' and then replaced them with an interpolated voltage value. This value is the average voltage of surrounding nearby electrodes and is based on the assumption that electrodes in close proximity to each other will have similar data.

2.5.6 Averaging

During the process of individual averaging, all ‘good’ trials (i.e. those that were not rejected during the artifact detection phase of data analysis) from each condition were pooled together to produce a composite of the neural responses that are elicited by the stimulus. By averaging all trials in a specific condition, the neural activity that is time-locked to the stimulus in this condition to be enhanced, whilst background EEG is reduced.

I then computed a grand average for purposes of visualizing the data and waveforms. A grand average contains data from all participants; all trials in a condition were averaged together to create a cross-participant ERP waveform.

2.6 Analysing ERP waveforms

2.6.1 Identifying spatial and temporal regions of interest

Before any statistical analyses could be run on the data, I first needed to identify the brain region (scalp site) and time window of the neural activity of interest, which usually relies quite heavily on the previous literature in the field.

2.6.1.1 Identifying spatial regions of interest

For all ERP experiments in this thesis (Experiments 4a, 4b, 5 and 7), I focused on somatosensory areas contralateral to the side of stimulation, in which maximal SEPs were likely to be found (namely, central regions of the brain where the somatosensory areas are housed).

A crucial process in deciding the spatial (and also temporal, but I will detail this in the following section) characteristics of interest in ERPs is that of visualizing the data. Inspecting the grand average helped to identify the scalp distribution of the neural activity. As previous research had confirmed that central electrodes (over somatosensory areas), were of particular relevance when tactile stimuli was applied to the body, I visually inspected electrodes within this area.

Due to the fact that the EGI system has a dense array of electrodes, it is common practice to look at a cluster of electrodes and average these electrodes, as opposed to simply inspecting a single electrode in isolation (de Haan, 2007; Johnson et al., 2001), so in general I visually inspected between 3 and 4 electrodes, that were in close proximity to each other, for similar looking waveforms in each of the experimental conditions. When inspecting these electrodes, I looked for certain characteristics in these waveforms, namely a clear somatosensory evoked potential that was contralateral to the hand that received the tactile stimulus. Additionally, the chosen electrodes showed a negative going deflection close to 140 ms in the waveform, resembling the N140 component in adults. The chosen electrodes in all experiments fulfilled these criteria.

2.6.1.2 Identifying temporal regions of interest

Previous work with adults from the research detailed above have been informative in helping determine which scalp sites to be investigated, however this was to a lesser extent when identifying the temporal region of interest. This is due to the fact that whilst data in the adult literature can be informative regarding the latency of certain components and processes, these components and latencies may not be the same for an infant population. For example, whilst adult ERPs often take the form of well defined peaks, this is not true of infant ERP data; the peaks are less well defined, resulting from greater slow wave activity due to reduced synaptic efficiency (DeBoer et al., 2007). It is only at approximately 4 years of age that ERPs take on an adult-like peaked form (Friedman, Brown, Cornblatt, Vaughan, & Erlenmeyer-Kimling, 1984; Nelson & Luciana, 1998).

To make an informed decision in determining the temporal region of interest, I focused on research related to somatosensory processing in young infants. Although this research could not indicate when effects of somatosensory remapping or the cueing of exogenous attention would occur in a waveform, such studies were informative in illustrating the latency and morphology of a somatosensory evoked potential in infants. Research has found both early and late processing components in response to median nerve stimulation. For example, Karniski (1992) found that newborns elicited three key components – the N1/P1, the P2 and the P3 within 450 ms of stimulus onset, a finding replicated by Taylor, Boor and Ekert (1996) in a group of premature newborns. The N1 and P2 were also found by Pihko and Lauronen (2004), with full term newborns during different stages of sleep, although there were differences in component latency (both within and between studies) across infants of different ages. Indeed, Pihko, Nevalainen, Stephen, Okada and Lauronen (2009) have demonstrated systematic changes in the morphology of SEPs and the latencies of the components that comprise this waveform as infants age from newborns (0 months) to become toddlers (24 months). Between the newborn and 6-month stage of life, the M60 shifts in latency (occurring earlier) to become the M30, which is then followed by the M50 (with this component emerging at 6 months of age). The authors propose that this change in latency (and morphology, given the occurrence of the M50 component; thus illustrating two peaks as opposed to one) is a result of cortical maturation that occurs in the first two years of life.

With these considerations in mind, I also reviewed the adult literature concerning somatosensory processing. The N140 component (a negative going peak in the waveform occurring 140 ms after a tactile stimulus) has been found in several experimental paradigms in which posture of the hands was manipulated (e.g., Rigato et al., 2013; Kennett, Eimer, Spence & Driver, 2001). Whilst the N140 component is well established in adults, I anticipated that (given the arguments presented above), that it would be unlikely that this early component would be observed in infants at this latency. However, as SEP components had been found as early as 60 to 100 ms (Pihko et al., 2009; Pihko & Laurenon, 2004; Karniski, 1992;) and as late as 450 ms post tactile stimulus (in studies which did not manipulate posture), I decided that the entire 700 ms segment following stimulus onset would be analysed. By selecting this wider window, this allowed me to examine both early and late processing of somatosensory stimuli, in full term infants aged between 6 and 8 months.

Below I detail the specific electrodes that were used in the statistical analyses conducted in each ERP experiment. These electrodes corresponded to the C3/C4 areas on the 10-20 net system. The electrode I selected for analysis, although similar with some overlap, did differ between experiments. I selected those electrodes where the SEP was most apparent (and largest). A possible explanation for differences between experiments could be due to the fact that different age groups were used in Experiments 4a (6- and 8-month-olds), 4b (8-month-olds), 5 (6-month-olds) and 7 (7-month-olds). Head size and shape varies across age groups (and of course, there is some variability between individual babies within the same age group), which would then result in slight differences in net placement. Additionally, experimenter skill in placing the net correctly may have also contributed to these slight differences in where the maximal SEPs were found and why different electrodes were chosen between different experiments. Although there are small differences in which electrodes were chosen for analyses, all electrodes that were included were located over the C3/C4 somatosensory areas of the brain.

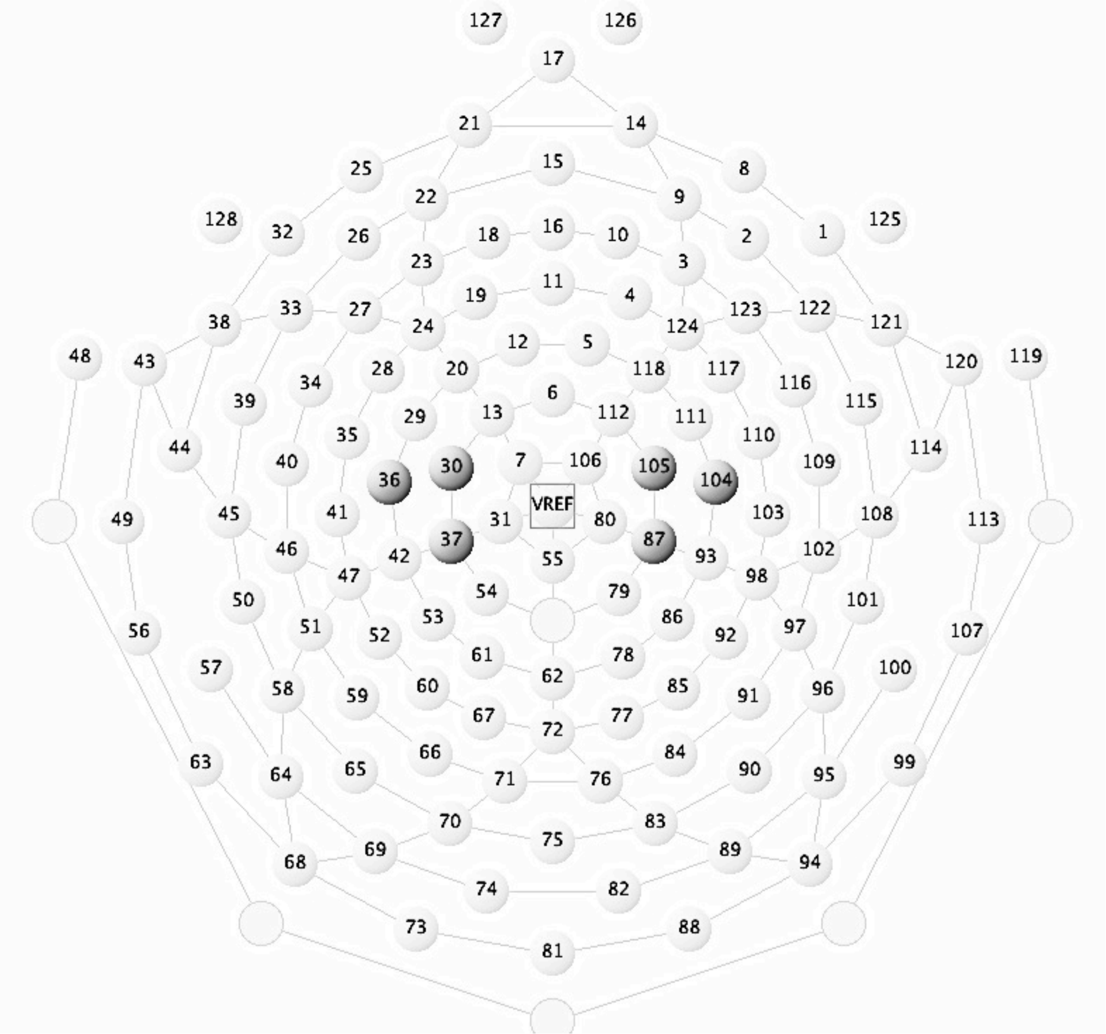


Figure 2.2: Location of electrodes used in statistical analyses in Experiment 4a

In Experiment 4a, the individual electrodes that were included were: 30, 36 and 37 for the right hand and 87, 104 and 105 for the left hand (Figure 2.2). In Experiment 4b, the individual electrodes that were included were: 29, 30, 35 and 36 (for the right hand) and 104, 105, 110 and 111 (for the left hand) (see Figure 2.3). In Experiment 5, the individual electrodes included were: 29, 30 and 35 (for the right hand) and 105, 110, 111 (for the left hand) (see Figure 2.4). In Experiment 7, the individual electrodes included were: 7, 13, 29 and 30 (for the right hand) and 105, 106, 111 and 112 (for the left hand) (see Figure 2.5).

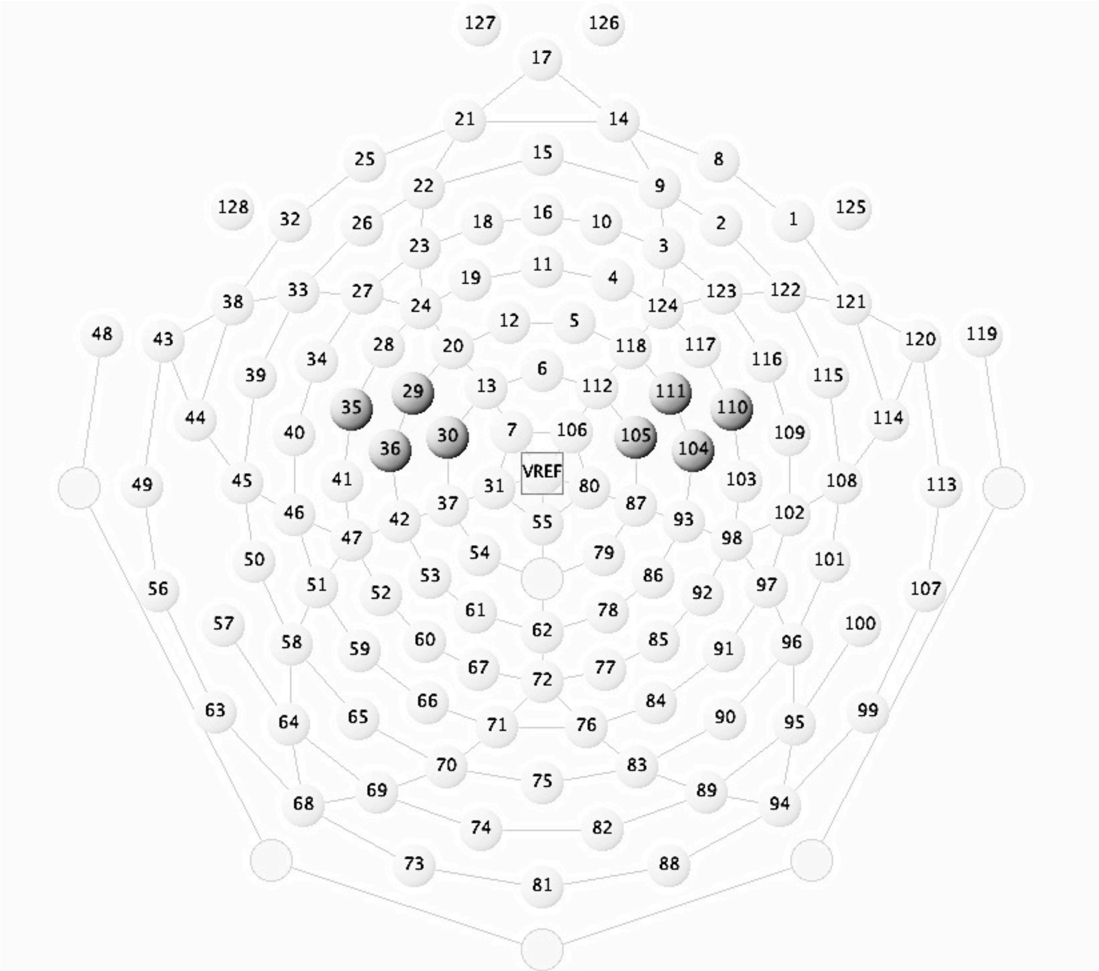


Figure 2.3: Location of electrodes used in statistical analyses in Experiment 4b

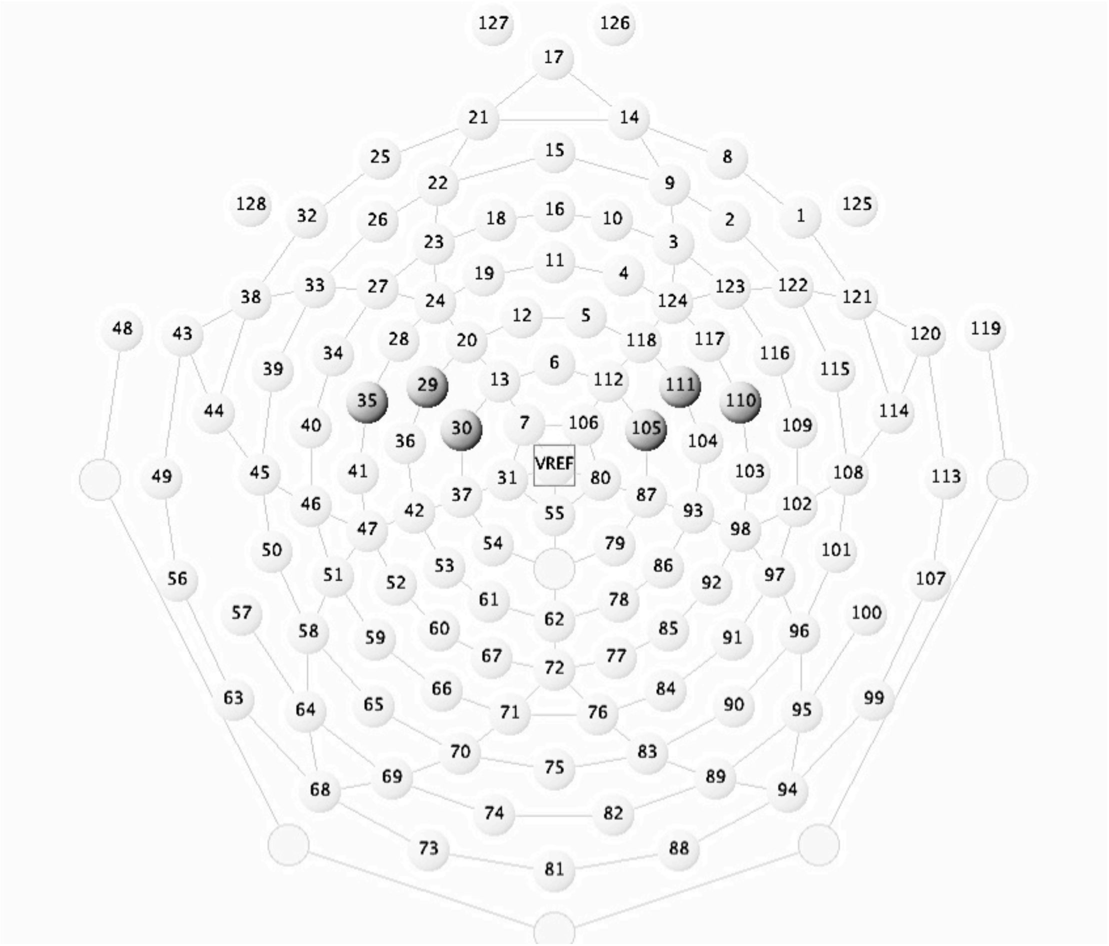


Figure 2.4: Location of electrodes used in statistical analyses in Experiment 5

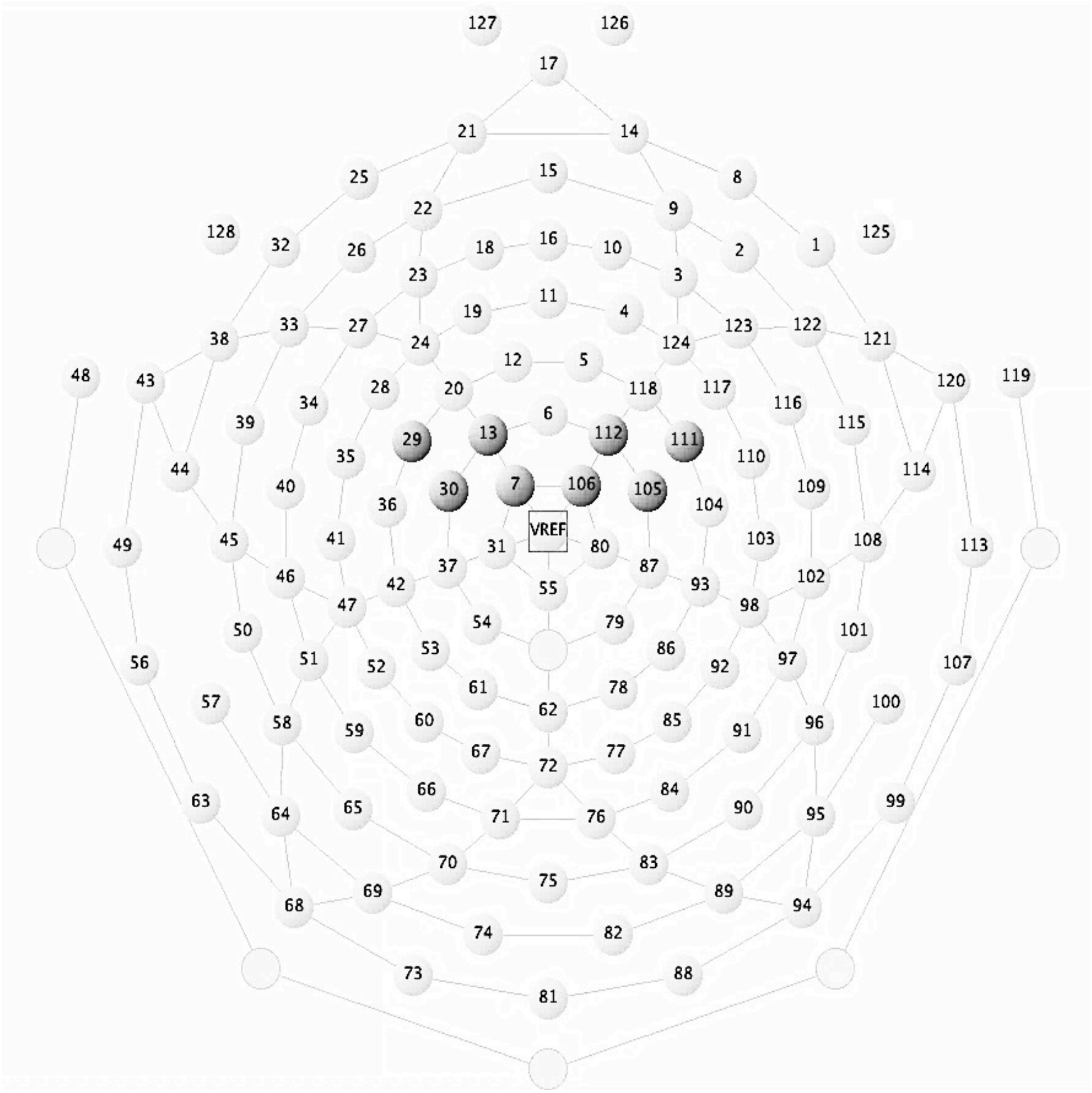


Figure 2.5: Location of electrodes used in statistical analyses in Experiment 7

2.6.2 Statistical analyses

There are several methods that can be employed to analyse ERP waveforms. The most common are peak amplitude and mean amplitude analyses. Peak amplitude analyses measure the voltage of peaks (both positive and negative going) in the waveform and are most typically used in adult data, which contains well-defined peaks. By contrast, another approach is to measure of the average voltage of a waveform within a specific time window. This method can be particularly useful when peaks are less distinct in the ERP.

Although the peak amplitude, and mean amplitude methods are able to assess the onset of effects of condition on an ERP, with less certainty regarding exactly what time interval of neural activity would be of interest (in terms of illustrating the onset of the effect), the number of potential tests which need to be run increases dramatically, along with the possibility of type 1 errors. In order to implement an exploratory analysis of effects of condition across the ERPs I used a more data-driven analysis which nonetheless employed appropriate controls to limit type 1 error. To this purpose I used a sample point by sample point comparison method, in which a Monte Carlo simulation is used to determine at which time point ERP waveforms differ significantly according to condition. In Experiments 4b and 5, this analysis examined the onset and time course of significant effects of posture in the SEPs. In Experiment 7, this analysis examined at the onset and time course of significant effects of a visual cue on a subsequent tactile stimulus to either the same or different hands.

The sample point method which uses a Monte Carlo simulation process (e.g., Guthrie & Buckwald, 1991; Mooney, 1997) does this by estimating the average first order autocorrelation present in the real difference waveforms across the 700 ms following stimulus onset (the mean first order autocorrelation at lag 1 was .99 for all datasets analysed). Following this, the method used 1000 datasets of randomly generated waveforms, each waveform having a mean and unit variance of zero at each time point, but having the same level of autocorrelation as seen on average in the observed data. Each simulated dataset also had the same number of participants and time-samples as in the real data. The Monte Carlo method applied two-tailed one-sample t-tests (vs. zero; alpha = .05, uncorrected) to the simulated data at each time point, recording significant vs. non-significant outcomes. In each of the 1000 simulations the longest sequence of consecutive significant t-test outcomes was computed. The 95th percentile of that simulated distribution of "longest sequence lengths" was then used to determine a significant difference waveform in the real data; specifically, I noted any sequences of significant t-tests in my real data, which exceeded this 95th percentile value. This method thus avoids the difficulties associated with multiple comparisons and preserves the type 1 error rate at .05 for each difference waveform analysed.

In addition to the sample point analyses described above, I also conducted comparisons of mean amplitude across conditions within 100 ms segments across the 700 ms after stimulus onset for any experiments that showed significant differences between conditions in the sample point analysis. This involved conducting pairwise t-tests of averages of ERP data for certain intervals of the segment (0-100 ms, 100-200 ms, 200-300 ms, 300-400 ms, 400-500 ms, 500-600 ms and 600-700 ms for Experiment 4b, Chapter 4, Section 4.3.3.2 and 100-150 ms and 200-300 ms for Experiment 7; Chapter 6, Section 6.3).

Chapter 3:

Spatial frames of reference for touch in children and infants

3.1 Experiment 1: The emergence of an external reference frame for touch in childhood

In the following chapter, I will examine the emergence of an ability to perceive tactile stimuli in external space in early life (both in childhood and infancy). As previously discussed in Chapter 1 (Section 1.5.1), there are two particular spatial frames of reference for touch that are relevant to the specific questions that are asked in this chapter: anatomical and external reference frames. By anatomical reference frame I mean a reference frame linked to a somatotopic coordinates on the body surface. By external reference frame, I mean a reference frame in external space which is not affected by changes in the posture of the observer's sense organs (i.e., changes in the posture of their arms, head and eyes). The specific questions under investigation in this chapter thus relate to how children and infants represent tactile stimuli with respect to these reference frames, which provide the spatial structure of their environments and bodies.

One method that can be used to investigate the spatial frames of reference which are used for locating tactile stimuli, is by examining the effect of changing the posture of the sense organs on tactile localisation. One way of doing this is by measuring the effect of crossing the hands. Performance on a tactile localization task can be compared across familiar (such as uncrossed hands) and less familiar postures (such as crossed hands). Studies have shown that adult humans demonstrate impaired tactile localization accuracy in the crossed hands posture, relative to the uncrossed hands posture (Shore et al*.,* 2002; Yamamoto & Kitazawa, 2001a; Groh & Sparks, 1996). Researchers have argued that this deficit in performance is due to the fact that when the hands are crossed over and in the contralateral side of space to their usual location, this creates a conflict between the location of the touch in its usual location with respect to the body (i.e. the anatomical location of the touch) and its location in external space.

The developmental literature investigating the "crossed hands" effect has attempted to trace the emergence of an ability to perceive the location of touch in external space in young children. Evidence of the crossed hands effect has been used to argue that, rather than simply mapping touches on the skin surface, young children of particular ages are able to locate touches with respect to the external environment. Pagel, Röder and Heed (2009) used a tactile TOJ task with children aged 4 to 10 years. Children were required to indicate the location of the first tactile stimulus by saying which hand they had felt the vibration on. As young children are notorious for confusing the 'left' and 'right' hand labels, animal stickers ('dog' and 'cat') were put on the backs of their hands, substituting the hand labels.

The researchers found that children aged 5.5 years and above displayed the "crossed hands effect", in that they were poorer at locating the site of the initial tactile stimulus in the crossed hands posture, relative to the uncrossed hands posture. Pagel et al. (2009) argued that this was a result of developmental improvements in tactile localization accuracy in the uncrossed posture; as children increase in age they become more reliant on their body being in usual postures in order to locate touches that occur on the body. As a result of this increased reliance, children are able to take advantage of the benefit they would gain in tactile localization accuracy when their body is in a canonical posture. Indeed, some accounts conceptualise the crossed hands effect is as an enhancement of tactile localization accuracy when the body is in canonical postures (e.g., with hands uncrossed), rather than as a deficit when the body is in less usual posture (such as with hands crossed; Pagel et al., 2009).

The findings of Pagel et al. (2009) suggest that children begin to map touches on their body in external co-ordinates at the age of 5.5 years, with this external reference frame possibly enhancing tactile localization performance when children adopt usual body postures (when arms are uncrossed). However, other research has found that an external reference frame emerges in the first half year of life. Bremner et al. (2008) found that when single touches were applied to infants' (aged 6.5 and 10 months) hands in the uncrossed and crossed posture, 6.5-month-old infants were less able to manually orient correctly (by way of moving the stimulated hand) towards the hand that received the tactile stimulus when in the crossed hands position compared to the uncrossed posture. In comparison, 10-month-old infants were able to accurately manually orient to, or look at the stimulated hand, with the same degree of accuracy regardless of hand posture, indicating that they do not show the “crossed hands effect”.

Bremner et al. (2008) interpreted their findings as showing that at 6.5 months of age, infants demonstrated poorer tactile localization accuracy in the crossed hands posture (relative to the uncrossed hands posture), due to the use of an external frame of reference in which touches were coded. In comparison, they argued that 10-month-olds infants were able to overcome the “crossed-hands” deficit, in this particular manual orienting task, by accurately and proficiently remapping touch with respect to the external environment by taking into account current limb position. Considering that the crossed hands deficit persists in adulthood (demonstrated using tactile TOJ paradigms), it is likely that the crossed hands deficit remains in the 10-month-olds, but that the manual orienting measure used by Bremner et al. (2008) may not have been sufficiently sensitive to observe this.

The presence of the crossed-hands effect on tactile localization (and subsequent claims of an ability to locate touches in external space) sits somewhat at odds with the claims made by Pagel et al. (2009) who argued that it is not until 5.5 years that children begin to code touches to the body in an external reference frame. A potential explanation for the discrepancy in the findings of the two studies could be methodological. For example, the children in Pagel et al. (2009) took part in a speeded tactile TOJ task, whereas the infants in Bremner et al. (2008) only had one tactile stimulus applied to their hand per trial with plenty of time to respond.

These two studies described above highlight the inconsistencies in the developmental literature, suggesting that more research needs to be conducted to discover when infants, and children, begin to use an external frame of reference to locate touches to their body. Indeed, these queries also relate to a wider set of questions in regards to the developmental process of spatial representation of the body.

Of course, infants, children and even adults do not process touches on the body in isolation; often if we feel a touch on the arm, we will look at the site of the impinging touch. Indeed, research has shown that when individuals have vision of their limbs being touched, this can modulate the processing of the tactile stimulus. Studies of the rubber hand illusion (RHI) have demonstrated that vision of a fake hand being stroked can capture tactile sensations to the visual location of the stroke (Botvinick & Cohen, 1998; Pavani, Spence & Driver, 2000). Additionally, viewing a hand receiving a tactile stimulus modulates processing in the somatosensory cortex (Longo, Pernigo & Haggard, 2011; Taylor-Clark, Kennett & Haggard, 2002; Cardini, Longo & Haggard, 2011), improves tactile acuity (Longo, Cardozo & Haggard, 2008; Press, Taylor-Clark, Kennett & Haggard, 2004), and can even reduce the intensity of acute pain (Longo, Iannetti, Mancini, Driver & Haggard, 2012).

The studies described above show that vision of the body can modulate tactile perception. However vision of a stimulated limb can also inform individuals about limb posture and location (Graziano, 1999), and change the ways in which limb position is represented in the brain (Lloyd et al., 2003; Rigato et al., 2013). Studies with children have shown that there are substantial improvements in the use of vision to reach in early childhood (Ferrell-Chapus, Hay, Olivier, Bard and Fleury, 2002; Renshaw, 1930). Recent studies have also shown that the sensory weightings, which children use to locate their limbs, undergo a number of noticeable developmental changes in early childhood. Bremner et al. (2013) have shown marked increases in the influence of visual cues on perceived hand location between 4 and 6 years. Investigating the development of children's responses to the rubber hand illusion, Cowie, Makin, & Bremner (2013) have demonstrated a particularly strong influence of a visual illusory hand on the perceived location of the real hand in middle childhood, which becomes more moderate into adulthood.

Thus, in addition to attempting to clarify the, at present, conflicting literature on the development of tactile spatial representation I also sought to investigate the influence of visual cues to the body on children's developing tactile spatial skills. Given the recent observations of changes in the visual weighting of hand position across childhood (e.g., Bremner et al., 2013; Cowie et al., 2013), I decided to investigate whether the presence of visual cues to hand position (in addition to proprioceptive cues) varied in their effect on tactile spatial localization across early childhood. To do this, children's tactile localization accuracy across postures either with, or without, sight of their hands was compared. It was anticipated that children would perform better with their hands in the uncrossed posture, compared to the crossed posture.

Rather than adopt the tactile TOJ paradigm used by Pagel et al. (2009), I decided that the most suitable context in which to study the crossed-hands deficit in children is a task which requires a judgment about the location of a single tactile stimulus (rather than 2 stimuli as in the tactile TOJ tasks discussed previously). This is because processing demands (and the task instructions) are simpler with single stimuli. Additionally, presenting a single tactile stimulus allows a more straightforward comparison with studies of tactile localization in infants (Bremner et al., 2008b), as such studies also only used single stimulus presentations.

Therefore, the following study used a task in which a single vibrotactile stimulus was applied to children's index fingers across several trials, in which their hands were either in an uncrossed- or crossed-hands posture (effects of posture were compared within participants). We also included within participants conditions which compared effects of posture when the hands and arms were either covered or directly visible. To avoid any confusion regarding the 'left' and 'right' labels of the hands, a (different) stuffed animal was placed directly above the left and right hands and children were asked which of the animals was responsible for the ‘tickling’ of their fingers.

3.2 Methods

3.2.1 Participants

Ninety-one participants aged 4 to 6 years (51 male) took part in the study. 14 participants were excluded prior to analyses, as they either did not respond correctly on five consecutive trials in the practice session (4-year-olds: n = 7; 5-year-olds: n = 3; 6-year-olds: n = 3), or did not appear to understand task instructions (4-year-olds: n = 1) leaving 77 participants (see Table 3.1 for further characteristics of the included participants).

Table 3.1: Participant characteristics

Age group (years)	n	Gender split	Mean age (years)	SD of age (years)
4	22	11m, 11f	4.52	.24
5	25	19m, 6f	5.57	.27
6	30	13m, 17f	6.42	.25

3.2.2 Apparatus and Materials

Two voice coils (30 x 40 mm) driven with a 220 Hz sine wave and controlled by custom software scripted in E-Prime acted as vibrotactile stimulators (tactors). These two tactors were fixed to a board 30 cm apart. A ledge covered this board, on which were placed a stuffed toy hedgehog and penguin (both 13 x 10 cm), the hedgehog over the right tactor, and the penguin over the left tactor. A detachable cover (35 x 40 cm) was attachable to the front edge enabling the experimenter to conceal participants' arms and hands and, by extension, their arm posture (Figure 3.1). This cover was made of faux fur and due to the thickness of the material, the postures of the children's arms posture were fully masked from view.

The experiment was conducted in the participant's classroom. The tactors emitted a noise of 49.7 dBA, whilst the average ambient noise in the classroom was 65.5 dBA. We conducted a short study on a subset of participants aged between 5 and 6 years (mean age = 5.8 years, SD = .66) in which they were asked to locate the stimulated tactor using only auditory cues. The participants were seated with the equipment set up in front of them and their hands in their laps. The experimenter triggered a trial and asked: "Which animal made a sound: the penguin or the hedgehog?" If a participant was unable to provide an answer, the experimenter prompted them to guess. Participants completed 12 trials, with a mean auditory localisation accuracy of 54.12% (SD = 13.35%). A one sample t test showed that the participants were performing at chance [t(7) = .87, n.s., d=.66].

Figure 3.1: The experimental set up with hands crossed and visible. In other conditions of the study I varied whether the participants' hands were crossed or uncrossed and covered or visible.

3.2.3 Procedure

In a short practice phase, I placed the participant's index fingers on the tactors, whilst the participant adopted an uncrossed-hands posture with their hands visible. Each vibrotactile stimulus was presented for 200 ms. The practice phase consisted of 6 trials. On each practice trial only one of the participant’s hands was stimulated. Across the 6 practice trials, each hand was stimulated three times, in a randomized order. Following each of these practice stimuli, the researcher asked the participant: “Who tickled your fingers: the penguin or the hedgehog?” In order to proceed to the experimental phase, participants were required to correctly locate the stimulus on 5 consecutive trials. If participants were unable to meet this criterion, they did not continue with the study.

The experimental trials were identical to the practice trials except that I was blind to the accuracy of the child’s answer during the experimental trials. Participants’ verbal responses were recorded by myself on a computer. In the experimental phase, there were four separate blocks of trials: (i) Uncrossed-hands, Visible (ii) Uncrossed-hands, Covered (iii) Crossed-hands, Visible (iv) Crossed-hands, Covered. Between blocks, the child’s hands were moved into a different posture and/or covered or uncovered their arms. Each block consisted of 20 trials (10 vibrotactile stimulations to each hand), across which the order of left and right stimuli was randomized. Thus, across the whole experimental session (4 blocks) there were 80 trials. The order of the blocks was fully counterbalanced across participants, yielding 24 separate order conditions. Due to an oversight, there were not enough participants in my 4-year-old group to fulfill the 24 different counterbalancing sequences. However, the counterbalancing order did not impact on children’s tactile location discrimination ($p = .73$).

3.3 Results

A measure of the children's tactile localization accuracy was derived by calculating the percentage of trials on which they made a correct response in each condition. One-sample t-tests of this percentage accuracy score showed that all three age groups were performing reliably above chance (50%) in all conditions (see Table 3.2).

Table 3.2: Results from one sample t-tests comparing children's tactile localisation accuracy with 50% (chance performance), across age groups and experimental conditions

Age (years)	**View condition**	**Posture**	**t(df)**	**p**	**d**
4 (*n* = 22)	Visible	Uncrossed	7.75(21)	<.001	2.37
	Visible	Crossed	7.55(21)	<.001	1.53
	Covered	Uncrossed	11.1(21)	<.001	1.65
	Covered	Crossed	7.19(21)	<.001	1.61
5 (*n* = 25)	Visible	Uncrossed	27.55(24)	<.001	5.07
	Visible	Crossed	11.80(24)	<.001	3.26
	Covered	Uncrossed	25.34(24)	<.001	5.51
	Covered	Crossed	16.29(24)	<.001	2.36
6 (*n* = 30)	Visible	Uncrossed	39.78(29)	<.001	7.47
	Visible	Crossed	23.64(29)	<.001	4.27
	Covered	Uncrossed	40.29(29)	<.001	7.26
	Covered	Crossed	25.35(29)	<.001	4.32

Figure 3.2 shows children's percentage accuracy across both the posture conditions and the two hand conditions (in which their hands were either visible or not). We used a mixed measures 2 x 2 x 3 ANOVA to investigate the effects of the within-subjects factors of Posture (Uncrossed-hands / Crossed-hands), and View (Covered / Visible), and the between-subjects factor of Age (4-year-olds / 5-year-olds / 6-year-olds) on children's percentage accuracy scores. This revealed a main effect of Age [$F(2, 74) = 12.00$, $p < .001$, $\eta_p^2 = .25$], showing that, across conditions, the older children were more accurate when localizing tactile stimuli. Tukey's HSD tests showed that this effect was driven by poorer performance in the 4-year-olds (M =80.3%, SD =14.55%) than both the 5-year-olds (M = 89.29%, SD = 6.8%) (p = .004) and the 6-year-olds (M = 92.78%, SD = 4.96%) ($p < .001$). There was no reliable difference in performance between the 5- and the 6-year-olds. A main effect of Posture was also observed [$F(1, 74) = 13.61$, $p = .001$, $\eta_p^2 = .16$], indicating that the children were reliably better at localizing touches in the uncrossed hands posture than the crossed hands posture (the crossed-hands deficit), across age-groups. We also observed an interaction of Posture x View [$F(1, 74) = 5.09$, $p = .027$, $\eta_p^2 = .06$], and a marginally significant interaction of Age x Posture x View [$F(2, 74) = 2.78$, $p = .069$, $\eta_p^2 = .07$].

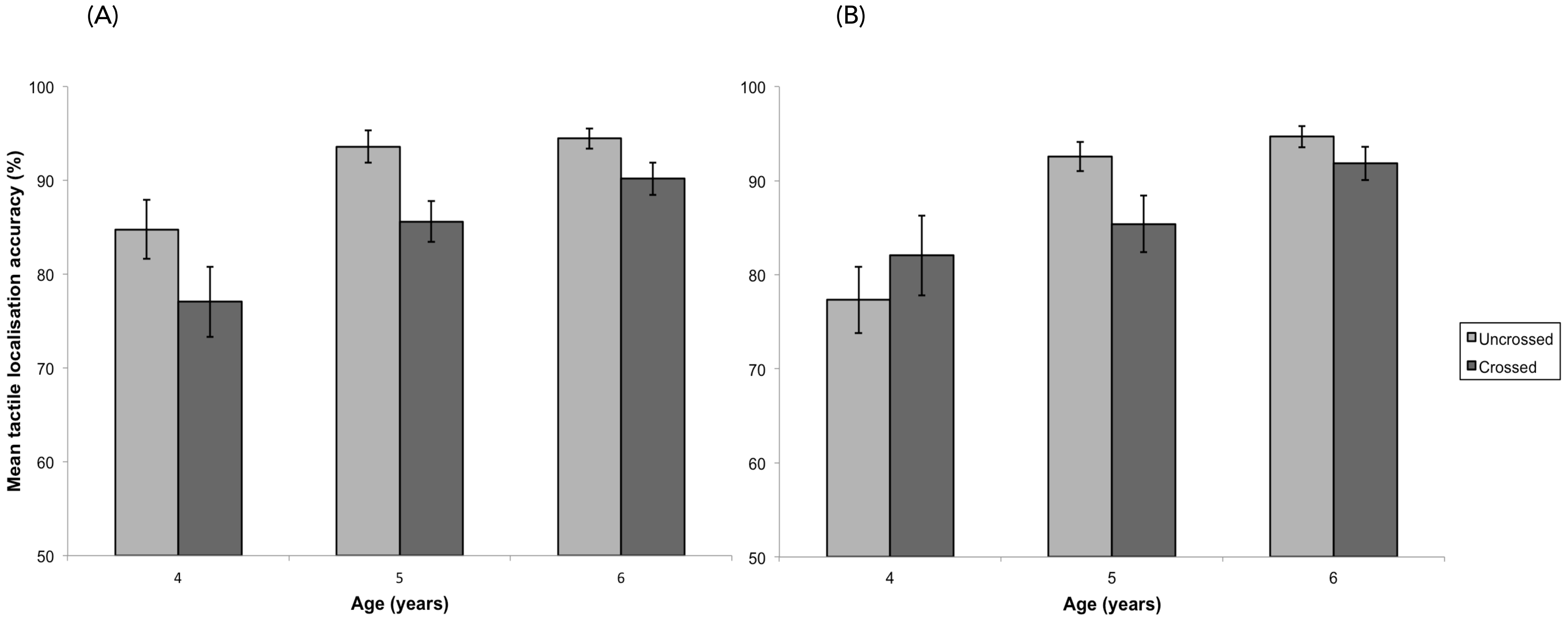


Figure 3.2: Mean tactile localization accuracy (percentage correct) of 4 to 6-year-olds in the crossed-hands and uncrossed-hands posture. Error bars indicate the standard error of the mean. Panel A indicates performance in the Hands-covered condition. Panel B shows performance in the Hands-visible condition

I first investigated the Posture x View interaction with four post-hoc comparisons. To control for type 1 error, the alpha value was bonferroni corrected to $\underline{p} = .013$. First, I conducted two comparisons looking at the effect of posture on tactile localisation. These comparisons were one-tailed because I predicted better performance in the uncrossed-hands posture than in the crossed-hands posture. When participants did not have sight of their hands, their tactile localization was worse in the crossed-hands posture than in the uncrossed-hands posture [$\underline{t}(76) = 4.33$, one-tailed $\underline{p} < .001$, $\underline{d} = .53$], i.e., they showed the “Crossed-hands deficit”. However, this effect disappeared when participants had sight of their hands [$\underline{t}(76) = 1.12$, n.s., $\underline{d} = .15$]. To further explore the interaction of Posture x View, we examined the effect of View within each of the posture conditions using paired sample t-tests. Thus, two further post-hoc t-tests were conducted. No differences between visible and covered conditions were found in the uncrossed posture [$\underline{t}(76) = 2.03$, n.s., $\underline{d} = .20$], or the crossed posture [$\underline{t}(76) = 1.21$, n.s., $\underline{d} = .14$].

Given that the interaction of Age x Posture x View was very close to the significance level of $p = .05$, I proceeded with post-hoc analyses. To do this I conducted three repeated measures 2 x 2 ANOVA (Posture: Uncrossed-hands / Crossed-hands x View condition: Hands covered / Hands visible), one for each age group. In order to avoid an increase in type 1 error associated with these multiple analyses the α value for these ANOVAs was corrected to $p = .017$. The 6-year-olds and 5-year-olds both showed significant main effects of Posture [$\underline{F}(1, 29) = 6.74$ $\underline{p} = .015$, $\underline{\eta_p{}^2} =$

.19] and [F(1, 25) = 13.49, p = .001, η_p^2 = .36] respectively, but no other main effects or interactions. However, the 4-year-old group demonstrated a significant interaction of Posture x View [F(1, 21) = 7.14, p = .014, η_p^2 = .25].

Four post-hoc paired sample t-tests were used to investigate this interaction and so the alpha value was bonferroni corrected to p = .013. First, we conducted two one-tailed comparisons looking at the effect of posture on tactile localisation. These showed that, as above, 4-year-olds' tactile localization accuracy was worse in the crossed-hands posture when they were unable to see their hands [t(21) = 2.53, one-tailed p = .009, d = .48]. However, once again, this effect was not present when participants had visual information about their current hand posture [t(21) = 1.22, n.s., d = .26].

I again further explored the interaction of View and Posture, with additional post-hoc tests to examine the effect of View within each of the posture conditions. The 4-year-olds also performed worse in the uncrossed posture when their hands are visible, compared to when their hands are covered [t(21) = 2.78, two-tailed p = .011, d = .48]. No difference between visible and covered conditions was found in the crossed-hands posture for this age group [t(21) = 1.51, n.s., d = .27]. Figure 3.3 demonstrates the interaction of Posture and View on the 4-year-olds's performance, by displaying percentage accuracy with visible and covered hands on a participant-by-participant basis (plotted separately for uncrossed and crossed hands posture conditions; 4-year-olds). This figure highlights the fact that, specifically in the uncrossed hands posture, 4-year-olds' were worse at localizing tactile stimuli when their hands were visible than when they were covered.

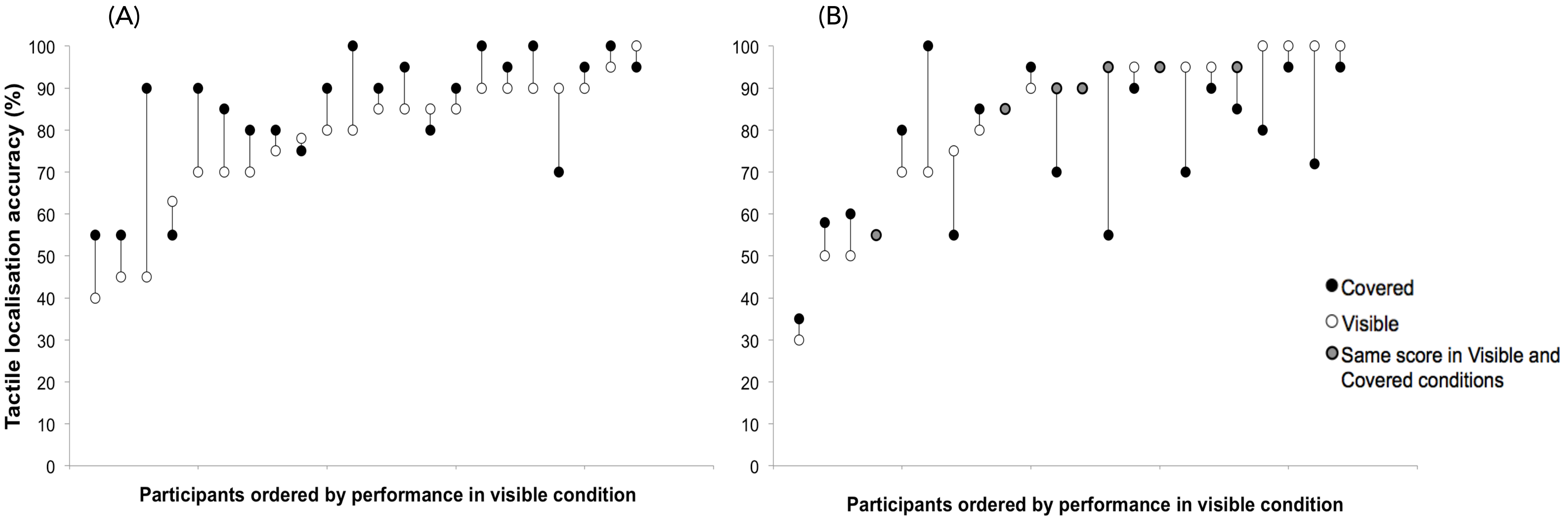


Figure 3.3: Individual tactile localisation accuracy scores (percentage correct) of the 4-year-olds in the Hands covered and Hands visible conditions. Panel A indicates performance in the Uncrossed-hands condition. Panel B shows performance in the Crossed-hands condition. Some participants performed at the same accuracy levels across View conditions in the crossed-hands posture (see 'same score in visible and covered conditions' in the legend).

3.4 Discussion

The current study found that all age groups demonstrated the “crossed hands” deficit (i.e. were not as accurate at locating the site of a tactile stimulus in the crossed hands posture, relative to the uncrossed hands posture), albeit with hands covered. The fact that the youngest children tested, 4-year-olds, exhibited the crossed-hands deficit demonstrates that an external frame of reference for localizing touches to the body is already in use by this age. Additionally, a significant interaction of Posture and View was also found in this age group indicating that sight of the stimulated limb modulates tactile localization accuracy.

This is a somewhat different pattern of results than that found in Pagel et al.’s (2009) study, in which 5.5-year-olds were the youngest age group to demonstrate the “crossed hands deficit". However there could be several potential explanations for the difference in findings. One such possible explanation could appeal to the different tasks used. Firstly, Pagel et al.’s, (2009) study involved children making judgements regarding the temporal order of two successive tactile stimulations to the hand. In this study, however, the children only responded to a single touch applied to their hands. The later emerging crossed-hands effect in Pagel et al.'s study may be a result of the task that was used. It has been proposed that in the crossed hands posture, as the anatomical and external reference frames are in conflict, it takes longer to compute the location of touches. Therefore, errors in tactile TOJs, with very short SOAs, could be a result of the second stimulus occurring before the somatotopic coding of the initial stimulus is complete (Röder et al., 2004). In comparison, in our study, the children were required to only locate one touch; therefore there is not a subsequent touch to interfere with the coding of the first touch stimulus. This would have made the task less demanding for the children, which could then allow participants fully showcase their capabilities (as was evidenced by the near ceiling performance of the 5- and 6-year-old children in the covered uncrossed hands condition).

Secondly, the children taking part in Pagel et al.'s (2009) study were required to take part in 2 sessions, each lasting between 1 and 1.5 hours. In comparison, the current experiment lasted less than 10 minutes per child. Children were sufficiently interested and energized, attending to the task and task instructions for the full length of the testing session. While it is not possible to know whether the children in Pagel et al.'s study were "no task", the children were engaged with (and enjoyed) the current task. Better performance may have made the current task more sensitive to effects of posture in young children.

The third possible explanation, and perhaps the most plausible, is that this study involved a manipulation in which children either did, or did not, have vision of the stimulated limbs. Throughout Pagel et al.'s study, the children had sight of their limbs, however in the current study, there were conditions in which children's arms were covered. This experimental manipulation yielded significantly different results in this study; it was only when children did not have sight of their hands did a difference between the posture conditions arise (i.e. they demonstrate the crossed-hands deficit). When the hands and arms were visible, the children's discriminatory abilities were comparable across the two arm postures. However, this comparable performance was driven by children's poor tactile localization accuracy in the *uncrossed* posture (rather than an increased accuracy in the crossed posture when hands were visible). Performance in the uncrossed-hands posture was enhanced when the children's hands were hidden; i.e., when only proprioceptive cues to posture were available, with accuracy decreasing in the uncrossed-hands posture when children had sight of their hands. As such, it seems unlikely that having vision of the hands actually improves tactile remapping. This is a somewhat surprising finding; especially when considering that using two sensory modalities (both vision and proprioception) to locate the site of a touch should result in greater accuracy.

So what is exactly happening in the youngest age group in terms of the role of vision in locating touch? First, we must consider the explanation of the "crossed-hands" effect that contends that the effect arises due to an increased tactile localisation accuracy in performance in the uncrossed-hands posture, as opposed to poorer performance in the crossed-hands posture (i.e. a deficit in tactile localization accuracy in the less familiar posture). This is consistent with Pagel et al.'s observation that development of tactile localization in early childhood proceeds via an enhancement of localization in the typical layout of the body.

However, this still does not account for the findings that 4-year-olds performed worse in the uncrossed-hands posture when they had vision of their limbs. One potential explanation for these surprising findings could be that, particularly in early childhood, due to difficulties in integrating visual cues into the body schema, under certain circumstances sight of the hands and arms may actually interfere with the localization of touch.

The ability to integrate visual cues of the body into a body schema develops throughout infancy and childhood. Indeed researchers have articulated the anecdotal observation of an infant viewing their hand, but also attempting to grasp this *visual* hand with the very same hand. It is as though young infants seem not to understand that their hand that they see is the same hand that can be used to reach and grab things (Hall, 1898), thus do not seem to incorporate visual cues of their limbs within their body schema. This is consistent with a view in which the integration of visual cues of posture into the body schema develops gradually throughout infancy and early childhood (Bremner & Cowie, 2013).

As adults it may seem almost an automatic reaction to look towards a felt touch on the body. However an ability to visually orient towards a tactile stimulus only emerges slowly across the first year of life (Bremner et al., 2008). In addition to this, vision of the hands is similarly irrelevant to the first successful reaches which infants make; these are performed equally well with sight of the hands or in the dark (e.g., Robin, Berthier & Clifton, 1996). The beginnings of visually-directed reaching emerge in the second year of life at the earliest (Carrico & Berthier, 2008; although see

Babinsky, Braddick & Atkinson, 2012, and Pogetta, de Souza, Tudella & Teixera, 2013 who have shown that infants at 5 months perform slightly less accurate reaches when their hands are occluded) and developments in visual guidance of reaching continue into middle childhood. Additionally, it is not until well into childhood (approximately at 9 years) that children use visual feedback (regarding hand movements) when accommodating for prismatic shifts in visual targets (Hay, 1979; Ferrel-Chappus, Hay, Olivier, Bar & Fleury, 2002; see also Smyth, Peacock & Katamba, 2004).

Furthermore, visual information about the body and where limbs lie in space becomes more important through childhood. Research with visual illusions has shown that young children (at around 5.5 years of age) become increasingly reliant on visual feedback of limb location (Bremner et al., 2013) and it is not until approximately 9 years of age that children are adult-like in the extent to which they use visual cues to hand position (Cowie et al., 2013).

Given the relatively long trajectory over which children learn to use visual cues to limb position, it may be that the poorer performance that 4-year-olds in this experiment when they could see their hands was due to a lack of integration of visual cues to the hand interfering with tactile localisation. Importantly, the visual cues only exerted their influence in the uncrossed hands posture. This suggests that visual cues interfered particularly with the advantages bestowed by the hands being in a canonical position (i.e. the representation of the canonical layout of the body). Thus, it is possible that children, without sight of their hands, are able to make use of a spatial prior (in this case, the statistical likelihood of a limb occupying a certain side of space) for where a touch is in the external coordinates to locate it on their body. However, when their hands are visible, they behave as if there was no spatial prior and so do not gain a benefit from the hands being in the uncrossed posture. But why do children not use a prior when they see their hands?

Therefore, this difficulty in integrating the *visual* hand within the body schema disrupts the benefit children would initially gain from referring to the canonical representation of the body. Thus, explaining the significantly poorer performance of the 4-year-olds in the uncrossed posture when their hands were visible.

As discussed above, children of the ages tested in this experiment (4- to 6-year-olds) are in a period of sensorimotor development in which they are novices at using visual cues to locate the limbs and reach to visual targets. The findings from the 4-year-olds tested above indicate that visual cues to the posture of the hands may lead them into invoking a representation of current limb posture (the body schema) in preference to the heuristics provided by the canonical body representation. As children are no longer referring to a canonical representation of their limbs, they are losing the benefit they would normally have from this representation, which then leads to poorer performance specifically in the uncrossed hands posture.

This study has established that from at least 4 years of age (and likely much earlier) children automatically locate tactile stimuli to locations on their limbs in external spatial coordinates, rather than just relative to anatomically defined locations on the body surface. But children's ability to locate touches on the body also seems to be affected by visual information concerning the limb being touched.

The fact that the youngest age group tested in this study (children aged 4 years) performed worse on a tactile localization accuracy task when they viewed their hands suggests that visual cues to the hands interfere with tactile localization. Visual interference leads us to make the strong prediction that even if illusory visual cues to hand position are provided, these will interfere with tactile localization in the uncrossed posture. In order to investigate this prediction further, I conducted an experiment in which it was possible to more directly manipulate visual information of current arm posture, using artificial hands.

Experiment 1 has been published in the following article:

Begum Ali, J., Cowie, D. & Bremner, A.J. (2014). Effects of posture on tactile localization by 4 years of age are modulated by sight of the hands: evidence for an early acquired external spatial frame of reference for touch. *Developmental science, 17*(6), 935-943

3.5 Experiment 2: Tactile localization across posture changes of artificial hands

How can the RHI be used as a means of investigating the localization of tactile stimuli to the body using an external frame of reference? In the above study (Experiment 1; Begum Ali, Cowie & Bremner, 2014), it was found that vision of the hands interfered with tactile localization, especially in the uncrossed hands posture. I go onto test this idea further in an experiment where it was possible to more directly manipulate visual cues to hand position, via artificial hands.

As previously mentioned, the RHI is an illusion in which bodily sensations of touches to the hand are referred to a limb like object which is nonetheless external to the body. Botvinick and Cohen (1998) were the first to empirically investigate the RHI using a series of studies in a group of healthy adults. Here, participants were seated with their hands on a table, their left hand and arm hidden from view by a screen and an artificial hand and arm in the space their left hand would usually occupy. Following this, the participant's left hand was stroked with a paintbrush, in synchrony with a paintbrush that was used to stroke the artificial hand; thus they were receiving tactile information from the felt touch to their real hand and visual information from the stroking of the fake hand they were fixating on. Both before and after this period of synchronous stroking, participants were asked to close their eyes and, using their right hand, underneath the table point to the location of the index finger of their left hand. It was found that participants demonstrated a drift in their proprioceptive sensations of where their real hand was, in that after the illusion was induced, their judgements of where their index finger lay in space was displaced towards the artificial hand. Additionally, participants quickly began to gain a sense of ownership over this alien limb, often reporting that the artificial hand "felt like [their] own" (Botvinick & Cohen, 1998, p. 756).

Interestingly, the intermanual reach displacement only occurred when participants' viewed synchronous stroking of their real and the fake hand. If there was a disparity in the timings of the seen and the felt touch (i.e. an asynchrony between visual tactile information), the illusion was not induced and did not affect participant's accuracy in locating the index finger of their left hand. Further conditions, that are a requisite in order to induce the illusion, include that the artificial limb should be in a similar orientation as participant's real hand (Ehrsson, Spence & Passingham, 2004; Tsakiris & Haggard, 2005), the size of the artificial limb cannot be smaller than participant's own hands (Pavani & Zampini, 2007; although see Bruno & Bertamini, 2010) and the distance between the real and artificial hand must not be greater than 30 cm (Lloyd, 2007).

The RHI has also been demonstrated in a variety of experimental situations, indicating the robust nature of the illusion in adult populations. For example, the illusion prevails even when there is not an alien limb, but an empty space receives a tactile stimulus (Guterstam, Gentile & Ehrsson, 2013), when the artificial limb is larger than an individual's own hand (Pavani & Zampini, 2007) or when the skin tone of the fake hand differs (Farmer, Tajadura-Jiménez & Tsakiris, 2012). The RHI demonstrates that intermodal correspondences (particularly between a seen and a felt touch, in this case) can lead to individuals accepting non-limb like objects within the body schema. However, there are a number of certain conditions that first need to be met (outlined above). These conditions relate to acceptable degrees of freedom of the body; for example, individuals can accept a larger artificial hand as their own, but not a smaller hand – your hand can grow in size, but it cannot shrink. Ultimately, the RHI has illustrated the flexible nature of the way in which individuals construct the body schema.

As mentioned above, the majority of RHI studies have been conducted on an adult population. However, recently there has been much interest in the developmental trajectory of visual-tactile correspondences and how children use these to infer knowledge of their bodies. Cowie, Makin and Bremner (2013) conducted a rubber hand study with children aged 4-9 years. As expected, the authors found that children were susceptible to the rubber hand illusion when presented with contingent visual-tactile information, by way of proprioceptive drift towards, and a sense of ownership of, the fake hand. A particularly important conclusion drawn from this study was that children are more susceptible to the RHI and demonstrate more of the illusion than adults. From this, it could be understood that young children rely more on visual information to depict hand position than adults.

One way to assess the exact role of current vision of limbs in tactile localisation is to introduce a conflict between visual and proprioceptive information (as has been previously done in RHI studies). Azañón and Soto-Faraco (2007) did just that; in their study participants' hands were placed in either the uncrossed or crossed-hands posture whilst they viewed rubber hands in a posture that either corresponded with the posture of their real hands, or was incongruent. In a tactile TOJ task (Yamamoto & Kitazawa, 2001a; Shore et al., 2002; Pagel et al., 2009), participants then had to judge the location of the first of two tactile stimuli to the hands.

The researchers replicated previous findings showing that participants' accuracy and response speed was impaired when their hands were crossed (relative to their performance in the uncrossed posture). The novel finding in this study was that participants demonstrated a decreased crossed-hands deficit (with improved accuracy and shorter response times in the crossed-hands posture) when individuals viewed a pair of uncrossed rubber hands, above their own hidden crossed hands.

A question to consider is if this pattern of findings would also emerge for developmental populations. As mentioned previously, from the findings of Azañón and Soto-Faraco (2007) and my findings in Experiment 1 (Begum Ali et al., 2014), two potential hypotheses arise. First, it is possible that the crossed-hands deficit will be eliminated due to better performance in the crossed posture when viewing uncrossed rubber hands (as in Azañón and Soto-Faraco, 2007). An alternative (and not necessarily opposing) hypothesis is that visual information of the rubber limbs in the uncrossed-hands posture, whilst children's hands are also in the uncrossed-hands posture, will impair localisation accuracy in this posture, eliminating the crossed-hands deficit in children as the difference in accuracy between postures would be reduced.

In order to investigate and disentangle potential explanations for the role of vision of current posture in localising tactile stimuli to the hands, I ran a variation of Experiment 1, this time with artificial hands in either a corresponding or an incongruous hands posture or without artificial hands at all. The first condition was a direct replication of the Hands Covered condition in Experiment 1 and I expected to replicate those findings (i.e. 4-year-olds would demonstrate a crossed-hands deficit, with a poorer localisation accuracy in the crossed-hands posture relative to the uncrossed-hands posture). Further to this, given the findings and conclusions of Experiment 1, I expected that when children had vision of uncrossed artificial hands, with their own hands in the corresponding posture, their tactile localisation accuracy would be impaired relative to the situation in which they could not see their own hands.

3.6 Methods

3.6.1 Participants

Seventeen participants aged 4 years (M = 4.55 years, SD = .36 years) took part in this study. Three males and 14 females took part. An additional 5 participants (all male) were excluded prior to analyses for failing to understand task instructions (3 participants) or repeatedly removing their hands out of the assigned posture (2 participants).

3.6.2 Apparatus and Materials

This study used the same apparatus as Experiment 1, however there were a few differences with additional equipment. For example, the small ledge on which the stuffed animals were attached was replaced with a larger ledge (measuring 32 cm by 42 cm by 11 cm) to accommodate the length of the fake rubber hands (see Figure 3.4). An additional length of faux fur (measuring 30 cm by 46 cm) was used to cover the ends of the rubber hands.

The experiment was conducted in a quiet room at either a nursery or at the Goldsmiths InfantLab. Although in the previous study it was found that children could not locate the tactors using only auditory cues (see Experiment 1), as an added precaution a centrally placed speaker playing grey noise was used to mask any sound the tactors made.

Figure 3.4: Experimental set up of Experiment 2. Panel A shows the No Rubber Hands condition. Panel B shows the Uncrossed Rubber Hands condition and Panel C shows the Crossed Rubber Hands condition. Participants' hands are beneath the black cover.

3.6.3 Procedure

This experiment used the same procedure for the practice phase as in Experiment 1 (see Section 3.2.3). The participant's hands were placed on the buzzers in the uncrossed posture, underneath the black covering cloth. Once again, each participant was required to correctly locate the stimulus on 5 consecutive trials in order to continue to the experimental trials.

The experimental trials took a similar format to the practice trials except that the experimenter was blind to the accuracy of the child's answer during the experimental trials and some experimental trials included the presence of rubber hands. Participants' verbal responses were recorded by the experimenter on a computer. In the experimental phase, there were six separate blocks of trials: (i) Uncrossed-hands, No rubber hands; (ii) Crossed-hands, No rubber hands; (iii) Uncrossed-hands, Uncrossed rubber hands; (iv) Crossed-hands, Uncrossed rubber hands; (v) Uncrossed-hands, Crossed rubber hands; and (vi) Crossed-hands, Crossed rubber hands. The order of the blocks was counterbalanced across participants, yielding 12 separate order conditions (see Appendix B).

Between blocks, the experimenter always moved the child's hands into a different posture. Additionally, the children were asked to close their eyes between all blocks (both when the rubber hands were either introduced to, or removed from, the ledge and also between blocks in which there were no rubber hands). Each block consisted of 20 trials (10 vibrotactile stimulations to each hand), across which the order of left and right stimuli was randomized. Thus, across the whole experimental session (6 blocks) there were 120 trials.

3.7 Results

A measure of the children's tactile localisation accuracy was derived by calculating the percentage of trials on which they made a correct response in each condition. One-sample t-tests of this percentage accuracy score showed that participants were performing reliably above chance (50%) in all conditions, except the Rubber Hands Crossed / Real Hands Crossed condition where the difference between chance and performance was marginally significant (see Table 3.3 below).

Table 3.3: Results from one sample t-tests comparing children's tactile localisation accuracy with 50% (chance performance) across experimental conditions.

Rubber hand Posture	**Real hands Posture**	**t**	**df**	**p**	**d**
None	Uncrossed	5.08	16	<.001	2.54
None	Crossed	2.48	16	.024	1.24
Uncrossed	Uncrossed	2.64	16	.018	1.32
Uncrossed	Crossed	3.68	16	.002	1.84
Crossed	Uncrossed	3.54	16	.003	1.77
Crossed	Crossed	2.08	16	.054	1.04

I used a repeated measures 2 x 3 ANOVA to investigate the effects of the within-subjects factors of Posture (Uncrossed-hands / Crossed-hands) and Rubber Hand (None / Uncrossed / Crossed). This revealed a main effect of Posture [$F(1, 16) = 4.59$, $p = .048$, $\eta_p^2 = .22$], showing that, across all conditions, children were more accurate when localizing tactile stimuli in the uncrossed-hands posture compared to the crossed-hands posture. Additionally, an interaction effect of Posture x Rubber Hand condition was also significant [$F(2, 32) = 3.41$, $p = .046$, $\eta_p^2 = .1$]. No other main effects were found.

As I had quite specific hypotheses to test, I conducted three planned paired sample t-tests looking at the effect of Posture in each of the No Rubber Hand and Rubber Hands Uncrossed conditions and so the alpha value was bonferroni corrected to $p = .017$. First I conducted a one tailed comparison looking at the effect of Posture on tactile localization in the No Rubber Hand condition; as expected I replicated the results of Experiment 1 - the children had poorer tactile localization accuracy in the Crossed-hands posture compared to the Uncrossed-hands posture [$t(16) = 2.57$, $p = .003$, $d = .72$], demonstrating the “crossed-hands” effect (see Figure 3.5). However, two further planned comparisons (also one-tailed) revealed that this effect was not present when participants viewed Uncrossed Rubber Hands [$t(16) = .45$, n.s.] or Crossed Rubber Hands [$t(16) = 1.08$, n.s.] with means indicating that children were performing comparably across postures when they viewed either Uncrossed or Crossed Rubber Hands (see Figure 3.5).

As I was particularly interested in whether viewing the Rubber Hands in an Uncrossed posture would disrupt children's tactile localization accuracy when their hands were in that same uncrossed posture, I ran a one-tailed comparison between the Uncrossed posture in the Rubber Hand Uncrossed condition with the Real Hands Uncrossed condition in which participants did not have visual information of any hands (i.e. the No Rubber Hands condition). I found a significant difference in tactile localization accuracy between these conditions [t(16) = 2.32, p = .017, d = .51), with means indicating that children's performance in the tactile localization task in Uncrossed postures was significantly impaired when they viewed Uncrossed Rubber Hands.

I now go on to a more exploratory analysis of the comparisons between other conditions in this study. First, I examined the role of seeing Rubber Hand (No Rubber Hands and Rubber Hands Uncrossed) on localization performance when the hands were Crossed (as in Azañón & Soto-Faraco, 2007) and found no significant difference [t(16) = 1.43, n.s.]. I then investigated whether having visual cues to the hands in a novel posture affects performance, examining the effect of Crossed Rubber Hands (compared to hidden hands) on tactile localization in both Postures (Uncrossed and Crossed). The comparison between Crossed Rubber Hands and No Rubber Hands in the Crossed posture yielded no significant difference in performance [t(16) = .15, n.s.]. However, a trend towards decrease in localization performance between conditions in which participants observed Crossed Rubber Hands compared to No Rubber

Hands when their real hands were in the Uncrossed posture produced a marginally significant effect [t(16) = 1.87, p = .08].

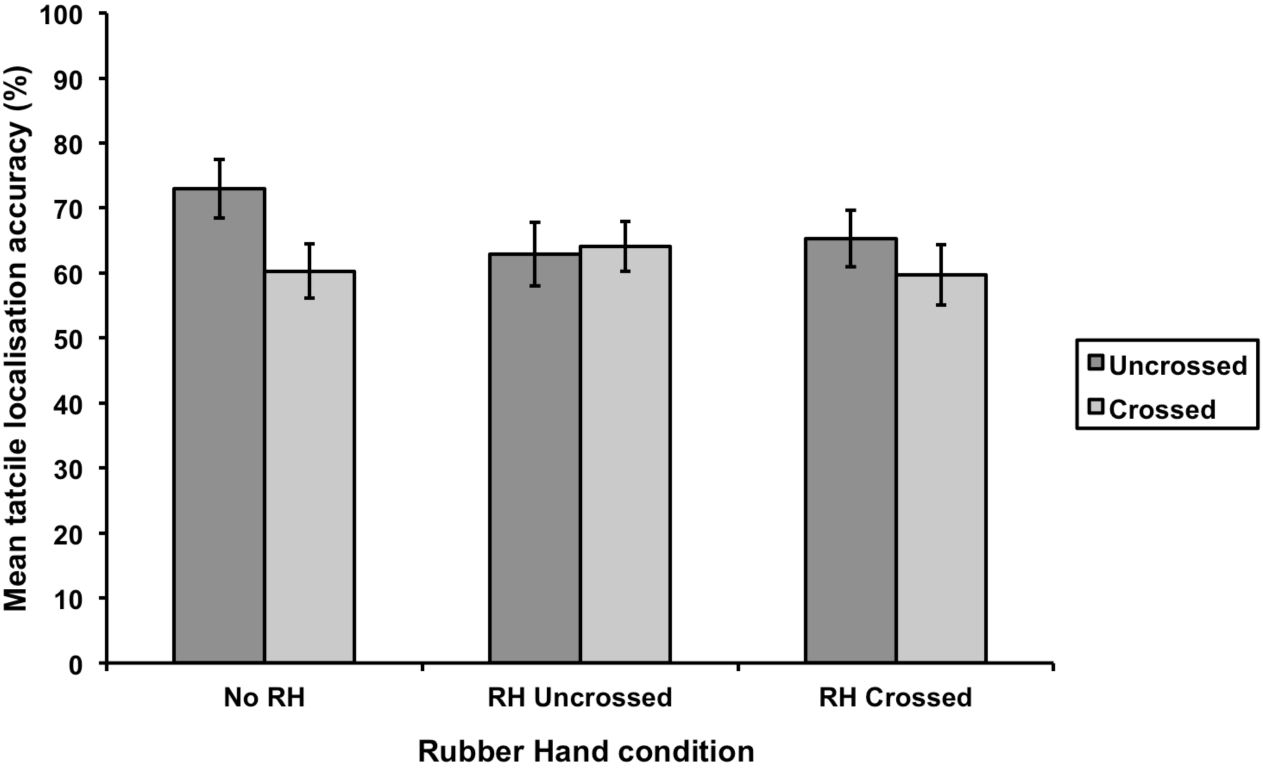


Figure 3.5: Mean tactile localization accuracy (percentage correct) of 4-year-olds in the crossed-hands and uncrossed-hands posture across conditions where they viewed rubber hands in an uncrossed- or crossed-hands posture or no rubber hands. Error bars indicate the standard error of the mean.

3.8 Discussion

As hypothesized, this study found that, when sight of the hands is not available, 4-year-olds demonstrated the "crossed hands" deficit (i.e. were not as accurate at locating the site of a tactile stimulus in the crossed hands posture, relative to the uncrossed hands posture). This confirms the findings from the previous study (Experiment 1), demonstrating that children of 4 years use an external reference frame to code touches to the body. Further to this, a significant interaction of Posture and Rubber Hand was also found in this age group indicating that sight of fake hands modulates tactile localization accuracy: when participants had visual information of a pair of (fake) hands in the uncrossed posture, the "crossed hands" effect disappeared.

What was interesting about the reduction of the effect of posture when participants could see uncrossed rubber hands, was that rather than this being the result of *improved* performance in the crossed posture (as was found in a study of adults by Azañón & Soto-Faraco, 2007), it was the result of a *reduced* accuracy in the uncrossed posture. This is consistent with the findings of Experiment 1, in that when children see hands in the uncrossed posture, tactile localization accuracy in this posture decreases.

In Experiment , I argued that this pattern of results was due to the fact that children of 4 years demonstrate visual interference when they see their arms. I proposed that when 4-year-olds have current sight of hand posture (specifically the uncrossed posture), they no longer rely on prior information regarding the canonical posture of their bodies, and as a result of this, they do not benefit from having their hands in this posture. It has been argued that this also means that young children are unable to incorporate visual cues of their own body within their body schema (Begum Ali et al., 2014). The current study extends this finding, in showing that even artificial hands placed in the uncrossed posture disrupt the advantage children would usually have when their hands are in anatomical locations in space. It appears that visual information specifying the position of the hands, rather than benefitting performance as it does in adults (Longo & Haggard, 2011; Longo et al., 2011) actually impairs it in early childhood.

A surprising element of this disruption is that it occurred without ownership of the limb being manipulated i.e. without experimental conditions in which the researchers prompted children to adopt the artificial hands as part of their own bodies. When designing the study, it was decided not to induce the rubber hand illusion by way of contingent visual-tactile information. This was decided in order to avoid any carry over effects (i.e. the effects of the contingent visual-tactile stimuli could affect not only the condition that immediately followed this stimulation, but other conditions as well) between conditions. Carryover effects would make it difficult to tease apart potential explanations for different patterns of findings.

Additionally, a further reason for not inducing the rubber hand illusion was in order to make the current study more comparable with

Azañón and Soto-Faraco (2007), as those researchers did not induce the rubber hand illusion, via contingent visual-tactile stimulation, with their adult participants.

There are several potential explanations for why seeing uncrossed rubber hands disrupted the 4-year-olds' performance even when the rubber hand illusion was not induced. It is possible that in this young age group, children are more susceptible to accepting artificial limbs as their own and do not need to see and feel contingent stroking of their own and the rubber hand. Given the main effect of age group in Cowie et al. (2013), which suggests that children experienced the RHI, regardless of whether they received contingent visual-tactile stimuli or not, this is a plausible explanation.

Most likely, and most consistent with the findings from Experiment 1 and the current experiment, is that children are especially captured by visual information of the limbs, be that their own or artificial limbs. This is an assertion that has been demonstrated throughout the psychological literature from various areas (Hay, 1979; Ferrel-Chappus et al., 2002; Smyth et al., 2004; Bremner et al., 2013).

Thus, it is my proposal that, at this young age, viewing uncrossed rubber hands prompts children to use representations of their current body posture, rather than the heuristics provided by the canonical body representation. Therefore, children are not bestowed with the enhancement in tactile localization accuracy that is specific to the uncrossed hands posture (due to the limbs being in a canonical location).

Without this enhancement in accuracy with hands uncrossed, the difference in performance across postures is dramatically reduced and the crossed hands deficit is no longer evident.

So a question for future research relates to the causes of this visual interference. Is visual interference the result of ownership of the hand or are visual cues to hand position sufficient to result in this interference? Either of these explanations are plausible, given that both ownership of the limb and visual capture of hand position have been demonstrated by Cowie et al. (2013) in this age group. However, considering that children at 4 years of age are still relatively immature at using visual cues to locate the limbs, with this ability developing throughout infancy and childhood (see Cowie & Bremner, 2013), it may be that the answer to the cause of visual interference is not straightforward.

This also relates to the wider question of when children begin to successfully integrate visual cues of the limbs (either their own or artificial limbs) to locate the limbs in space, thus deriving a benefit from viewing uncrossed rubber hands whilst their own were in the crossed posture. A series of studies that could be conducted to further investigate the effect of vision of limbs could be to manipulate ownership over the rubber hands by inducing the rubber hand illusion. This would be interesting across all variations of posture (of both real and artificial hands), but particularly interesting in conditions in which participants' real hands are in a posture that is incongruent to that of the artificial hands and the subsequent effect the illusion would have on tactile localization accuracy. Again, investigating the developmental trajectory and the pattern of the crossed hands deficit would be especially interesting in terms of determining the progress of developing integration of visual cues to the limbs.

In summary, this study has confirmed that by 4 years of age, children use an external frame of reference in which touches to the body are coded. This is in accordance with previous research (Experiment 1; Begum Ali et al., 2014). Further to this, it has been shown that when visual information of the uncrossed posture is provided (via artificial limbs), children demonstrated decreased tactile localization accuracy when their own hands were in the corresponding posture. It seems that when visual cues are provided, this disrupts the benefit children would gain from their limbs being in a canonical posture. This is the case when children either see their own hands (as in Experiment 1) or artificial hands. Therefore, this suggests that visual cues to hand position interferes with a representation of the layout of the body in external space.

The last two experiments have shown how current visual information of a limb (whether a participant's limb or an artificial one) can modulate tactile localization accuracy across different arm postures. Additionally, these experiments have shown that children as young as 4 years of age are able to code touches within an external frame of reference. This is a younger age than that found by Pagel et al. (2009), however as previously stated, Bremner et al. (2008) have demonstrated that infants within the first year of life demonstrate the crossed-hands effect and thus use an external reference frame to map touches on the body. The next study investigates exactly when an external reference frame emerges in infancy.

3.9 Experiment 3: The emergence of an external reference frame for touch in infancy

Locating a touch on the body is not a simple task; we do not simply locate touch on the skin surface but also within the external environment. In order to represent the location of a touch in external coordinates, adults dynamically remap the relation between tactile stimuli and external coordinates (Azañón & Soto-Faraco, 2008; Azañón & Soto-Faraco, 2011; Graziano et al., 2004; Kitazawa, 2002; Overvliet et al., 2011).

As previously related, studies investigating the crossed-hands effect have shown that adults and children make errors in localizing tactile stimuli that are applied to the hands, often making errors in localization, when their hands are crossed over and in the side of space contralateral to their usual placement (Pagel et al., 2009; Overvliet, Azañón & Soto-Faraco, 2011; Groh & Sparks, 1996; Begum Ali et al., 2014 and Experiment 2 of this thesis). This has been attributed to conflict between the anatomical and the external frames of reference for locating a touch when the hands are crossed.

Research from congenitally and late blind individuals indicates that early visual experience plays an important role in the emergence of external spatial reference for touch. Röder, Rössler and Spence (2004) investigated the “crossed-hands” deficit in a population of visually impaired individuals and found that those that were congenitally blind (i.e. blind from birth so did not have any experience of vision) did not show the “crossed-hands” deficit. However, those individuals who had acquired a visual impairment (and thus, had some visual experience in infancy and early childhood before losing their vision) performed comparably to typical, blindfolded adults without any visual impairments. In other words, the late blind participants accuracy in locating the site of the initial tactile stimulus was significantly reduced in the crossed-hands posture, compared to when the hands were uncrossed.

Röder et al. (2004) suggested that a possible explanation for this pattern of results is that congenitally blind adults may use solely an anatomical reference frame when locating touches on the body. According to this account, without an external frame of reference for touch, a conflict between the anatomical and external reference frames does not occur in the crossed hands posture and thus accuracy is comparable across postures. From these findings, the researchers concluded that early visual experience is paramount to the development of an external reference frame for locating tactile stimuli.

According to Röder et al. (2004) the comparable performance of the late-blind with control participants is the result of visual experience in early life prior to the onset of blindness. The researchers argue that even just a few years of visual experience may drive the emergence of an external reference frame for coding touches to the body. Recent research indicates that there is a critical period in early development within which visual experience impacts on tactile spatial perception. Ley, Bottari, Shenoy, Kekunnaya and Röder (2013) report a case study of H. S., a 33-year-old male who was completely blind in the first 2 years of his life, as a result of congenital cataracts. At 2, after undergoing surgery to remove his cataracts, normal vision was restored. H. S. took part in a tactile TOJ experiment and it was found that even after his sight was restored at 2 years of age, he did not demonstrate using an external reference frame to locate touches on the body in this particular tactile localization TOJ task. H. S.'s tactile localization accuracy did not differ across the two arm postures and was comparable to that of congenitally blind individuals in Röder et al. (2004), even though normal vision had been restored for thirty years. This supports the argument that the external frame of reference in which touches to the body are coded is influenced by visual experience in early life, with this sensitive period constrained to the first 2 years of life.

So, in regards to the sensitive period in which vision is particularly important in the emergence of an external reference frame, this raises the question of when and at what stage in the first two years does visual experience give rise to the acquisition of external spatial coding? Research with typically developing human infants suggests that the first half year of life may be important. Bremner, Mareschal, Lloyd-Fox and Spence (2008) have shown that 6.5-month-old infants manual orienting behaviour to touches was significantly worse when their hands were crossed.

Bremner et al. (2008) concluded that 6.5 months are able to use an external reference frame to code touches to the body.

In Experiment 1, the developmental trajectory (in childhood) for the use of an external reference frame when locating touches to the limbs was investigated. In this particular study, I investigated the emergence of an external reference frame for touch within the first half year of life. In order to do this, I looked at the crossed hands deficit in 4- and 6-month-old infants (Experiment 3). From previous pilot work conducted, it was found that it is difficult to persuade young infants to cross their hands over. In comparison, the legs appear to have more postural freedom. Previous research has shown that crossing the feet also elicits deficits in tactile localization in adults (Schicke & Röder, 2006), so it was decided instead to cross infants' feet.

3.10 Methods

3.10.1 Participants

Eighteen 4-month-olds (9 males), aged between 104 and 134 days (M = 116 days; SD = 8 days) took part in this study. One female participant was excluded from the final analyses, due to equipment errors, leaving a total of 9 male and 8 female participants in this age group. Additionally, fourteen 6-month-olds (5 male), aged between 177 and 220 days (M= 196 days; SD=13 days) also participated. One male 6-month-old was excluded prior to analyses due to his fussy behaviour in the testing session, thus leaving 4 male and 9 female participants in the 6-month-old age group.

Informed consent was obtained from the parents before testing commenced. The testing took place only if the infant was awake and appeared to be in an alert and content state. Ethical approval was gained from the Ethics Committee of the Department of Psychology, Goldsmiths University of London.

3.10.2 Apparatus and Materials

Infants were seated in a specialist baby chair (Bloom Loft high chair). The seat was reclined in a horizontal position with the back-rest parallel to the floor. Adjustable straps secured the infant in the seat. Cotton padding around the trunk and a head-rest were used to secure the posture of the infant's head and trunk. A digital video camera located 80 cm in front of, and 60 cm above, the chair, facing the infant's frontal midline recorded the movements of the infant's foot. Video data were recorded for offline coding. The vibrotactile stimuli were delivered by two voice coil tactors (that the experimenter placed on the soles of the infant's feet, securing them in place with cohesive bandage) driven by a 220 Hz sine wave and controlled by custom software scripted in E-Prime. The E-Prime script also sent commands to a serial-controlled video titler so that the infants' stimulus-locked behaviour could be observed and coded. Any noise emitted by the tactors was masked with grey noise played from a centrally placed loudspeaker. This masked sound cues for both the infant and experimenter.

3.10.3 Design

Infants were presented with a maximum of three blocks of experimental trials. Each block contained 10 experimental trials in which a 1000 ms vibrotactile stimulus was presented to one of the infant's feet in pseudorandom order (which was R, L, L, L, R, R, L, L, R, R). This 1000 ms vibrotactile stimulus was followed by an 8000 ms interval to allow sufficient time for the infant to react to the stimulus. Every 5 trials, the posture of the infants' legs was alternated between crossed and uncrossed. Whether crossed or uncrossed posture was adopted in the start of each block was counterbalanced between participants.

3.10.4 Procedure

On each trial, one experimenter (Experimenter A) held the infant's legs around the ankle placing them in the assigned posture (uncrossed or crossed, with feet approximately 10 cm apart, see Figure 3.6), whilst a second experimenter (Experimenter B) controlled the delivery of stimuli within the E-Prime program. At the beginning of each trial, Experimenter A placed the infant's legs in the required posture. A trial was then triggered by the Experimenter B. During the stimulus delivery, Experimenter A gently held the infant's legs in the assigned posture until the infant either moved their legs, or 8000 ms had elapsed, at which point the trial was terminated. In the 8 second period following each stimulus, Experimenter A oriented her face to the floor, in order not to distract the infant. If the infant became fussy, they were entertained with musical toys and/or bubbles until they were settled enough to continue with the study. The study continued for as long as the infant was willing to participate, with included participants completing a minimum of one block (10 trials), and maximum of three blocks (30 trials).

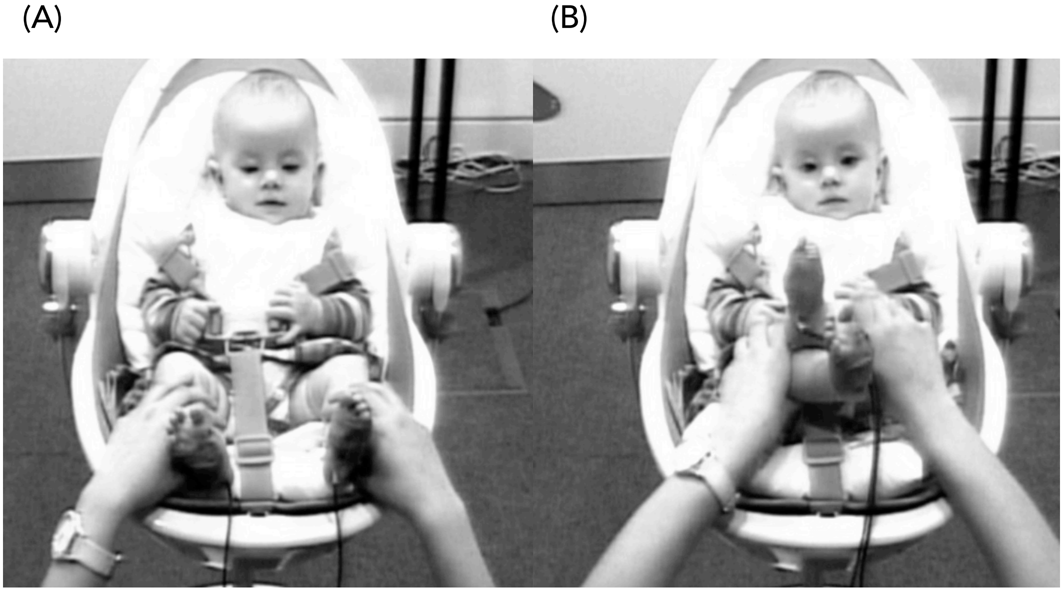


Figure 3.6: Experimental set up showing infant in the reclined baby seat. Panel A shows an infant in the uncrossed-feet posture and Panel B shows the infant in the crossed-feet posture.

3.11 Data coding

The direction and latency of infants' first foot responses to the tactile stimuli were coded from the video records. Both raters were blind to the side of stimulus presentation, but were provided with stimulus onset and offset information. The initial 133 ms following stimulus presentation on each trial were not coded as any movement during this period was considered to be anticipatory. After this period, the first foot to move independently (of the other) was accepted as a directional (orienting) foot response to the tactile stimulus. Additionally, the latency of the first directional foot response to the tactile stimulus was also noted. A second rater coded a proportion of the total trials across all participants, with trial-by-trial agreement at 85% for both the 4- and 6-month-old age groups.

3.12 Results

The proportion of foot orienting responses which were made to the side which had received the tactile stimulus (i.e., correct directional responses/total number of responses) were computed for both crossed and uncrossed postures (see Figure 3.7). One-sample t-tests of the proportion tactile localization accuracy scores in each age group and condition showed that 4-month-olds were performing reliably above chance (0.5) in both posture conditions, whereas the 6-month-olds were only performing above chance in the uncrossed feet posture condition (see Table 3.4)

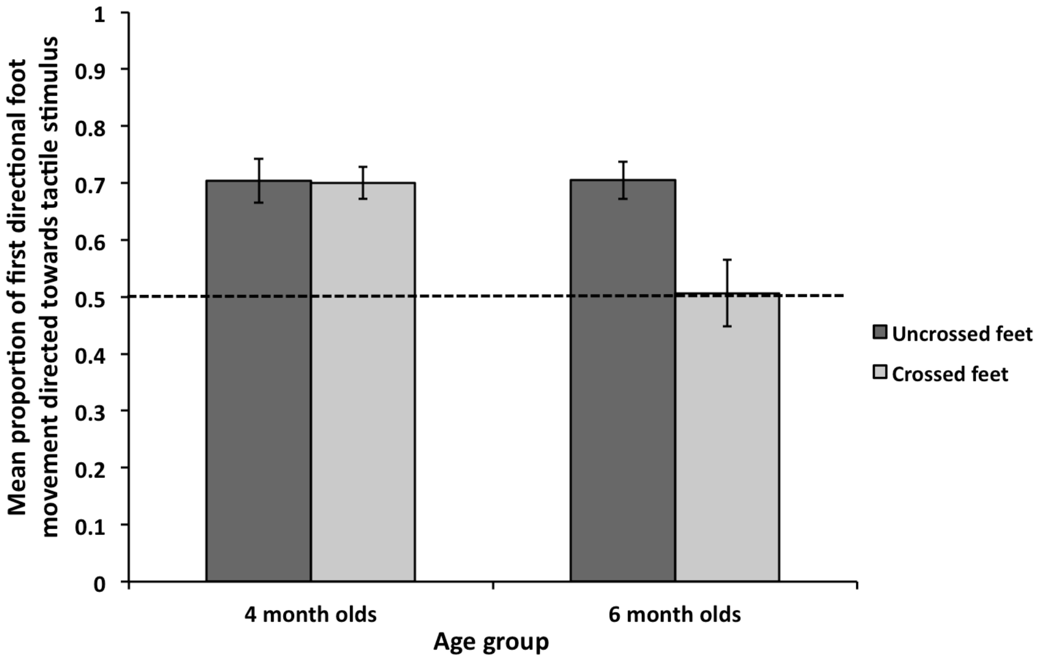


Figure 3.7: Mean tactile localization accuracy (proportion of correct first directional foot movements to vibrotactile stimulus) of 4- and 6-month-olds in the crossed-feet and uncrossed-feet posture.

Table 3.4: Results from one sample t-tests comparing infant's tactile localization accuracy with 0.50 (chance performance) across age groups and experimental conditions

			Uncrossed feet		Crossed feet	
Age group	**n**	**df**	**t**	**p**	**t**	**p**
4-month-olds	17	16	5.28	<.001	6.15	<.001
6-month-olds	13	12	7.36	<.001	.1	.92

To investigate developmental changes in the use of an external reference frame for touch, a 2 x 2 mixed measures ANOVA of tactile localization accuracy with the within-participants factors of Posture (Uncrossed-feet / Crossed-feet) and the between-participants factor of Age (4-month-olds / 6-month-olds) was conducted. This revealed a main effect of Age [F(1, 28) = 4.504, p = .043, η_p^2 = .14], and a main effect of Posture [F(1, 28) = 8.604, p =.007, η_p^2 = .24] (Uncrossed posture: M = .7, SD = .13; Crossed posture: M = .62, SD = .19), which was qualified by the significant interaction of Posture x Age [F(1, 28) = 7.92, p = .009, η_p^2 = .22]. I investigated this interaction with four post-hoc comparisons (alpha was set at p = .0125). First, we conducted a comparison looking at the effect of posture on tactile localization in each of the age groups. This revealed a significant effect of posture in the 6-month-olds [t(12) = 3.31, p = .006, d = 1.28], but not the 4-month-olds, [t(16) = .104, n.s.]. Next, I examined the effect of Age within each of the posture conditions using paired sample t-tests. There was no difference between the 4- and 6-month-olds in the uncrossed posture [t(28)

= .01, n.s.]. However, the 4-month-olds significantly outperformed the 6-month-olds in the crossed posture [t(28) = 3.07, p = .002, d = 1.12].

I also examined the latencies of infants' foot orienting responses. Figure 3.9 plots the cumulative timings (following tactile stimulation) of directional responses to tactile stimuli across trials. The 4-month-olds responded more quickly, and more often to tactile stimuli on their feet. The mean latencies of the infants' foot responses (Figure 3.8) were entered into a mixed 2 x 2 ANOVA with Posture (Uncrossed-feet / Crossed-feet) and Age (4-month-olds / 6-month-olds) as independent variables. This revealed a main effect of Age [F(1, 28) = 24.62, p < 001, η_p^2 = .47]. No other main effects or interactions were significant (all Fs < 2).

There is the possibility that the tactile stimuli activated more of a protective withdrawal system in the 4-month-old infants. To investigate this I compared the frequency of the two types of foot orienting responses produced by the two age groups. I found that the withdrawal response only contributed to a small proportion of the overall foot responses (M = .12, SD = .11 and M = .12, SD = .09 for the 4- and 6-month-olds respectively) in comparison to the exploratory foot "wriggle" (M = .88, SD = .11 and M = .88, SD = .09 respectively). I found no significant differences between the groups in the extent to which they responded with either an exploratory foot "wriggle" [t(28) = .01, n.s.] or a withdrawal foot response [t(28) = .1, n.s.].

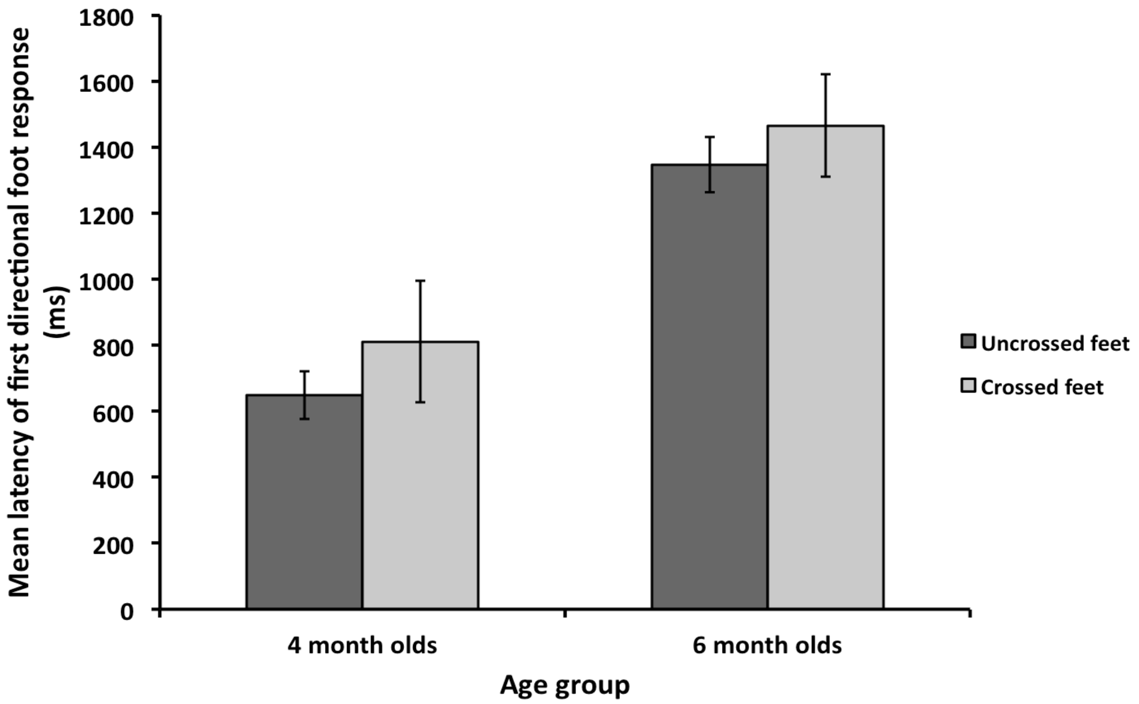


Figure 3.8: Mean latency of first directional foot response to vibrotactile stimuli of 4- and 6-month-olds in the crossed-feet and uncrossed-feet posture.

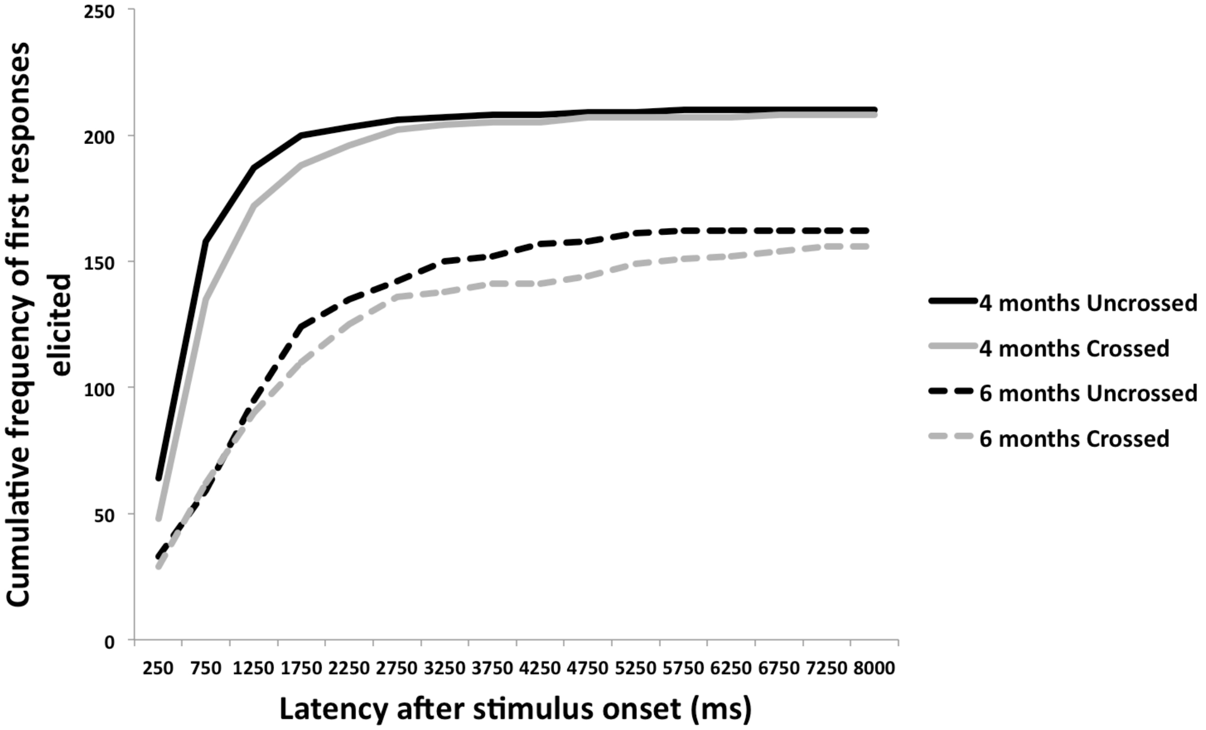


Figure 3.9: Cumulative frequency of first response latency to vibrotactile stimuli of 4- and 6-month-olds in the crossed-feet and uncrossed-feet posture.

3.13 Discussion

The youngest infants (4-month-olds) in Experiment 3 demonstrated the ability to correctly locate and respond to a tactile stimulus presented to one of their feet, regardless of the posture (i.e. they did not demonstrate a "crossed-feet deficit"). This extends previous findings on tactile localization in early life which have shown that infants as young as 6 months of age make manual orienting responses to tactile stimuli on the hand (Bremner et al., 2008). However, I found no effect of posture; the 4-month-olds whom I tested were equally accurate at orienting a foot motor response to a tactile stimulus whether their feet were placed in an uncrossed-feet posture, or a crossed-legs posture.

There could be two potential explanations of this finding. Firstly, it may be that infants may locate touches to the feet in external spatial coordinates, but they may be more competent at doing this across changes in posture of the legs than they are for the hands (Bremner et al., 2008). Therefore, one would expect a general trend towards external coding in early infancy, and expect both 4- and 6-month-olds to show an effect of posture on tactile localization to the feet (as has already been established with the hands; Bremner et al., 2008). However, this explanation is unlikely given that this pattern of results was *not* found – the 6-month-old infants in this study showed poorer tactile localization with crossed feet (compared to uncrossed feet), thus demonstrating the crossed feet deficit. It is not that infants are better at localizing tactile stimuli to the feet (in anatomical space), but there are age related changes in the way in which infants in the first half year of life locate touches to the body.

Indeed, a second and more likely explanation for this pattern of results is that, at 4 months of age, infants have not yet acquired the ability to code tactile locations in an external spatial frame of reference, irrespective of the locus of tactile stimuli on the body. In the absence of external coding, a reliance on anatomical coordinates to make their response would explain the lack of a posture effect, as anatomical spatial coding is unaffected by posture (*e.g.*, a touch on the right foot is always considered as a touch on the right foot, irrespective of where that foot lies in space).

Further to this, when scrutinizing data concerning the latency of foot responses to the touch stimulus, I found that the younger infants were much quicker to respond to the stimuli compared to the older age group across posture conditions. There could be several potential explanations for this. One possible explanation could be that due to the fact that the younger infants had shorter limbs. It is possible that the signals sent from the skin receptors to the brain and then effector muscles had a shorter distance to travel, thus resulting in faster responses. However, considering the small differences in the length of these limbs between 4 and 6 months of age and the large differences between response latencies in these age groups, this explanation seems unlikely.

Conversely, a much more interesting and plausible explanation could be related to the way in which infants at different stages in the first half year of life process touches to the body, with longer processing and response times reflecting more complex processes. This theory is in accordance with Kitazawa (2002), who argued that, when using an external reference frame to locate touches to the body, individuals first map the touch in space before mapping the touch on the body. Alternatively, others have suggested that this process is reversed, with individuals mapping touches in somatosensory co-ordinates and then in external space (Azañón & Soto-Faraco, 2008). Regardless of the exact order of these events, this is a more complex process than simply mapping touch directly onto the skin surface, and the increase in response time of the 6-month-olds (compared to the 4-month-olds) illustrates this.

This study has shown that influences of external spatial coordinates on tactile localization emerge in human infancy between 4 and 6 months of age. It is at 6 months that infants show a marked decrease in accurate orienting to a stimulated foot in the crossed-feet posture (in comparison to the uncrossed-feet posture), that is they demonstrate the “crossed-feet effect” and the use of an external reference frame to code touches to the body. In comparison, the youngest age group tested showed no such effect, performing to a high level of orienting accuracy regardless of their leg posture.

From this, it seems reasonable to conclude that it is during the two month period between the ages of 4 and 6 months that infants begin to code touches on their bodies with respect to external space. As proposed by Röder et al. (2004) and Ley et al. (2013), I consider it very likely that this reference frame emerges as a consequence of visual experience in the first months of life. I have been able to support this argument and also demonstrate that early visual-tactile experience is particularly important in the narrow time frame in which infants are aged between 4 and 6 months. If infants are deprived of visual experience during this time (as in the case of congenitally blind infants or those with cataracts), I would expect that these infants would not locate touches to their bodies with respect to the external world, simply locating touches on the skin surface.

Chapter 4

Sensorimotor developmental drivers of somatosensory remapping

4.1 Introduction

In the previous chapter, I reported studies that investigated the development of an ability to localise touches in external space. However, once this is possible we also have to be able to remap to external space across a variety of limb postures (i.e. resolving the problems produced by having the hands in less usual postures, such as crossed at the forearm).

A factor that complicates this resolution is that our bodies do not lie static in space. We are in constant motion; not only do we move around our environments, but our limbs also move with respect to the body. Therefore, in order to accurately locate a touch with respect to external space, we must also dynamically remap the relations between somatosensory coordinates and locations in external space by taking account of the current position of the limbs. Here I will refer to this process as "somatosensory remapping".

In adults, behavioural studies investigating somatosensory remapping of touch have found that this process begins approximately 60 ms following stimulus onset (Azañón & Soto-Faraco, 2008). In this crossmodal spatial cueing paradigm, participants were presented with a tactile stimulus to one hand, followed by a visual stimulus (a flash of light) presented on the top or bottom of either the same, or opposite, hand. Participants were required to judge the location of the visual stimuli (e.g. either top or bottom), irrespective of hand. The researchers found that when the visual stimulus was presented between 30-60 ms to the hand that did not receive the tactile stimulus (the opposite hand), participants' reaction times for localizing the visual stimulus was faster when (i.e. when the location of the stimuli were anatomically congruent, but spatially incongruent). However, if after 60 ms, the visual stimulus was presented to the same hand (that which received the tactile stimulus), participants' reaction times to the visual stimulus were faster as the location of the stimuli (both visual and tactile) were now spatially congruent. From these results, Azañón and Soto-Faraco (2008) argued that initially participants' locate touch within an anatomical reference frame, before the remapping process begins after 60 ms following stimulus onset.

Studies using neuroimaging methodologies have not only been able to determine which brain areas are recruited during this process, but have also been able to identify the time course according to which the brain remaps somatosensory stimuli to the current posture of the body (Rigato et al., 2013; Lloyd et al., 2003; Azañón & Soto-Faraco, 2013).

The above research has been conducted with adult populations. However there is still very little known about the development of an ability to keep track of the location of a touch over changes in limb posture. This is a striking omission, considering that the developing infant must keep track of where their limbs lie in space in order to execute actions in an adaptive way. For example, to be able to feed themselves, the infant must not only be aware of where their hand lies in relation to food, but also where it lies in relation to their mouth in order to successfully bring the hand (and food) to the mouth.

Although there have been very few research studies investigating somatosensory remapping in infancy, there are two key studies that have examined this. The first, Bremner et al. (2008b), used a behavioural paradigm with infants in the first year of life. As previously mentioned (in Chapter 1, Section 1.6), single touches were applied to the palms of infants, aged 6.5 and 10-months, in either the uncrossed-hands or the crossed-hands posture. Whilst 6.5-month-old infants made more manual orienting errors in the crossed-hands posture relative to the uncrossed-hands posture, this was not the case for the 10-month-olds. This older group of infants localised touches in an accurate manner across both arm postures with both manual and visual orienting responses. As such the authors argued that infants develop in their ability to update the locations of felt touches across changes in limb posture between 6.5 and 10 months of age.

In a more recent study, infants' somatosensory remapping was examined using ERP methods. Rigato, Begum Ali, van Velzen and Bremner (2014) investigated modulations of somatosensory processing across changes in limb posture in 6.5 and 10-month-old infants. This study involved presenting vibrotactile stimuli to the infant's hands while they were in either the crossed-, or uncrossed-hands, posture. They found that 10-month-old infants' somatosensory evoked potentials (recorded at central electrode sites which were contralateral to the stimulated hand) were modulated by the posture of the hands. The SEPs elicited by somatosensory stimuli when hands were uncrossed and crossed, demonstrated significant differences as early as 58 ms following stimulus onset (see Figure 4.1). Vibrotactile stimulations in the crossed-hands posture evoked a SEP waveform that was greater in amplitude, compared to the uncrossed hands posture. In comparison, infants aged 6.5 months did not show any difference in the amplitude of somatosensory evoked potentials across postures.

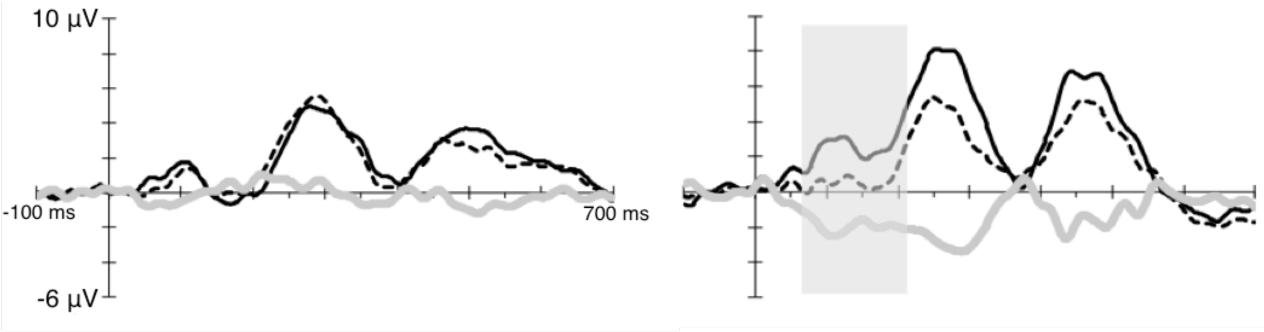


Figure 4.1: Grand averaged SEPS in the Uncrossed (dashed lines) and Crossed (solid black line) hands postures for 6.5-month-olds (left panel) and 10-month-olds (right panel). Grey lines indicate the difference of the two conditions (Uncrossed – Crossed). The shaded area indicates the time course of significant effects of Posture on somatosensory processing. There was no effect of Posture in the 6.5-month-olds, but a reliable effect was found between 58 and 220 ms in the 10-month-olds. Figure taken from Rigato *et al.,* (2014).

From the physiological and behavioural data reported in these two studies (Bremner et al., 2008; Rigato et al., 2014), Rigato et al. (2014)

argued that the neural networks underlying the ability to remap tactile events in external space across changes in limb position become functional at least by 10 months of age. The postural modulations in the SEP waveforms were observed particularly early in somatosensory processing in this age group: 58 ms after stimulus onset. This demonstrated that the posture of the limbs influenced the early feedforward stages of somatosensory processing.

In a further experiment, Rigato et al. (2014) investigated the role of the perceptual information that are required by infants to successfully remap somatosensory information across changes in posture. In this study, they examined the modulatory effect of vision on remapping. Here, the 10-month-old infants' hands and arms were covered by a cloth. This obscured their view of the current posture of their hands. Vibrotactile stimuli were then delivered to the infants' hands in the uncrossed- and crossed-hands postures. This time no effect of posture was observed in the SEP. This suggests that sight of the limbs is a necessary prerequisite for 10-month-olds to remap tactile stimuli.

4.1.1 The role of experience in somatosensory remapping: midline crossing

Bremner et al. (2008) postulated that the ability to remap somatosensory information to accurately locate a touch on the body across changes in limb posture might be driven by experience. Specifically, they proposed that sensorimotor experience of crossing the body midline might be important in giving rise to an ability to remap somatosensory stimuli across the midline also. Midline crossing denotes the act of placing one's hand in the contralateral side of space. By completing this action, the individual is reaching across themselves and thus, their midline.

Several studies have investigated the ability to cross the hands into contralateral space in infants and children. For example, Cermak, Quintero and Cohen (1980) looked at midline crossing abilities in 150 children aged between 4 and 8 years using the Space Visualisation Test. The test involved observing the number of times children used their ipsilateral or contralateral hand to pick up blocks and computed a ratio that was based on these two frequencies. Although, the researchers observed a trend in which spontaneous midline crossing increased with age, the study ultimately yielded non-significant results.

In comparison, Carlier, Doyen and Lamard (2006) found a statistically significant developmental trend of midline crossing from the ages of 3 to 8 years. They studied 432 children aged 3-10 years (using the Bishop Card Reaching Task; Bishop, Ross, Daniels & Bright 1996) and found that older children spontaneously crossed their midline when reaching for objects at a higher frequency than younger children, with the age factor explaining 4.9% of the variance observed in the observed reaching behaviours. Additionally, Doyen, Dufour, Caroff, Cherfough and Carlier (2008) found that children aged between 7 and 11 years performed a greater number of midline crossings compared to both younger and older participants.

These studies have been useful in tracking the developmental trajectory of midline crossing reaching in childhood. In order to understand how sensorimotor experience might influence the development of the postural schema, it is important to look at the earlier origins of an ability to reach across the body midline. Studies investigating this type of reaching in infants may shed some light on this.

Provine and Westerman (1979) investigated the initial emergence of midline crossing in infants aged between 9 and 20 weeks. The infants were seated in a suitable chair and a swaddling blanket wrapped around them was used to restrain one arm. The researcher then presented infants with a brightly coloured object with a bell, placing the toy alternately in front of the infant's midline or opposite their shoulder which was ipsilateral to their free hand or opposite their shoulder which was contralateral to their reaching hand for 60 seconds. Provine and Westerman (1979) found that that a large majority (71%) of infants aged between 15 and 17 weeks were able to touch the object when it was placed in the contralateral position. However it was only within the 18-20 week age bracket were all infants able to touch the stimulus when it was at the contralateral shoulder. Although this study demonstrates that midline crossing can emerge as early as 15 to 17 weeks after birth, it must be noted that one of the infant's arms was restrained during the experimental procedure. The fact that one arm was rendered immobile may have actively encouraged (and may have even induced) midline crossing at an age when it would not normally happen. Thus, the authors contend that midline crossing may develop at a later age if the arms of the infants were unrestrained, as in their natural environment.

Other studies investigating midline crossing in infancy have used paradigms in which the infants' arms have not been restrained and found differing results. For example, Morange and Bloch (1996) used a similar task as above with infants aged 4-7 months, however this study differed in that infants' arms were not restrained. The researchers found that midline crossing occurred at 7 months, a much later age than that found by Provine and Westerman (1979).

In contrast to the above studies, where the focus has primarily been on one handed reaches across the midline, van Hof, van der Kamp and Savelsbergh (2003) used a different paradigm and observed midline crossing frequency when either one or both hands were employed. The researchers examined midline crossing frequency in relation to the development of bimanual reaching behaviours in infants aged 12, 18 and 26 weeks. Van Hof et al. (2003) found that midline crossing reaching behaviours initially emerged at 18 weeks, but became more fully developed at 26 weeks. Fundamentally, it was found that the majority of midline crossing instances occurred when the infants needed both hands to grasp the object. Initially, regardless of the size of the object to be grasped, reaches at the earliest ages were predominantly unimanual, however there was a shift to using both hands to grasp the larger object as age increased. Thus, the researchers concluded that midline crossing reaching behaviours occurs as a result of the necessity for bimanual handling as infants require both hands to successfully grasp larger objects.

So how do reaches across the midline relate to the ability to remap tactile stimuli to the hands when the hands are placed in less usual postures (i.e. crossed over at the forearm, with the hands in the opposite side of space to their usual location)? As mentioned in the opening of this section, it may be that as the infant grows their brain matures, especially the corpus callosum (Ballesteros, Hansen & Solia, 1993; Teicher, Dumont, Ito, Vaituzis, Giedd & Andersen, 2004; Barkovich & Kjos, 1988). Increased connections between the hemispheres of the brain may account for infants' abilities to detect, and update, changes in their posture. However, as already mentioned, an alternative (but not mutually exclusive) hypothesis, that was also raised in Chapter 1, is that sensorimotor experience may be particularly related to the emergence of somatosensory remapping in the infant brain. It may be that the more an infant engages in adopting different postures, and is aware of the postures their body is *able* to assume, then they are more likely to be able track these changes in bodily posture, and thus the location of a limb in space.

I have investigated the relationship between sensorimotor experience and somatosensory remapping in the first year of life with the following set of experiments (see Experiments 4a, 4b and 5).

4.2 Experiment 4a: Sensorimotor drivers of somatosensory remapping

In order to address the question of how sensorimotor experience may relate to somatosensory remapping across changes in posture, I conducted a correlational study to investigate the relationship between across the midline reaching and remapping in the infant brain across changes in arm posture (e.g., uncrossed vs. crossed hands). By engaging in reaching behaviours that cross the midline, the infant's hand is now in the contralateral side of space to its usual placement; where the other hand would usually lie. The more experience the infant has of crossing their hands over (via reaching behaviours), the more likely it is that the infant is able to track any changes in their limb posture (specifically when their hands are crossed over at the forearm). And so I measured both postural modulation of somatosensory processing in an ERP study, and examined the extent to which postural modulation of the SEP was correlated with a predilection to cross the midline in a behavioural reaching task. I predicted that infants who were more likely to cross the midline would also show a greater postural modulation of their SEPs.

4.2.1 Methods

4.2.1.1 Participants

Sixteen 6.5-month-old infants (8 males) aged between 155 and 218 days (M = 186 days; SD = 20.56 days) took part in Experiment 4a. An additional three infants were excluded from the analyses because of fussy behaviour (1 participant), equipment failure (1 participant) or because they did not produce any reaches during the reaching task so could not be classified into a reaching group (1 participant). Nine 8-month-old infants (4 male) aged between 240 and 261 days (M = 253 days; SD = 6.87 days) also took part in this experiment. An additional two infants were excluded from analyses due to fussy behaviour. Informed consent was obtained from the parents. The testing took place only if the infant was awake and in an alert state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London,

4.2.1.2 Midline crossing reaching task

Infants were seated in a specialist baby chair (Bloom Loft high chair). The seat was placed in a reclined position at a 90° angle from the cradle (horizontal) position. Adjustable straps secured the infant in the seat. 2 security cameras (mounted on tripods) were used to record the reaching behaviours of the infants for offline coding at a later date. One camera was placed 80cm in front of where the infant would be seated, whilst the second camera was placed 117 cm away at a 30° angle from the midpoint of the baby seat (see Figure 4.2). The two cameras were connected to a mixer (Edirol V-4), a titler and a hard disk recorder (Data Video DV/HDV Recorder) that recorded and stored the video footage.

Once secured in the seat (with adjustable straps) infants were presented with an inflatable ball. The ball was attractive in appearance. Standing behind the baby chair, the researcher presented the toy at the infant's left shoulder, right shoulder and midline, making sure that on each trial the toy was within the infant's reach. Infants were presented with a total of 9 reaching trials (3 trials in the respective reach locations) for either a maximum of 30 seconds or until the infant touched, or their hand was within a fist sized distance from, the toy. Infants' reaching behaviour was recorded on each trial focussing on whether the reach was unimanual or bimanual, and whether they reached across the body midline or not (whether the reach was contralateral or ipsilateral).

Figure 4.2: 6-month-old infant taking part in the midline crossing reaching task and demonstrating a reach into the contralateral side of space (left panel).

4.2.1.3 Tactile ERP task

Following the completion of the reaching task, the infants were taken out of the testing room to engage in a few minutes of play during a short break. It was during this break that the EEG net was applied to the infant's head. Infants were then brought back into the testing room with the parent. At this point the researcher began the tactile localisation task.

With the infant seated on a parent's lap, the researcher placed the tactors in the infant's palms. These solenoid tactors were custom built in house. The tactors were secured with an adjustable strap and covered with scratch mittens.

Experimenter A, who was blind to the side of stimulus presentation, held the infant by each wrist and bounced his or her hands three times while saying "One, two, three, woo!". On reaching "woo!", Experimenter A held the infant's attention with an engaging facial expression and direct gaze, and at the same time placed and held the infant's hands into the appropriate posture (crossed-hands or uncrossed-hands), approximately 10 cm apart, one on either side of the midline. At this point, Experimenter B triggered the presentation of a trial (a sequence of four tactile stimuli, each stimulus lasting 200 ms with an interstimulus interval varying randomly between 800 and 1400 ms). Between every trial the posture of the baby's arms was changed (the starting posture was counterbalanced between participants).

If the infant became fussy, they were entertained with musical toys and/or bubbles until they were settled enough to continue with the study. When the babies became too fussy to continue with the study (e.g. crying and/or moving excessively), the study was terminated. Throughout this task, infant's brain activity was recorded using the 128 electrode Hydrocel Geodesic Sensor Nets (Electrical Geodesic Inc.).

4.2.2 Results

4.2.2.1 Analyses and results of behavioural data

Data was coded offline from the recorded videos. In order for a reach to be counted, infants had to either grasp the toy (with one or both hands) or to have brought one or both of their hands within a fist sized distance of the toy (the same criteria were used by Van Hof et al., 2002). Unimanual reaches across the midline and reaches across the midline which formed part of a bimanual reach were both counted as midline crossing. Those participants who crossed their midline at least once were allocated to the "Crossers" group. The remaining participants who did not cross the midline once were allocated to the "Non-crossers" group.

Infants were presented with a maximum of 9 reaching trials (3 trials in each of the reach locations). The majority of infants, in both age groups, performed reaches in all trials (see Tables 4.2 and 4.3 below). In the group of 6-month-olds, eight of the infants tested made no midline crossing reaches at all. The other eight infants made at least 1 and a maximum of 3 midline crossing reaches. In the sample of 8-month-olds, seven infants did not produce a midline crossing reach. Only two infants reached into the contralateral side of space, with a minimum of 1 and maximum of 3 reaches (see Figure 4.3 for an average of midline crosses across age group).

Those participants who crossed their midline at least once were allocated to the "Crossers" group. The remaining participants who did not cross the midline once were allocated to the "Non-crossers" group (see Table 4.1 below).

Table 4.1: Participant characteristics across reaching and age group

Group	**n**	**Sex**	**Mean age (days)**	**Age range (days)**
6-month-old Crossers	8	3f, 5m	191 (SD = 22.7)	158-218
6-month-old Non-crossers	8	5f, 3m	182 (SD = 19.1)	155-209
8-month-olds Crossers	2	1f, 1m	256 (SD = 4.9)	253-260
8-month-old Non-Crossers	7	4f, 3m	252 (SD = 7.4)	240-261

Table 4.2: Reaching performance in the 6-month-old infants across reaching group

Variable	Means (SD)		t-test statistics			
	Crossers (n = 8)	Non-crossers (n = 8)	t	df	p	d
No. of midline crosses	1.75 (.9)	.0 (.0)				
% of midline crosses	29.1 (14.7)	.0 (.0)				
Age (days)	193.1 (21.6)	184.9 (18.2)	.8	14	.5	.4
Trials presented	9	9	0	14	1	
Reaches made	8.86 (.35)	8.63 (.74)	.8	14	.4	.4

Table 4.3: Reaching performance in the 8-month-old infants across reaching group

Variable	**Means (SD)**		**t-test statistics**			
	Crossers (n = 2)	Non-crossers (n = 9)	t	df	p	d
No. of midline crosses	2 (1.4)	.0 (.0)				
% of midline crosses	33.3 (23.5)	.0 (.0)				
Age (days)	256.5 (4.9)	253.2 (8.2)	.5	9	.6	.3
Trials presented	9	9	.0	9	1	
Reaches made	9 (.0)	8.3 (1.1)	.8	9	.4	.5

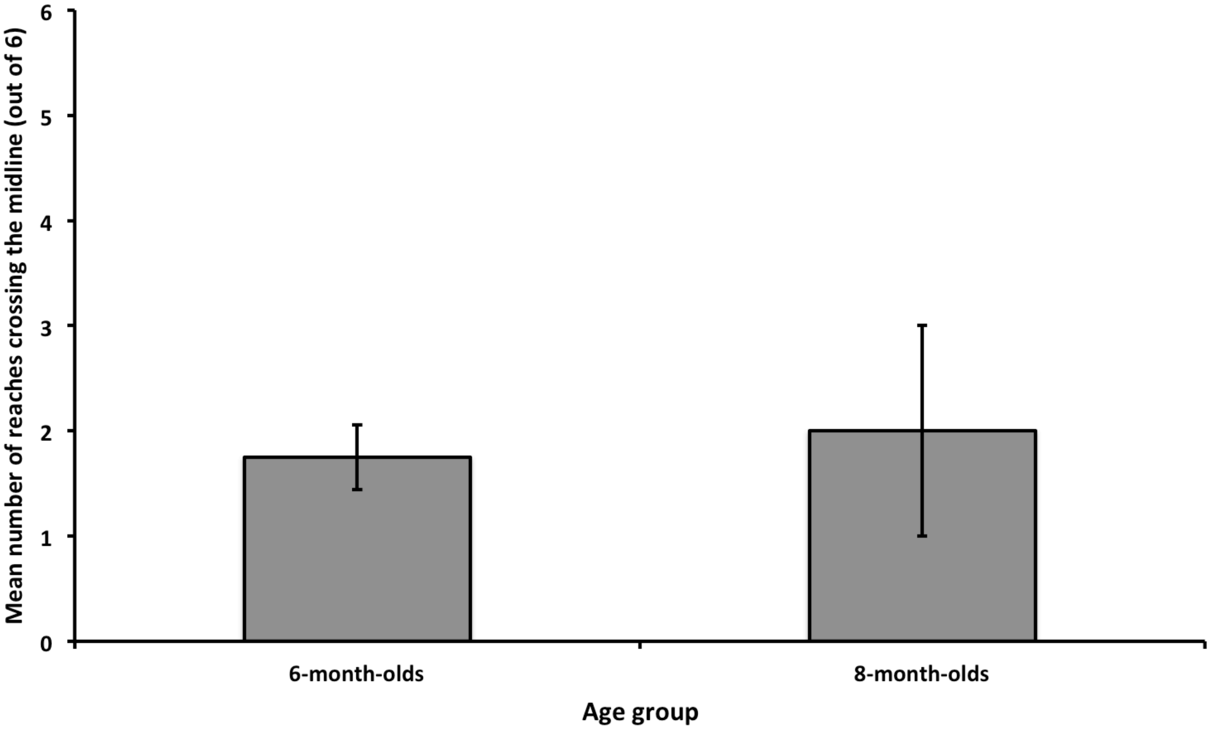


Figure 4.3: Mean number of reaches that involved crossing the midline (out of a possible 6 trials). Error bars indicate the standard error of the mean

I conducted an one way ANOVA comparing the number of reaches that involved crossing the midline across Age (6-month-olds vs. 8-month-olds). There was no effect of Age group [F(1, 25) = 1.62, n.s.].

4.2.2.2 Analyses of EEG data

The data was processed offline (see Chapter 2 for details). When visually inspecting the data on a trial-by-trial and grand average basis, a stimulus locked artefact became apparent (see Figure 4.4). After careful testing of equipment, it was found that the tactors used in this study (solenoid tactors which, when triggered, produced a "buzz" like vibration) were producing an artefact that appeared in all electrodes and was long lasting following stimulus onset. As such, no further EEG analyses were conducted.

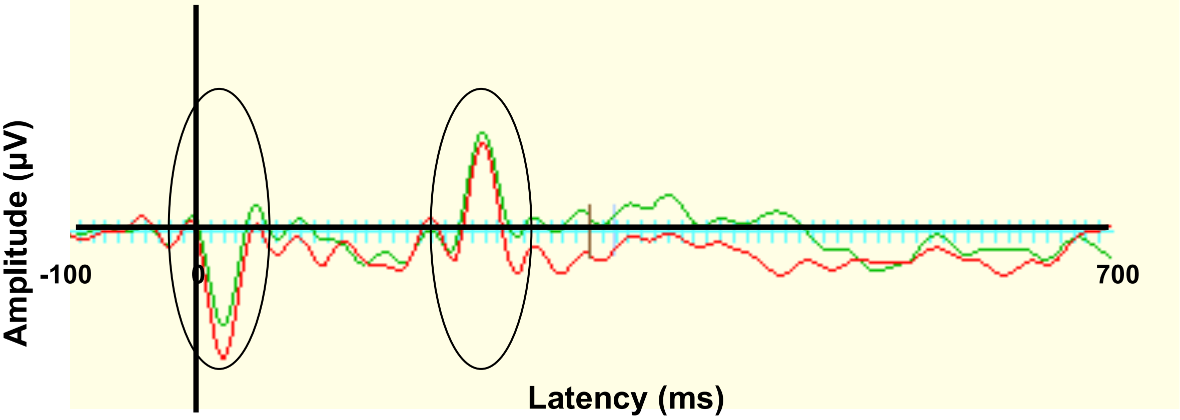


Figure 4.4: Electrodes in the C4 area showing a long lasting artefact produced at stimulus onset and offset (circled). Red and green lines indicate vibrotactile stimuli applied to the right (red) and left (green) hands. This artefact was seen in the majority of electrodes across the scalp, with amplitudes exceeding 100 microvolts. These properties suggested that the waveforms were not true neural responses to the stimulus, thus no further EEG data analyses were conducted on this dataset.

4.2.3 Discussion

This study was conducted to investigate the relationship between sensorimotor experience (specifically reaches that involved crossing the body midline) and the somatosensory remapping of touch across changes in arm posture. To do this, we assigned infants to different groups depending on their performance on a reaching task. If infants produced at least one reach that involved placing the hand in the contralateral side of space, they were considered 'Crossers'. If, however, infants were producing only ipsilateral reaches, they were considered to be 'Non-crossers'. This was assessed in two age groups: 6- and 8-month-old infants.

The aim of this study was to then examine whether these two reaching groups (within each age group) differed in the extent to which somatosensory processing in the brain was modulated by the current posture of their hands (an index of somatosensory remapping of touch in external space). However, upon inspection of the ERP data, it was found that a large, long lasting artefact (time-locked to the onset and offset of the vibrotactile stimuli applied to infants' hands) was present in the data. This artefact exceeded 100 microvolts at the peaks and thus could not reflect true brain responses. Additionally, as this artefact was long lasting, it completely obscured the first 200 ms of the SEP. As effects of posture on 10-month-olds' SEPs were found at an early point in somatosensory processing in Rigato et al. (2014) (at 58 ms post-stimulus for the 10-month-olds), this artefact was especially problematic as it could not be simply removed. Additionally, due to the large microvoltage of this artefact, it would be difficult to conclude that any reliable effects between reaching groups were not being driven by it. Therefore, it was decided that this ERP data would not be analysed. As such, I will only discuss the results from the reaching task.

The data from the behavioural (reaching) task indicated that the number of 8-month-olds that were producing reaches that crossed their midlines differed from that of the 6-month-old participants; 2 infants in the 8 month age group compared to 8 infants in the 6 month age group (see Tables 4.2 and 4.3). This seemed strange given that Van Hof et al. (2002) found older infants were more likely to produce contralateral reaches than younger infants and by the age of 26 weeks, the majority of infants in their sample (16 out of 17 infants) were engaging in midline crossing reaching. One possible explanation for a reduction in midline crossing reaching in 8-month-olds could have been that infants' limbs are heavier at this age (compared to at 6 months) and when lying prone, reaching across the midline may be particularly effortful. Therefore, at 8 months, infants may have used a more efficient, and less taxing, reaching approach to contact the toy; namely ipsilateral reaching. So, it may be that 8-month-olds do engage in midline crossing reaching behaviours, however the task that was used in this study did not capture this ability.

Therefore, this study was able to support the findings of previous research demonstrating that midline crossing is present by six months of age. However, the data from this study demonstrated that midline crossing declined between 6 and 8 months of age. As suggested above, the most parsimonious reason for this decline may be that we had placed the infant in a prone position during the reaching task.

In order to, more effectively, investigate how sensorimotor experience, specifically midline crossing reaching, relates to somatosensory remapping of touch across changes in arm posture, I conducted a further study (Experiment 4b), which was largely similar to the current study. However, Experiment 4b used a slightly different behavioural reaching task and also included motor assessments to match for motor abilities across the two reaching groups (Crossers vs. Non-crossers). This motor battery was included so as to be sure that any group differences were based solely in midline crossing reaching ability and not any other gross and/or fine motor abilities. I provide the details of Experiment 4b in the following section.

4.3 Experiment 4b: Sensorimotor drivers of somatosensory remapping

This study addressed the issues that occurred in Experiment 4a, as such several changes were made (detailed below). One such change involved the age group of infants tested for this study. In the previous study (Experiment 4a), I included a sample of both 6- and 8-month-old infants. However, as other findings which were emerging in our laboratory had shown that 6-month-olds do not show evidence of somatosensory remapping in their somatosensory evoked potentials (Rigato et al., 2014), I decided to focus on only a group of 8-month-olds for the current study.

Additionally, in order to control for any differences in motor abilities between the two reaching groups (Crossers and Non-crossers), I included two motor assessments that measured gross and fine motor abilities in infants. These motor scales were included to be sure that any differences in somatosensory remapping of touch was related to midline crossing reaching specifically and not general motor ability.

4.3.1 Methods

4.3.1.1 Participants

Twenty-six 8-month-old infants (11 males) aged between 241 and 283 days (M = 257 days; SD = 13.1 days) took part in Experiment 4b. An additional five 8-month-olds were excluded from the analyses because of fussy behaviour (4 participants) or equipment failure (1 participant). Informed consent was obtained from the parents. The testing took place only if the infant was awake and in an alert state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London,

4.3.1.2 Stimuli and procedure

The stimuli and procedure for this experiment was largely similar to those used in Experiment 4a. However, there were a number of significant changes made to refine the tasks and procedure. As such, a detailed description of the full methods used in this study is provided below.

4.3.1.3 Motor assessment battery

In this experiment I gathered background measures of the infants' motor development. The infants were tested on: i) the Mullen Scales of Early

Learning (current edition, 1995) and ii) the Vineland Adaptive Behaviour Scale (VABS, current edition, Sparrow, Balla & Cicchetti, 1984). The Mullen and VABS are assessment scales for infants and toddlers measuring overall cognitive development using domains including language, visual reception and motor abilities. Largely, these assessment scales are similar, however the VABS relies more heavily on parent report of particular motor behaviours (such as distance of crawling and how often this motor behaviour occurs). For this study, I used only the gross and fine motor scales from each battery. For the Mullen Scales, I observed whether the infant was able to perform certain gross motor (e.g. sitting without support, crawling) and fine motor tasks (e.g., using a pincer grip to pick up small items) and scored them accordingly. This method was also used for the VABS, however there were some items on the scale that were parent reported as it was not feasible to test them in the lab setting (e.g., I relied on parental report concerning whether infants could crawl up or down stairs).

4.3.1.4 Midline crossing reaching task

Infants were seated in a specialist baby chair (Bloom Loft high chair). The seat itself was placed in the upright position at a 90° angle from the cradle (horizontal) position. I decided to make this change as Experiment 4a showed that 8-month-olds were not producing reaches that crossed their midlines. This may have been due to the horizontal positioning of the chair in that as infants' limbs are heavier at 8 months, compared to younger infants, the prone positioning of their bodies in the chair may have made crossing the midline more effortful (as discussed in this chapter, Section 4.2.3).

Once seated in the baby chair, infants were presented with a customized stuffed tiger face toy. The toy was 7 cm in diameter and was fitted with bells that made a tinkling sound when shaken. I decided to use a smaller sized toy for which infants would reach, so as to keep the task as similar to Van Hof et al.'s study as possible (in their study they used a ball with a diameter of 7 cm).

Standing behind the baby chair, the researcher presented the toy at the infant's left shoulder, right shoulder and midline, making sure that on each trial the toy was within the infant's reach. Infants were presented with a minimum of 9 reaching trials (3 trials in each of the reach locations) and a maximum of 18 (6 trials in each of the locations) for either a maximum of 30 seconds or until the infant touched, or their hand was within a fist sized distance from, the toy. The number of reaching trials was increased from 9 to 18 trials, so as to give infant's plenty of opportunity to display their reaching behaviours.

4.3.1.5 Tactile ERP task

With the infant seated on a parent's lap, the researcher placed the tactors in the infant's palms. Instead of using solenoid tactors (as in Experiment

4a), I used custom in-house built vibrotactile stimulators. These tactors were driven by a 200Hz Sine wave for 200ms per stimulation. The tactors were secured with an adjustable strap and covered with scratch mittens.

Experimenter A, who was blind to the side of stimulus presentation, held the infant by each wrist and bounced his or her hands three times while saying “One, two, three, woo!”. On reaching “woo!”, Experimenter A held the infant’s attention with an engaging facial expression and direct gaze, and at the same time placed and held the infant’s hands into the appropriate posture (crossed-hands or uncrossed-hands), approximately 10 cm apart, one on either side of the midline. At this point, Experimenter B triggered the presentation of a trial (a sequence of four tactile stimuli, each stimulus lasting 200 ms with an interstimulus interval varying randomly between 800 and 1400 ms). Between every trial the posture of the baby’s arms was changed (the starting posture was counterbalanced between participants).

If the infant became fussy, they were entertained with musical toys and/or bubbles until they were settled enough to continue with the study. When the babies became too fussy to continue with the study (e.g. crying and/or moving excessively), the study was terminated. Throughout this task, infant’s brain activity was recorded using the 128 electrode Hydrocel Geodesic Sensor Nets (Electrical Geodesic Inc.).

4.3.2 Data coding and analysis

4.3.2.1 Motor battery assessment

As I only used the Gross and Fine Motor scales of both the Mullen and VABS assessments, we were unable to compute a composite score. For the Mullen scale, this composite score would usually include gross and fine motor, visual receptive as well as language skills. For the VABS, this score would usually include social, communication, motor and daily living skills. As I had only used the Gross and Fine Motor scales, a raw score was computed for these domains (by summing the number of motor milestones infants were able to demonstrate during the testing session). This was calculated separately for the Mullen and the VABS scales.

4.3.2.2 Midline crossing reaching task

Reaching data was coded offline from video records. In order for a reach to be counted, infants had to either grasp the toy (with one or both hands) or to have brought one or both of their hands within a fist sized distance of the toy (the same criteria were used by Van Hof et al. (2002). Unimanual reaches across the midline and reaches across the midline (which formed part of a bimanual reach) were both counted as midline crossing

4.3.2.3 Tactile ERP task: analysis

The data from this task was analysed using a Monte Carlo simulation technique. The Monte Carlo method which we used here, based on one employed by Guthrie and Buchwald (1991) and Mooney (1997), estimates the average first order autocorrelation present in the real difference waveforms across the 700 ms following stimulus onset. Following this, the method produced 1000 datasets of randomly generated waveforms. Each simulated difference waveform had a mean and unit variance of zero at each time point, but the same level of autocorrelation as seen on average in the observed data. Each simulated dataset also had the same number of participants and time-samples as in the real data. We then applied two-tailed one-sample t-tests (vs. zero; alpha = .05, uncorrected) to the simulated waveforms at each time point, recording significant vs. non-significant outcomes. In each of the 1000 simulations the longest sequence of consecutive significant t-test outcomes was computed. The 95th percentile of that simulated distribution of “longest sequence lengths” was then used to determine a significant difference waveform in the real data; specifically, I noted any sequences of significant t-tests in my real data, which exceeded this 95th percentile value. This method thus avoids the difficulties associated with multiple comparisons and preserves the type 1 error rate at .05 for each difference waveform analysed.

4.3.3 Results

4.3.3.1 Midline crossing reaching task

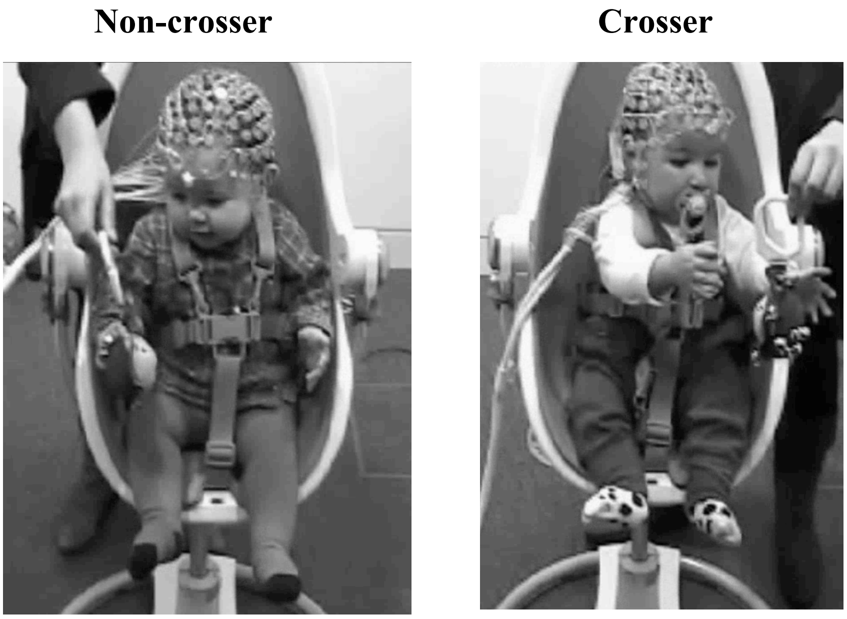
Infants were presented with a minimum of 9 reaching trials (3 trials in each of the reach locations) and a maximum of 18, and all made a reach response on virtually all of those trials. Eleven of the infants tested made no midline crossing reaches at all. The other 15 infants made at least 1 and a maximum of 7 midline crossing reaches. I thus divided the infants into "Crossers" and "Non-crossers" groups on the basis of whether they had made a single reach which crossed the midline during the reaching task (see Table 4.4 and Figure 4.6. below)

Table 4.4: Participant characteristics by reaching group

Group	n	Sex	Mean age (days)	Age range (days)
8-month-old Crossers	15	7f, 8m	258 (SD = 13.4)	243-279
8-month-old Non-crossers	11	8f, 3m	256 (SD = 13.3)	241-283

Infants in the two reaching groups (Crossers and Non-crossers) were compared on age, the number of reaching trials presented, number of reaches made and gross and fine motor abilities using the Mullen Scales of Early Learning and the Vineland Adaptive Behaviour Scale (VABS) (see

Table 4.5). Independent samples t-tests showed that the two groups did not differ on any of these measures (all ts <1, n.s, see Table 4.6).



Non-crosser **Crosser**

Figure 4.5: A "Crosser" and a "Non-crosser" 8-month-old showing distinctive reaches in the reaching task

Table 4.5: Reaching performance and motor ability scores in the 8-month-old infants across reaching group

Group	**Reaching task**				**Mullen motor scores**		**VABS motor scores**	
	Trials completed	*Reaches*	*Midline crosses*	*% midline crosses*	*Gross*	*Fine*	*Gross*	*Fine*
Crossers n = 15 (8m, 7f)	*M* = 10.6 *SD* = 2.2 *Range* = 6-12	*M* = 10.5 *SD* = 2.4 *Range* = 5-12	*M* = 2.2 *SD* = 1.7 *Range* = 1-7	*M* = 20 *SD* = 14 *Range* = 8-58	*M* = 12.5 *SD* = 1.2 *Range* = 7-15	*M* = 13.0 *SD* = 2.5 *Range* = 10-18	*M* = 15.6 *SD* = 3.7 *Range* = 7-24	*M* = 12.1 *SD* = 2.0 *Range* = 9-16
Non-crossers n = 11 (3m, 8f)	*M* = 11.4 *SD* = 1.8 *Range* = 6-12	*M* = 11.2 *SD* = 2.4 *Range* = 4-13	*M* = 0 *SD* = 0 *Range* = 0	*M* = 0 *SD* = 0 *Range* = 0	*M* = 13.1 *SD* = 1.9 *Range* = 11-15	*M* = 14.6 *SD* = 2.8 *Range* = 11-18	*M* = 15.6 *SD* = 4.5 *Range* = 12-24	*M* = 12.9 *SD* = 2.5 *Range* = 10-16

Table 4.6: Reaching performance and motor ability scores (means and t-test statistics) in the 8-month-old infants across reaching group

Variable	Means (SD)		t-test statistics			
	Crossers (n = 15)	*Non-crossers (n = 11)*	*t*	*df*	*p*	*d*
No. of midline crosses	2.2 (1.7)	.0 (.0)				
% of midline crosses	20.0 (13.8)	.0 (.0)				
Age (days)	257.9 (13.4)	255.7 (13.3)	.4	24	.4	.2
Trials presented	10.6 (2.2)	11.4 (1.8)	.93	24	.36	.4
Reaches made	10.5 (2.4)	11.2 (2.4)	.68	24	.50	.3
Mullen gross motor score	12.5 (1.2)	13.1 (1.9)	.47	24	.36	.5
Mullen fine motor score	13.0 (2.5)	14.6 (2.8)	.94	24	.16	.6
VABS gross motor score	15.6 (3.7)	15.6 (4.5)	0.0	24	1.0	0
VABS fine motor score	12.1 (2.0)	12.9 (2.5)	.79	24	.44	.4

4.3.3.2 ERP data analyses

The average number of ERP trials considered for analysis was 24 in the uncrossed-hands posture and 26 trials for the crossed-posture. In the Non-crossers group, the average number of trials used in the analyses were 26 in the uncrossed-hands posture and 27 in the crossed-hands posture. In the Crossers group, trial numbers were 22 and 25 respectively.

First, a grand average (see Chapter 2, section 2.5.6) of each experimental condition was used to plot topographic maps in the EEG software. From these, I was able to visually inspect the data and identify brain regions of interest. As expected (given that the study involved tactile sensations and the findings of Experiments 1 and 2 in Rigato et al., 2014), the somatosensory areas of C3 and C4 indicated hotspots of neural activity. After visual inspection of participants' individual averages (see Chapter 2, section 2.5.6), I found similar neural activity occurring in electrodes 104, 105, 110 and 111 in the right hemisphere and then looked at the symmetrically matched electrodes in the left hemisphere. These electrodes (29, 30, 35 and 36) in the left hemisphere elicited similar neuronal activity to each other and also similar activity to that seen in the right hemisphere electrodes.

A sample-point by sample-point analysis (the Monte Carlo simulation method described earlier) was carried out on the data for 700 ms following stimulus onset, investigating the presence of reliable postural modulations of SEPs for the Crossers and Non-crossers groups.

The mean first order autocorrelation at lag 1 (estimated from the data, and used for our Monte Carlo simulations) was 0.99 for the contralateral and 0.99 for the ipsilateral dataset for the 'Crossers', and 0.99 for the contralateral and 0.99 for the ipsilateral dataset for the 'Non-crossers'.

I expected greater posture effects in the Crossers group (see Figure 3.5). The shaded area in Figure 3.5 indicates the interval during which the difference wave deviated significantly from zero, and thus reveals the onset of statistically reliable effects of posture on somatosensory processing.

For the 'Crossers' at contralateral sites, the effect of Posture started at 298 ms and was observed until 392 ms (a sequence of consecutive significant t-tests over 86 ms in length was deemed significant by our Monte Carlo simulation). No effects were observed for the 'Non-crossers'. In addition to this, no effects were found at the sites ipsilateral to the stimulated hand for both the groups of infants.

I then examined whether there was a greater effect of Posture between these two groups of infants. To do this, I computed a "posture effect", which was simply the difference in amplitude between the two posture conditions (i.e. uncrossed hands mean amplitude – crossed hands mean amplitude). I compared the "posture effect" (μV difference) for the Crossers and Non-crossers groups within the interval which was significant in the Crossers group (298-392 ms), no reliable differences between the Crossers (M = 4.35, SD = 4.42) and the Non-crossers (M = 2.68, SD = 7.02 were found [$\underline{t}$(24) = .75, n.s.]. Furthermore, there was no significant correlation observed between the number of midline crosses and the posture effect in this SEP interval across all of the 8-month-olds [$\underline{r}$(26) = .19, n.s.].

In addition to these analyses, I also produced topographical plots[1] (see Figure 4.8) of the voltage distribution over the scalp in the Crossers. These maps are an average of the voltage distribution between 340 and 390 ms following a tactile stimulus. The topographical plots demonstrate that the effects of postural modulation arise from somatosensory areas of the brain. As the neural activity is focused around central areas, the observed modulations of activity cannot be the result of a posture related artifact.

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[1] Topographical plots of voltage distributions are only produced if statistically reliable effects are found

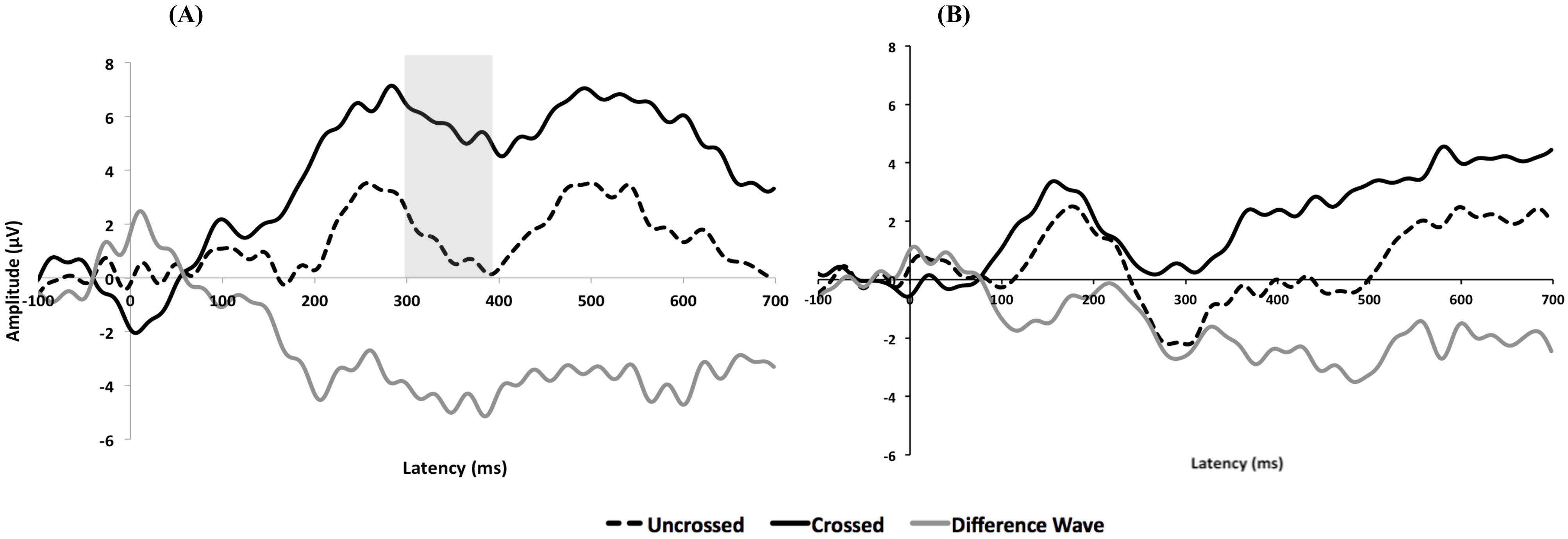


Figure 4.6: Grand averaged SEPs from central electrodes (C3, C4) contralateral (Panel A) and ipsilateral (Panel B) to the stimulated hand depicted for the Crossers group (n = 15) of 8-month-old infants. A posture effect difference waveform was obtained by subtracting the SEP waveform in crossed-hands posture from that in uncrossed-hands posture. The shaded area indicates the time course of reliable effects of posture on somatosensory processing. There was an effect of Posture in the Crossers, with this effect occurring between 298 and 392 ms.

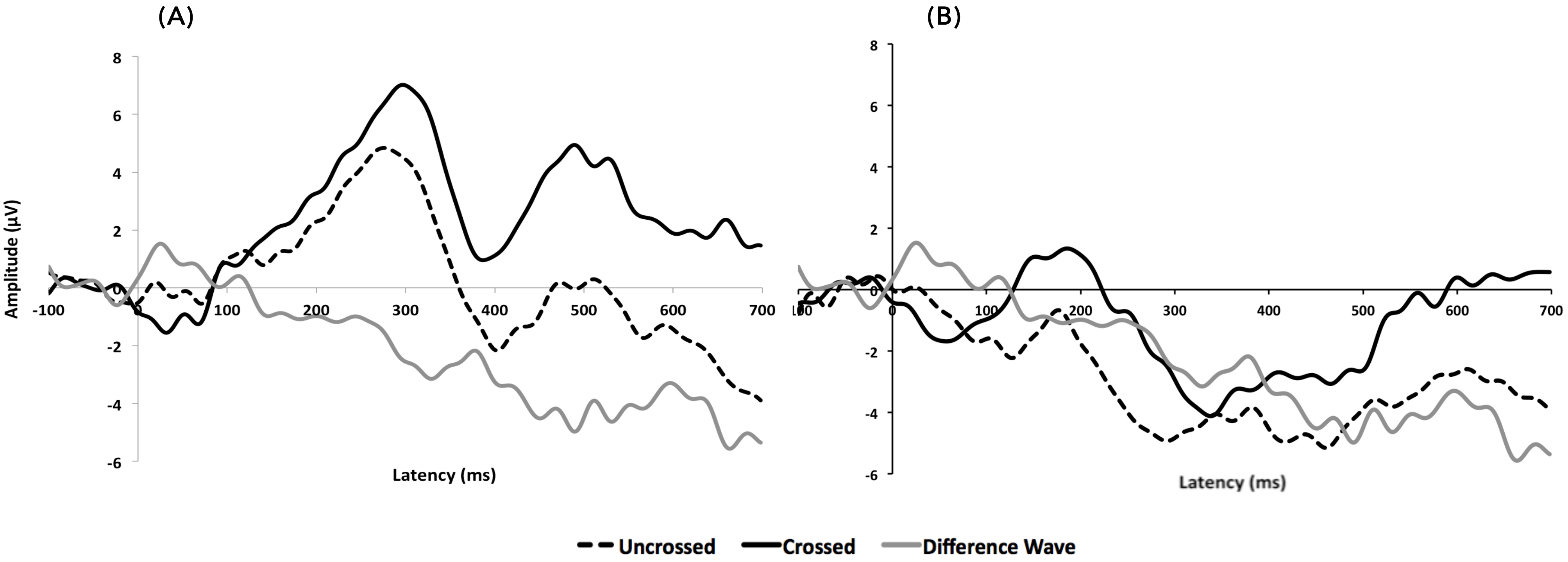


Figure 4.7: Grand averaged SEPs from central electrodes (C3, C4) contralateral (Panel A) and ipsilateral (Panel B) to the stimulated hand depicted for the Non-crossers (*n* = 11) group of 8-month-old infants. A posture effect difference waveform was obtained by subtracting the SEP waveform in crossed-hands posture from that in uncrossed-hands posture. There was no effect of Posture in the Non-crossers.

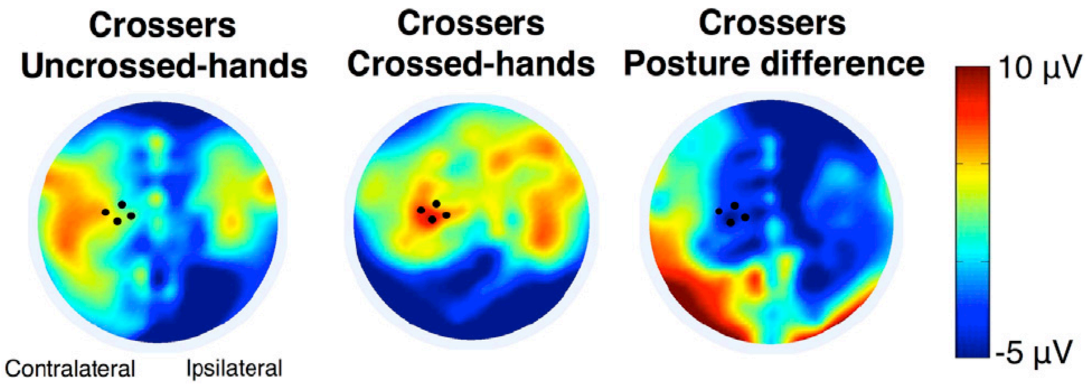


Figure 4.8: Topographical representations of the voltage distribution over the scalp in the Crossers from 340-390 ms following the tactile stimulus on trials in which the left hand was stimulated (contralateral effects are on the right of the maps). The map on the far right shows the effect of posture (Uncrossed – Crossed) over contralateral (right hemisphere) somatosensory sites. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

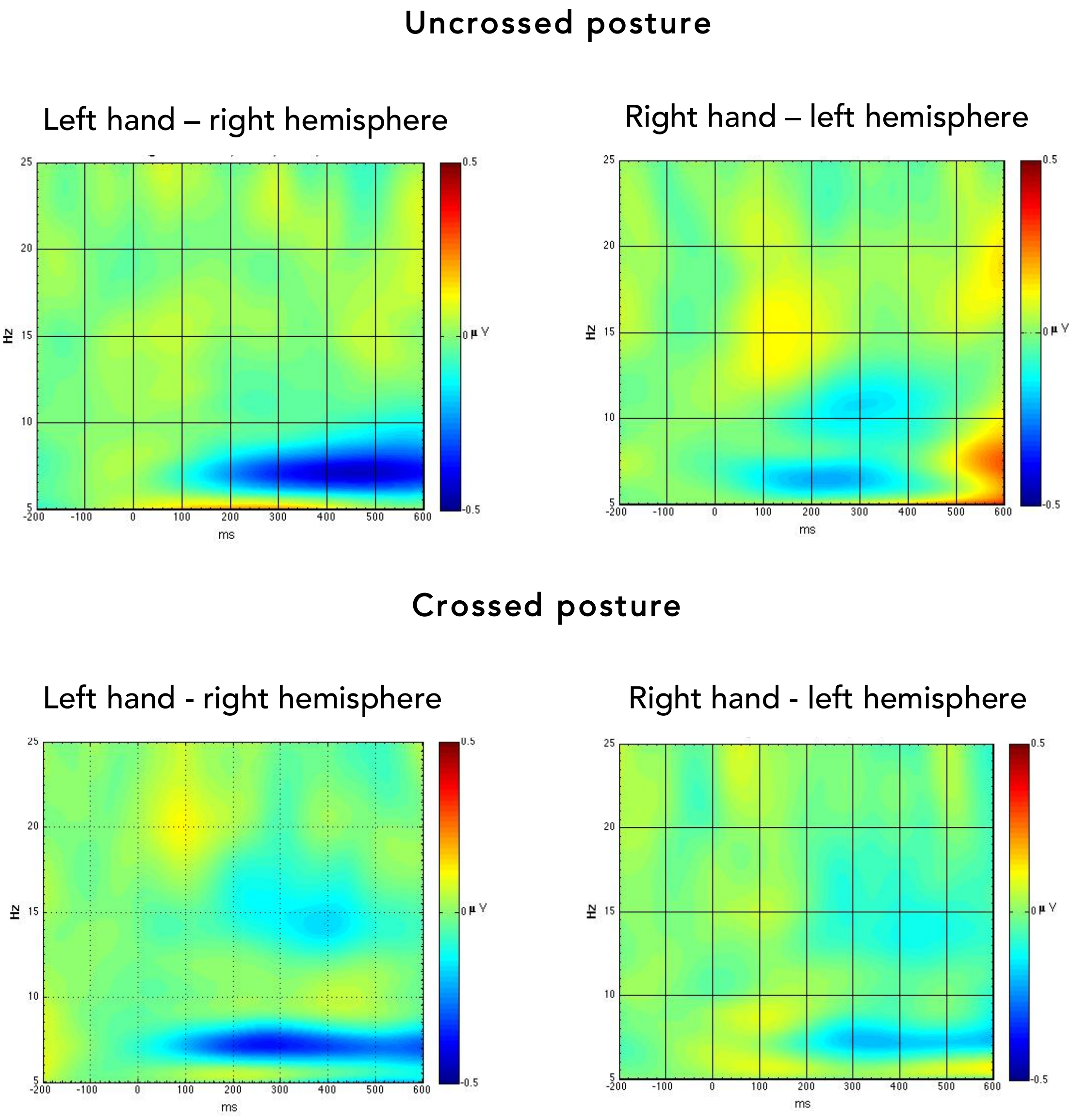
4.3.3.3 Time frequency analysis

A potential explanation for the posture effects on somatosensory processing observed in the Crossers group could be that movement artefacts are driving the difference in the Posture condition. It is possible that those infants who displayed more sophisticated reaching behaviours (the Crossers) may have been more resistant to arm crossing, resulting in greater movements which could themselves have influenced the SEPs I measured. To address this criticism, I conducted a series of analyses that examined alpha wave desynchronisation in the infants' EEG. Alpha waves rapidly decrease when movements are performed. Therefore, if there is no evidence of alpha wave desynchronisation within the EEG data, it would provide evidence against the criticism that any differences in ERP waveforms between posture conditions was the result of movement artifacts.

The time-frequency analyses were performed for the group of 8-month-old infants in which we observed an effect of Posture (i.e the ‘crossers’). These analyses were performed by wavelet transforms using Morlet wavelets at 1 Hz intervals in the 5 to 25 Hz range, and average wavelet coefficients within infants were calculated by taking the mean across trials. For each 1600 ms segment, the first and last 400 ms was removed to eliminate noise resulting from the wavelet transform, and the reported segment lengths reflect length after this truncation, i.e. 200 ms before until 600 ms after stimulus onset (800 ms). Artifact-free data were baseline-corrected to the average amplitude of the 200 ms interval preceding stimulus onset, and re-referenced to the average potential over the scalp.

I selected the same clusters of electrodes as used in the ERP analyses described above. Changes in amplitude between the crossed and uncrossed posture within the hemisphere contralateral to the stimulated hand were calculated within a frequency range between 6 and 9 Hz to encompass the reported lower end of the infancy alpha range and as suggested in previous studies (Stroganova & Orekhova, 2007). As significant effects of posture on somatosensory processing were only found at contralateral sites and only in the Crossers group, this hemisphere and group only were considered for analyses. The analyses revealed no difference in the alpha frequency band for the 8-month-old crossers: [t(14)

= .47, p = .65, M(contraUnx) = -.16; M(contraX) = -.14; see Figure 4.9 for time frequency plots].



Uncrossed posture

Left hand – right hemisphere

Right hand – left hemisphere

Crossed posture

Left hand - right hemisphere

Right hand - left hemisphere

Figure 4.9: Time-frequency plots of alpha levels across Posture and Hemisphere in the group of 8-month-olds 'Crossers'. I found no significant difference in alpha levels across the uncrossed or crossed-hands posture.

4.3.4 Discussion

From the findings of this study, it seems that posture modulates somatosensory processing in 8-month-olds who have a tendency to cross their hands over (into the contralateral side of space) when engaged in a prior reaching task. Conversely, in a group of virtually identical infants (in age and motor ability), but who did not engage in midline crossing reaching behaviours, there was no modulatory effect of posture on somatosensory processing. This pattern of findings is certainly consistent with a role for sensorimotor experience in the development of somatosensory remapping. However, as there was no interaction effect of reaching group and posture it is not possible to conclude that midline crossing experience was related to postural modulations of somatosensory processing. Indeed, there may be other factors that influence somatosensory remapping in 8-month-old infants. Here, I discuss potential explanations for these findings and alternative hypotheses.

This study investigated the relationship between reaching across the midline and the somatosensory remapping of tactile stimuli to the hands across different postures in the infant brain. I looked at two groups of 8-month-old infants who were virtually identical in age and motor ability. However, these infants differed in their ability to engage in reaching across the midline in a specific experimental reaching task. It was found that only those infants who produced at least one reach into the contralateral side of space that demonstrated somatosensory remapping (i.e. showed a greater neural response to having their arms crossed over than when they were uncrossed, illustrating that they were able to distinguish between these two arm posture and represent them accordingly). I found that the difference in amplitude between postures was not significantly larger in the Crossers than the Non-crossers. Thus, it is difficult to conclude that midline crossing is related to somatosensory remapping abilities.

Further to this, I also found that 8-month-old crossers demonstrated somatosensory remapping somewhat later than 10-month-old infants. The posture effect in the Crossers group occurred from 298 ms, markedly later than the effect observed by Rigato et al. (2014) in their study with 10-month-olds, who found differences in posture observed as early as at 58 ms. This demonstrates that in younger age groups, posture affects remapping at later stages of somatosensory processing, compared to earlier stages of processing in older infants.

Another potential explanation for this later effect in younger infants is that more brain areas are recruited, beyond the somatosensory cortex and SII (Pihko & Lauronen, 2004; Pihko, Laurenon, Wikström, Parkkonen & Okada, 2005). This can be seen in the topographical maps of the distribution of neural activity and may well be related to the greater time and processing required for 8-month-olds (in comparison to 10-month-old infants) to remap somatosensory stimuli across changes in posture.

Although the modulatory effect of posture was only found in the group of Crossers, there was no statistically significant difference between reaching groups. Therefore, whilst midline crossing may be involved in some way, there are likely other possible factors that may also be related to somatosensory remapping. For example, it may be that between the ages of 6- and 8-months, there is an increase in both intra and inter-hemispheric connections in the brain, with particular emphasis on increased connections within the somatosensory network (see Nevalainen, Lauronen & Pihko, 2014). Additionally, the maturation of the corpus callosum may be of importance (Ballesteros et al., 1993; Teicher et al., 2004; Barkovich & Kjos, 1988).

This increase in neural connections could be a contributing factor to, not only the somatosensory remapping process, but may also be involved in the range of motoric and limb movements and postures the developing infant is capable of adopting. Though, of course, this explanation is not necessarily independent of sensorimotor experience explanations as it is entirely possible that experience could be driving the development of these connections.

In terms of the midline crossing reach task itself, one could argue that perhaps this was not a sensitive enough measure that truly reflects infant's contralateral reaching capabilities. Perhaps infants were not given enough trials to showcase their midline crossing behaviours. Although this is possible, I presented infants with 12 trials that could potentially involve reaching across themselves for the attractive toy and this seemed the maximum number of trials that infants were happy to take part in, thus I feel this was an adequate number of trials for infants to take part in.

Ultimately, whilst this study was unable to support the hypothesis that midline crossing reaching is related to somatosensory remapping in infants, it has demonstrated that infants as young as 8 months of age are able to remap somatosensory information across changes in limb posture. Furthermore, I have ruled out an explanation in terms of a motor artefact resulting from posture manipulation. In order to disentangle the specific role of sensorimotor experience (considering that an association between midline crossing and somatosensory remapping cannot tell us about the direction of the developmental cause), a training or intervention study must be conducted.

4.4 Experiment 5: Effects of sensorimotor training on somatosensory remapping in infants

The previous experiment (Experiment 4b) demonstrated that, in a group of 8-month-old infants, (who engaged in reaching behaviours that involved reaching into the contralateral side of space), posture modulated somatosensory processing. In comparison, a separate group of 8-month-olds (who were identical in age and motor ability) did not show modulatory effects of posture. The findings from Experiment 4b were consistent with an (albeit tentative) association between midline crossing and somatosensory remapping. However, it is difficult to state the exact role of this sophisticated reaching behaviour on somatosensory remapping and the causal direction of this relationship.

One way to address this is to examine the causal relationship between midline crossing reaching and somatosensory remapping in the infant brain by conducting a motor training study in which infants reaching behaviour is manipulated. Specifically, if infants were trained on a contralateral reaching task, would this then drive the emergence of somatosensory remapping in the brain?

Below I discuss a select few infant studies that used a motor training paradigm. Although none of these studies relate to somatosensory remapping or even sensorimotor outcomes, the methodology employed for these studies can be particularly insightful.

Sommerville, Woodward and Needham (2005) conducted a study investigating infant's perceptions of their own actions versus other's actions. In this particular study, the training protocol took place within the lab over one session. Initially, 3-month-old infants interacted with a number of toys for 3 minutes. Following this, the researchers placed 'sticky mittens' (scratch mittens with Velcro that adhered to objects, allowing infants to 'pick up' these objects) on infants' hands and allowed them to play with specific objects for 200 seconds. Finally, a habituation task tested infant's transfer of knowledge from active experience to visually observed objects. This was a fairly short training session (approximately 3 minutes of active training during the sticky mittens reaching task). However, this was a sufficient amount of time to yield significant differences in looking time at an unexpected visually observed event (such as a new toy being the focal point of a reaching action) between motor training groups. It was found that, in this post-training task, those infants who had received sticky mittens training looked significantly longer at the unexpected action compared to control participants that did not take part in the sticky mittens task.

An advantage of this short training period allowed researchers to conduct the training protocol themselves and thus, was more controlled across participants. This also ameliorated participant attrition. However, a limitation (that is particular to the study I conduct) is that of whether the training needs to be carried out for multiple sessions to have an effect on the neural process under investigation.

Other behavioural studies have used longer periods of training. For example, Rovee and Fagen (1976) conducted the motor training (in which infants were trained to produce a leg movement) within the infant's home over a three-day period. In this study, 3-month-old infants' kicking (in their cot) behaviour was rewarded by the movement of a mobile that was connected to their feet. As such, kicking behaviour was trained using operant learning. Each training session lasted for 9 minutes a day. Within this three-day period, infants quickly learnt that the more they kicked, the longer the mobile chimed and moved; with kicking behaviour and attentiveness increasing with each successive training session. The researchers were successful in conditioning the infants' kicking behaviour and the study demonstrated that infants at 3 months of age, even with a 24-hour retention period, were able to distinguish between a novel and familiar reward for said kicking behaviour.

The above studies have shown that short periods of training, whether that it is one session or over a number of days, can successfully alter an infant's behaviour. In terms of motor training studies with older infants, Libertus and Needham (2010) investigated how active and passive reaching experience related to visual and manual exploration of objects and people performing actions. Here, infants aged 7 months of age wore sticky mittens and were trained to reach for, and manipulate, small toys. When the infant's mitten(s) made contact with the toy, the toy became attached to the velcro and the infant was able to haptically explore the toy for 10 seconds, before the toy was removed. This sequence of events occurred a number of times within a ten minute training period.

The training protocol was carried out at home (by the caregiver) for ten minutes every day for a two-week period. After two weeks of reaching training had been completed, the infant returned to the lab and carried out post-training tasks. A separate group of infants took part in a passive training session in which they viewed their caregivers manipulating the objects. It was found that only those infants that actively took part in the motor training sessions demonstrated an increased manual and visual exploration of the objects following the final training session.

All of the above studies have successfully carried out motor training paradigms with infants in the first year of life. The most useful component of this literature relates to the duration of motor training infants received. Considering that, for the current study, infants would take part in an at-home training protocol (in which infants would be trained to reach into the contralateral side of space), it was possible to maximise the amount of training infants could receive. If the current study used an in the lab training session design, the number of training sessions would be restricted as parents would be required to come in several times within a two week period, which would be time consuming (for both parents and the researcher). As such, at home motor training would be more suitable for this study and infants would be exposed to the training for a longer period. I decided to use the same duration of motor training as Libertus and Needham (2010); a period of two weeks.

In summary, the current study investigated the sensorimotor drivers of somatosensory remapping. A group of 6-month-old infants received at home motor training, which involved training to reach into the contralateral side of space for a period of two weeks. It was expected that this contralateral reaching training would drive somatosensory remapping of touch in the infant brain.

4.4.1 Methods

4.4.1.1 Participants

Twelve 6-month-old infants (8 males) aged between 181 and 196 days (*M*= 191 days; *SD*= 4.14 days) took part in Experiment 5. An additional three infants were excluded from the analyses because of fussy behaviour (1 participant) and failure to return for the second visit (2 participants). It was decided that 6-month-olds would be the ideal age group to use in this study due to the fact that evidence has shown that at this age, infants are not remapping tactile stimuli to the hands (Rigato et al., 2014). Additionally, it is at this age that midline crossing reaching behaviours become more frequent (Van Hof et al., 2002).

4.4.1.2 Stimuli and procedure

In this study, I looked at the causal effects of motor training (specifically across the midline reaching training) on somatosensory remapping of tactile stimuli across changes in arm posture. To do this, 6-month-old infants were required to take part in a number of tasks. For example, to gauge measures of motor and reaching ability, infants took part in motor assessments and a midline crossing task before and after motor training. Additionally, to measure somatosensory remapping, infants' brain responses to tactile stimuli on the palms of their hands (across changes in arm posture) were recorded. I discuss these tasks in more detail below.

The stimuli and procedure for this experiment are largely similar to the two experiments described earlier in the chapter, apart from a few minor changes. As such, I will provide a full and detailed description of all tasks. All of the following tasks were carried out with the infant both before and after the two week motor training period (conducted at home with their caregiver).

4.4.1.3 Midline crossing task

As in Experiments 4a and 4b, I measured the extent to which infants crossed their hands across the body midline using a reaching task. This task was carried out, just as described in Experiment 4b. However, I decided to limit reaching trials to a maximum of 12 (4 per location at the right and left shoulders and at the infant's midline), so as to maximise the number of trials infants would be able to complete in the tactile localisation ERP task. Previously, I had found that more trials conducted in the reaching task would negatively impact the time (and the number of trials) infants would take part in during the tactile localisation ERP task.

4.4.1.4 Tactile EEG task

This followed the same procedure as in Experiments 4a and 4b. However, I provide a full description of this task below.

With the infant seated on a parent's lap, the researcher placed the tactors in the infant's palms. Instead of using solenoid tactors (as in Experiment 4a), I used custom in-house built vibrotactile stimulators. These tactors were driven by a 200 Hz Sine wave for 200 ms per stimulation. The tactors were secured with an adjustable strap and covered with scratch mittens.

Experimenter A, who was blind to the side of stimulus presentation, held the infant by each wrist and bounced his or her hands three times while saying "One, two, three, woo!". On reaching "woo!", Experimenter A held the infant's attention with an engaging facial expression and direct gaze, and at the same time placed and held the infant's hands into the appropriate posture (crossed-hands or uncrossed-hands), approximately 10 cm apart, one on either side of the midline. At this point, Experimenter B triggered the presentation of a trial (a sequence of four tactile stimuli, each stimulus lasting 200 ms with an interstimulus interval varying randomly between 800 and 1400 ms). Between every trial the posture of the baby's arms was changed (the starting posture was counterbalanced between participants).

If the infant became fussy, they were entertained with musical toys and/or bubbles until they were settled enough to continue with the study.

When the babies became too fussy to continue with the study (e.g. crying and/or moving excessively), the study was terminated. Throughout this task, infant's brain activity was recorded using the 128 electrode Hydrocel Geodesic Sensor Nets (Electrical Geodesic Inc.).

4.4.1.5 Motor assessments

As in Experiment 4b, I used the Gross and Fine motor scales from the Mullen Scales of Early Learning (current edition; 1995) and the VABS (current edition, 1984). Additionally, I also created a Motor Milestones questionnaire (see Appendix H), which I will detail below.

This is a questionnaire that is carried out within the testing session and incorporates both parent report measures and behaviours that can be observed within the lab setting. Unlike the Mullen and the VABS, the Motor Milestones Questionnaire (see Appendix H) focused on behaviours specifically for infants aged 0-8 months (e.g., onset of sitting unaided, adopting a crawling posture and so on).

4.4.2 Motor training

Participants took part in a contralateral reaching training protocol. This took place at home with the primary caregiver, and parents were instructed to carry out the reaching training protocol, with the custom training toys, for ten minutes every day over a period of two weeks (14 days).

The custom training toys are comprised of a green bean bag with bells and a purple rubber ball that flashes when contacted. These toys are fixed a yellow wooden board, 15 cm apart (see Figure 4.10).

The parents were instructed to conduct the reaching training protocol as follows: all babies should be seated on the parent's lap, with the custom toys that were fixed to a board (see Figure 4.10) across the infant's legs. Following this, the parent should take hold of both hands. Whilst keeping one hand steady and away from the toys, the parent should moved the other hand into the contralateral side of space and place this hand on the toy (e.g. holding both hands and then moving the right hand onto the toy in the left side of space). If the infant withdrew their hand from the contralateral toy, then the parent was instructed to place the hand back on that toy again, up until ~60 seconds had elapsed since the first contralateral placement. This ~60 second training event should have been repeated 6 times, each time alternating between the left and right hand. Thus, parents were instructed to allow the infant a total manual exploration time of ~6 minutes.

Piloting indicated that when infants are presented with two toys side by side (either side of the midline), then this tends to elicit bimanual reaching behaviours to each toy in turn (and thus, midline crossing). Thus, as I was aiming to encourage midline crossing, following this training session, the infants were permitted to engage in a 'free play' session where they are able to play with the toys in any way they liked for up to 4 minutes.

Parents were asked to follow this protocol for fourteen consecutive days. In order to keep track of the number of sessions infants took part in, parents were required to complete a diary (see Appendix J) of their daily training sessions, writing down the start and end times of the training and the infant's general enthusiasm for the game. Following this two week period, the infants and parents were then invited back into the lab, for their post-training assessments (the same tasks they completed in the pre-training visit to the lab). Due to infant and/or parent sickness, only 7 infants returned to the lab after 14 days, whilst 5 returned to the lab after 21 days (M = 17.41, SD = 4.42 days).

Figure 4.10: Custom toys used in the motor training task of Experiment 5. A green bean bag with bells and a spiky rubber ball (that flashed with different colours when handled) were fixed to a wooden board, 15 cm apart.

4.4.3 Results

4.4.3.1 Motor assessments

Infants' scores on the Mullen, VABS and Motor Milestones scales were compared across sessions and, as expected (given that the infants would have developed certain motor skills within the two week period, regardless of the motor training) the infants showed a significant improvement in motor ability between the two testing sessions (see Table 4.7)

4.4.3.2 Midline crossing reaching task

Infants were presented with a maximum of 12 reaching trials (4 trials in each location) and all made a reach response on virtually all of those trials (Table 4.8 shows only reaches that could potentially elicit a midline crossing reach i.e. only those trials where the toy was presented at the infant's left and right shoulders and not at their midline). In both testing sessions (pre- and post-training), there was no difference in the number of reaches made by the infants, or indeed the number of reaches involving crossing the midline (see Table 4.8).

Table 4.7: Reaching performance and motor ability scores in the 6-month-old infants before and after motor training

Session	**Reaching task**				**Mullen motor scores**		**VABS motor scores**		**Motor Milestones Score**
	Trials completed	*Reaches*	*Midline crosses*	*% midline crosses*	*Gross*	*Fine*	*Gross*	*Fine*	
Pre-training	*M* = 7.7 *SD* = 1.2 *Range* = 4-8	*M* = 7.6 *SD* = 1.4 *Range* = 3-8	*M* = 1.2 *SD* = 1.6 *Range* = 0-5	*M* = 14.7 *SD* = 20.5 *Range* = 0-63	*M* = 10.7 *SD* = 1.3 *Range* = 9-13	*M* = 12.3 *SD* = 2.1 *Range* = 9-17	*M* = 9.3 *SD* = 2.3 *Range* = 6-14	*M* = 11 *SD* = 1.7 *Range* = 9-14	*M* = 9.9 *SD* = 2.3 *Range* = 7-15
Post-training	*M* = 8 *SD* = 0 *Range* = 0	*M* = 8 *SD* = 0 *Range* = 0	*M* = 1.5 *SD* = 1.9 *Range* = 0-6	*M* = 18.8 *SD* = 24.7 *Range* = 0-75	*M* = 11.5 *SD* = .9 *Range* = 10-13	*M* = 13.9 *SD* = 1.6 *Range* = 12-17	*M* = 10.7 *SD* = 1.9 *Range* = 7-14	*M* = 12.2 *SD* = 1.6 *Range* = 10-14	*M* = 13.1 *SD* = 2.8 *Range* = 10-19

Table 4.8: Reaching performance and motor ability scores (means and t-test statistics) in the 6-month-old infants before and after motor training

Variable	**Means (SD)**		**t-test statistics**			
	Pre-training	*Post-training*	*t*	*df*	*p*	*d*
No. of midline crosses	1.2 (1.6)	1.5 (1.9)	.52	11	.6	.2
% of midline crosses	14.7 (20.5)	18.8 (24.7)	.01	11	.9	0
Age (days)	191.58 (4.1)	209 (4.9)				
Trials presented	7.7 (1.2)	8 (0)	1	11	.3	.4
Reaches made	7.6 (1.4)	8 (0)	1	11	.3	.4
Mullen gross motor score	10.7 (1.3)	11.5 (.9)	2.3	11	.04	.9
Mullen fine motor score	12.3 (2.1)	13.9 (1.6)	2.5	11	.03	1
VABS gross motor score	9.3 (2.3)	10.7 (1.9)	2.2	11	.04	.9
VABS fine motor score	11 (1.7)	12.2 (1.6)	2.2	11	.05	.9
Motor Milestones motor score	9.9 (2.3)	13.1 (2.8)	4.5	11	.001	1.9

4.4.3.3 Tactile ERP task findings

The average number of trials considered for analysis was 31 in the uncrossed-hands posture and 33 trials for the crossed-hands posture in the pre-training session. For the post-training session, the average number of trials was 35 and 36 for the uncrossed and crossed-hands postures respectively.

Given the findings from the previous study (Experiment 4b), I expected hotspots of somatosensory evoked activity in the C3/C4 area. However, in order to identify electrodes of interest, I visually inspected the individual averages of participants within each session (pre-training vs. post-training). I found similar activity occurring in electrodes 105, 111 and 112 in the right hemisphere. I then looked at the symmetrically matched electrodes in the left hemisphere (electrodes 29, 30 and 13). These electrodes showed similar neural activity to those electrodes in the right hemisphere. This was the same method I used for the ERP data collected in the post-training session. As these same electrodes showed clear SEPs with the greatest amplitude, these were used for the post-training session analyses (see Figure 4.11 for grand averages of Posture conditions within each Session).

The Monte Carlo simulation method described in Experiment 4b above was conducted on this dataset (both contralateral and ipsilateral to the site of the tactile stimulus), looking at effects of Posture (uncrossed hands vs. crossed hands) and Session (pre vs. post training). No significant main effects or interaction effects of Posture and Session were found. As there were no reliable effects (of either Posture or Session), no further analyses were conducted and topographical plots of voltage distribution were not produced.

The above results show that contralateral reaching training did not affect somatosensory processing across hand posture in this group of 6-month-old infants. I discuss possible reasons for this in the following section.

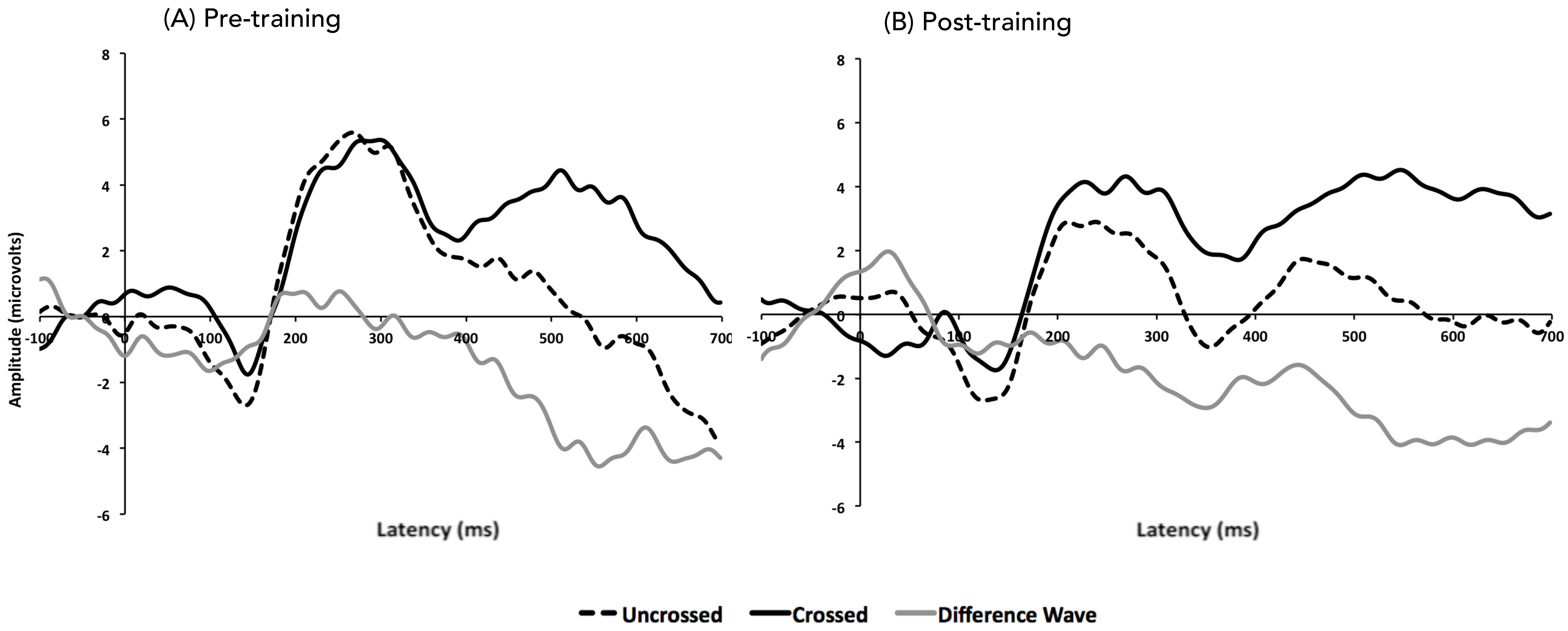


Figure 4.11: Figure 3.5: Grand averaged SEPs from central electrodes (C3, C4) contralateral to the stimulated hand depicted for 6-month-old infants across Sessions. A posture effect difference waveform was obtained in each group by subtracting the SEP waveform in crossed-hands posture from that in uncrossed-hands posture. There was no effect of Posture in either of the Sessions (pre-training vs. post-training) and no interactions effects of Posture and Session.

4.4.4 Discussion

In this study, I investigated a potential role for sensorimotor experience in the development of somatosensory remapping in 6-month-olds, specifically whether across the midline reaching behaviours contributed to somatosensory remapping. Previously, I have looked at the correlation between midline crossing reaching abilities and somatosensory remapping in 6- and 8-month-old infants (Experiment 4b), but here I investigated the causal relationship via a motor training protocol. Ultimately, I did not find a relationship between midline crossing reaching and somatosensory remapping in 6-month-olds, in that training 6-month-olds to reach across the midline did not promote somatosensory remapping of touch in the brain. Next, I will discuss potential explanations for the lack of effect of the motor training and improvements to the study that may yield different findings.

There are a number of potential reasons the contralateral reaching training did not impact somatosensory remapping in 6-month-old infants, which I will outline and discuss below. One possibility could be that of the small sample size. Due to the nature of longitudinal designs, there was some attrition in my sample; I was unable to collect data from 3 of my participants on their second visit due to fussy behaviour (1 participant) and 2 participants not returning. This limited my sample to 12 infants. Generally, EEG data collected from infants contains a high degree of variance, both between and within babies (e.g., De Haan, 2007) and this is all the more evident (and impactful) in very small samples. Given the small sample of babies in this study (12 infants), it may be that any effects of the training may be obscured by the large variability in the data. Indeed, calculating the required number of participants revealed that I needed to test 76 infants (calculated with G*Power, using the observed effect size, alpha and power values) to observe a significant finding of somatosensory remapping following contralateral reaching training.

Another potential explanation could be the age of the infants. I decided to conduct this study with 6-month-olds previous research had found that infants of this age do not show effects of postural modulation of SEPs (Rigato et al., 2014) and are not remapping tactile stimuli (Bremner et al., 2008b) but do engage in reaches involving crossing the midline (Van Hof et al., 2002; Experiment 4b of this thesis). Therefore, 6 months seemed the most appropriate age of infants to undertake the motor training. Additionally, any differences between somatosensory remapping abilities before and after training would unequivocally be the result of this experimental manipulation and not simply a result of maturation of the brain. On the return visit to the lab (after the two week contralateral reaching training period), infants would be aged, on average, 6.75 months. This is very close to the age group tested by Rigato et al., (2014), infants aged 6.5-months. Considering that these 6.5-month-olds in Rigato et al., (2014) did not show evidence of somatosensory remapping across changes in arm posture, if the infants in the current were to demonstrate somatosensory remapping, it could be argued that the motor training was a causal driver of somatosensory remapping.

However, it may be that there exists some delicate interplay between this sophisticated reaching behaviour, somatosensory remapping and brain maturation. Perhaps there is a sensitive period, at which point the brain is mature enough, and the infants are particularly receptive to the reaching training. Indeed, as Experiment 4b found that a subset of 8-month-olds who did not engage in across the midline reaches and did not show neural remapping of touch, it may have been useful to include a sample of 8-month-olds. Additionally, comparing the two age groups on midline crossing frequency and somatosensory remapping (pre and post motor training) may have yielded interesting findings regarding the developmental trajectory of somatosensory remapping.

A further possibility could be that the time frame for the motor training maybe be either too short or too long, so that I was missing the crucial period when the midline crossing reaching training was most influential. However, several of the motor training studies described in Section 4.4.1 of this chapter used much shorter training periods of an in the lab training session, where the infant was tested on post-training tasks either straight away (Sommerville et al., 2005 or after a period of 3 days (Rovee & Fagen, 1976). This did not seem to be an issue for Libertus & Needham (2010), who conducted a study in which infants received at home motor training over fourteen days. However, this study involved a behavioural post-training task. It may be that for EEG post training tasks, more exposure to the training protocol is necessary. To truly affect the underlying neural mechanisms of somatosensory remapping, perhaps the infant needs to be able to perform midline crossing reaching not only within this particular behavioural task at post-training test, but also within their everyday reaching behaviour (e.g., when reaching for food, toys and/or people in their immediate environment).

In the current study, infants returning at the two-week mark were a particular problem. Whilst I always endeavoured to do this, due to illness (on the part of either the parent or the child) five of the infants returned to the lab for their second visits three weeks after the initial session. Therefore, as they would not have carried on the motor training at home for that third week, any potential effects may have been diminished by the time of their return to the lab. For any future studies using this paradigm, a possible solution for this would be to instruct parents to carry on the motor training until the day of their second visit and compare these infants separately from those that completed two weeks of training.

Another potential explanation for the non-significant effect of the motor training lies in the training task itself. As I wanted to maximise the number of times infants crossed their midline to manipulate a toy, I asked parents to hold their infant's arms and guide their reaching behaviour. However, it may be that to truly affect somatosensory remapping, infants must engage in active reaching across the midline (whereas this task involved passive reaching). So, for any further studies, I would use a task that elicits spontaneous reaches across the midline guided by the infant, as opposed to the caregiver. A potential example could be in the form of grasping a toy moving in the contralateral side of space (whilst the caregiver restricts movement of the ipsilateral hand).

Another possible training activity I could introduce is one that includes the ‘sticky mittens’ (as described in Section 4.4.1 of this chapter). Using sticky mittens would allow infants to manipulate the objects they had reached for (as said object would stick to the infant’s mitten clad hand). Manipulation of the object may encourage infants to initiate reaches as retrieval of the toy could be viewed as a ‘reward’.

Parents could then remove the toy and place it back, eliciting further reaching attempts from the infants. It may be that these change would encourage infants to continue playing with the toys and completing the reaching training protocol.

In summary, the current study did not find significant effects of posture either before, or after, motor training. Additionally, motor (contralateral reaching) training did not appear to influence somatosensory remapping. The current study was informative in the potential issues that are linked with conducting a motor training study like this. If I were to further explore the causal relationship between midline crossing reaching and the somatosensory remapping of touch, there are a number of changes that I would enact which have been described above.

Experiment 4b has been published in the following article:

Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A. J. (2014). The neural basis of somatosensory remapping develops in human infancy. *Current Biology*, *24*(11), 1222-1226

Chapter 5

Perception of visual-tactile co-location in infancy

5.1 Visual-tactile co-location

In Chapters 3 and 4, I addressed the question of how infants and children map touches in external space. One of the main findings of the first series of experiments reported in Chapter 3, was that an ability to locate touches in external space appears to develop between 4 and 6 months after birth. It has now been established that visual experience in the first six months of life is necessary for the automatic external referencing of touch to emerge. Considering the role that vision plays in the development of an ability to locate touches in external space, a pertinent question concerns whether infants within the first half year of life become able to perceive touch and vision within the same space.

5.2 Experiment 6a: Visual-tactile co-location in 6-month-olds

Upon his/her arrival in the world, the human infant is bombarded with sensory stimuli. A question that has dominated developmental research, in various forms, has asked exactly how the infant makes sense of this multitude of sensory inputs, learning to pair information from the same environmental events or objects together and which stimuli to delineate as separate events (e.g., Körding, Beierholm, Ma, Quartz, Tenenbaum & Shams, 2007 and Shams & Kim, 2010). From previous research it has been shown that young infants do not experience sensory information in isolation. To take an example which is pertinent to bodily perception, Bahrick and Watson (1985) conducted a series of experiments with 5 month old infants that demonstrated that infants of this age are able to detect discrepancies in the spatial and temporal characteristics of the seen and the felt position of their limbs. Further to this, Rochat and Morgan (1995) have demonstrated that infants as young as 3 months of age are also capable of detecting these discrepancies (although see Bremner & Cowie, 2013 for a critique of the methods used to explore visual-tactile correspondences in this series of studies).

In a tradition spanning back to Molyneux and Locke over 300 years ago, it has been argued that, in early infancy, the sensory systems function independently and become integrated as the infant is exposed to different sensory stimuli occurring concurrently in everyday life. This is often referred to as the "Integration" view (Piaget, 1952; Birch & Lefford, 1963, 1967; Friedes, 1974). However a more recent argument has been that for many multisensory percepts integration is not necessary, and that young infants are able to detect multisensory invariants (e.g. equivalencies in sensory information such as duration, spatial location, texture, and intensity) via an amodal code (Gibson, 1969). This account has been referred to as the "differentiation" view and proposes that infants develop by learning to differentiate progressively more fine-grained aspects of multisensory stimulation.

There is an argument to be had that the differentiation account put forward by Gibson (1969; see also Bahrick & Lickliter, 2000, 2012) underestimates the complexity of perceiving crossmodal relationships (i.e. perceiving commonalities across sensory information). Even though the task of detecting crossmodal spatial and temporal relations might seem facile to the average human adult, this need not be the case in early life (Bremner & Cowie, 2013; Bremner et al., 2008). As discussed in Chapters 1 and 4, the task of keeping track of the location of touch in the visual field is complicated by the necessity of keeping track of where the limbs are across changes in posture.

Nonetheless, research has shown that infants learn about a range of crossmodal relationships quite early in the first year of life. For example, it has been found that 2-month-old infants are able to detect correspondences between auditory and visual information (loudness matched with brightness; Bahrick, 1992; Bahrick & Lickliter, 2002; Lewkowicz, 1996; Lewkowicz, 2000; Lewkowicz & Turkewitz, 1980; Spelke, 1979). Research investigating the perception of audio-visual spatial relations has shown that even newborns have the ability to orient to auditory sounds. When an auditory stimulus was presented, infants turned their heads towards or away from the location of the sound in space (Butterworth & Castillo, 1976; Wertheimer, 1961; Clifton, Morrongiello, Kulig, & Dowd, 1981; Muir & Field, 1979).

Also, it must be noted that age related differences in detecting crossmodal correspondences exist in the data; with younger infants/children abilities quite rudimentary and immature compared with older infants and children's (e.g. Fenwick & Morrongiello, 1998; Neil et al., 2006). For example, Fenwick and Morrongiello (1998) found that when 4-month-old infants were able to form paired associations between an object and a sound when the two stimuli were not precisely co-located in space. However, this was not the case for the 6-month-olds in this study. In this age group, in order to form an association between a visual and an auditory stimulus, those stimuli needed to be in the same spatial location.

Compared to the multitude of studies investigating audio-visual interactions, there has been very little research conducted on visual-tactile representations. One way in which researchers have tackled the question of whether children, infants and indeed newborns can make links between vision and touch is via crossmodal transfer tasks (Sann & Streri, 2007; Streri & Gentaz, 2003, 2004; Gottfried, Rose & Bridger, 1977; Maurer, Stager & Mondloch, 1999; Streri, 2003; reviewed in Bremner et al., 2012, and Streri, 2012). In crossmodal transfer paradigms, infants haptically explore an object until habituation occurs (the frequency with which they let go of the object increases to a criterion). Following habituation, the infant is visually presented with the familiar and a novel object, with researchers the extent to which the infants' visual preferences are influenced by novelty. Alternatively, infants can be presented with the visual object first, to which they are habituated. Following habituation, they are then presented with the physical object to explore haptically, with researchers examining the length of time they manually explore familiar and novel objects. This type of task yields a lot of information about representation of common properties across the senses (e.g., shape and texture), but little in terms of representing common locations of tactile and visual objects in peripersonal space.

So how would one go about tackling the research question at hand (do infants represent visual-tactile stimuli within a common spatial framework)? One suggestion is to use orienting paradigms, where infants are presented with tactile stimuli and their visual orienting behaviours are recorded. For example Bremner et al. (2008) used manual orienting measures to establish tactile localization abilities in infants in the first year of life. A particularly relevant observation to note from this study is the fact that it was not until 10 months of age that infants produced a visual orienting response (before a manual orienting response) to a tactile stimulus that was applied to the hands. In comparison, 6-month-olds infants produced much less visual orienting behaviours to the hand on which the tactile stimulus was applied.

In terms of the development of visual orienting to single touches on the body, this may also be indicative of the complex developmental changes that underpin the ability to map touches to the body in both tactile and *visual* space (which occurs in the second half year of life). In Chapter 1 (Section 1.2.2) of this thesis, I discussed research demonstrating that adult humans and primates are equipped with receptive fields that are sensitive to both visual and tactile incoming stimuli (e.g., Làdavas, 2002; Làdavas et al., 1998; Graziano, 1999; Graziano et al., 2000; Graziano & Gross, 1993, 1994; Graziano et al., 1994, 1995, 1997), which are continually updated so that limb position is taken into account in drawing visual and tactile receptive fields into spatial correspondence around the limb (e.g., Graziano et al., 1994, 1995, 1997). For adults, this computationally complex process seems effortless, however for the developing infant, there are also other factors to consider. For example, as the body of the infant grows, the spatial configuration of limbs within the body also change, which usually must be accounted for when locating touches both on the body and in space.

So why would this make it more difficult for the human infant to *visually* orient to a touch? A possible explanation could be that infants find it difficult to translate information from different sensory frames of reference within the spatial domain. Indeed, it may be that young infants require a concurrent (perhaps visual) stimulus to occur in order to aid them in determining the spatial frame of reference within which to locate a touch.

This was the line of investigation undertaken in a recent study in the Goldsmiths InfantLab by Freier, Mason and Bremner (in prep.). Here, the researchers presented concurrent visual and tactile stimuli to the hands of 6- and 10-month-old infants. These visual-tactile paired stimulations either occurred on the same hand (Congruent condition) or different hands (Incongruent condition) and the infants' preferential looking at their hands was recorded and coded. It was found that both age groups showed a preference for the incongruent display of visual-tactile stimuli, looking longer at their hands during this condition. From this, the researchers argued that infants from 6 months of age are able to detect spatial commonalities within the visual-tactile domain and are able to distinguish between co-located visual-tactile events and visual-tactile events that are disparate in space. Thus, infants within the first half year of life expect visual and tactile stimuli to occur in the same spatial location.

However, a criticism of Freier et al.'s study is that the 6- and 10-month-olds might simply have preferred to look at the incongruent presentations due to the larger spread of the stimuli in space (visual-tactile pairs were presented across two hands rather than within one). Therefore, before any further studies were run to investigate the onset of visual-tactile co-location (in 4- and 6-month-olds), I investigated this alternative interpretation.

Freier et al. (in prep.) had found a preference for events in which visual and tactile stimuli were not co-located, concluding that this preference was due to the infants' relative inexperience with spatially incongruent multisensory events. If this is the case then we would not expect infants' to prefer a control condition in which unisensory stimuli were presented across two hands.

The control condition involved either tactile or visual stimuli presented in one modality at a time, occurring on both hands simultaneously (and were as separated in space as the incongruent visual tactile stimuli). Infants' duration of looking time (at their hands) would then be compared with looking time durations in the data collected by Freier et al. (in prep). The crucial point is that if infants' looking was driven by a preference for the novelty of the spatially incongruent bimodal visual-tactile stimuluation then this control condition should show less looking than in the incongruent condition, as there is as no spatial incongruency in the control condition. I expected thus to observe that the preference for the incongruent trials over the congruent trials which was observed in Freier et al. (in preparation) should be maintained when the incongruent trials are compared with the unisensory control condition trials gathered and reported here.

5.3 Methods

5.3.1 Participants

Fourteen 6-month-olds (8 males), aged between 185 and 213 days (M = 198 days, SD = 8.79 days) took part in Experiment 6a. An additional two infants were excluded from the analyses due to equipment failures. Informed consent was obtained from the parents prior to commencement of the study. The testing took place only if the infant was awake and appeared to be in an alert and content state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London.

5.3.2 Design

Infants were presented with 10 stimulation events across both hands, in which pairs of visual flashes or vibrotactile stimuli were presented synchronously for 700 ms with a 1500 ms interstimulus interval. Each trial lasted for 20.5 seconds in total.

This study only included a control condition, with the aim to compare the results from this condition with the data collected by Freier et al. (in prep.) in which infants took part in the Congruent and Incongruent condition. The Congruent condition involved a visual and a tactile stimulus occurring synchronously in the same region of space (i.e. on the same hand), whilst the visual and tactile stimuli synchronously occurred in different regions of space (i.e. different hands) in the Incongruent condition (see Figure 5.1). These two conditions were not included in the current experiment, only the Control condition was included in Experiment 6a.

Thus, for the (only) Control trials in this study, one pair of stimuli from one modality (either visual or tactile) was presented to both hands (see Figure 5.2). Each trial consisted of 10 distinct events (of which pairs of visual or tactile stimuli were delivered to the hands). Infants looking duration at either hand was measured, this was irrespective of which hand received a visual stimulus or if a visual stimulus occurred in that trial at all.

To be included in the final analyses, participants had to complete one block of the Control condition (a total of 10 stimulations). Participants ultimately took part in a minimum of 4 trials, and maximum of 6 trials. The order of presentation (of whether infants received tactile or visual stimuli first to their hands) was counterbalanced across participants.

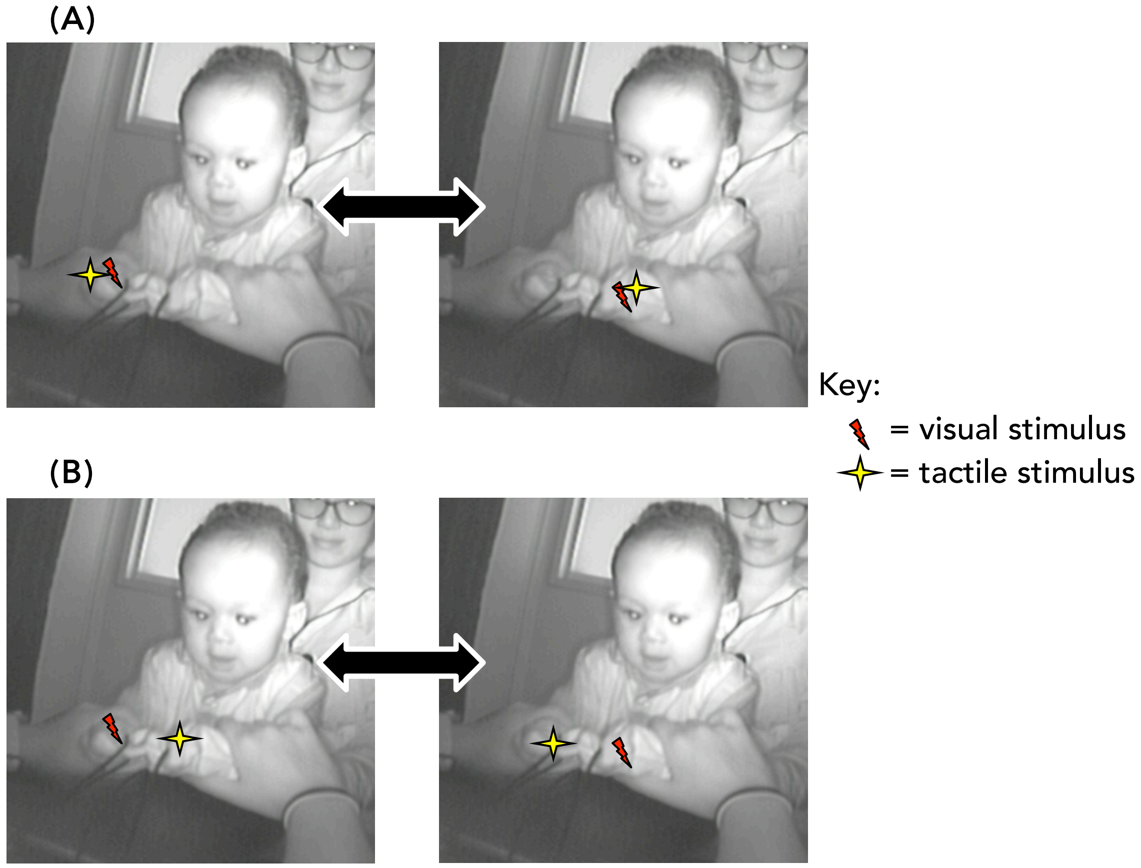


Figure 5.1: Pictures of experimental set up in Freier et al. (in prep.). Panel A depicts the Congruent condition in which infants received a visual and tactile stimulus to the same hand. Panel B depicts the Incongruent condition, in which infants received a visual stimulus to one hand and a tactile stimulus to the other. These conditions were not included for Experiment 6a.

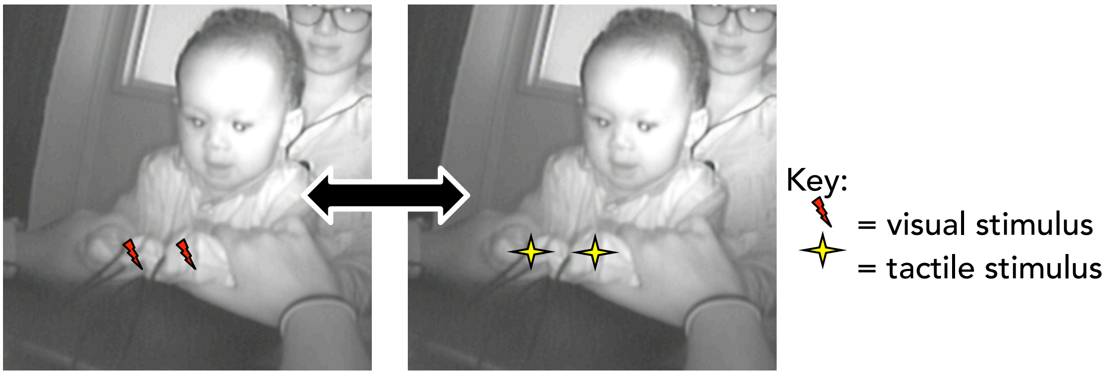


Figure 5.2: Pictures of experimental set up in which an infant has received a visual stimulus (flash of light) or a vibrotactile stimulus to the hands. The infant looks at their hands during, and following, stimulus presentation. Within each trial, pairs of stimuli (visual or tactile) were administered to the hands in 10 different synchronous events (each event was 700 ms in duration with an inter-event interval of 1500 ms). The trials were presented randomly.

5.3.3 Materials

Infants were seated on their parents lap in the dimly lit testing room. Following this, the tactors were positioned on the palms of their hands and secured with cohesive bandage before white cotton scratch mittens were placed over the hands. White LEDs had previously been sewn into the scratch mittens which were positioned so that the LEDs were placed on the top of the infant's hands. The scratch mitten was secured in place with a Velcro strap.

5.3.4 Procedure

On each trial, the experimenter held onto the infant's arms, keeping them approximately 10 cm apart, above a small table. The experimenter then engaged in a game of peek-a-boo with the infant, whilst keeping holding of the infants’ hands. The experimenter would use the infants’ hands to “hide” behind, which would direct infants’ gaze to the hands. After three "peek-a-boos", the experimenter would move out of sight, holding the infant’s hands and allowing their hands to rest on the small table. If the infant remained looking at their hands at this time, a second experimenter initiated a trial via the E-Prime script. If the infant was not looking at their hands, the second experimenter signaled (via an intercom) for the first experimenter to continue playing with the infant. Once again, this researcher would engage in a series of three peek-a-boos before ducking out of sight. The second experimenter would then initiate the trial when infants looked at their hands. Across all trials, two sets of three peek-a-boos at maximum were sufficient to direct the infant’s gaze to their hands.

In the time during a trial (a series of 10 paired stimulations lasting 20.5 seconds in total) the experimenter stayed out of sight and faced downwards to the floor and away from the infant, in order not to distract the infant. Once a trial had finished, the second experimenter signaled via intercom for the first experimenter to redirect the infant’s attention to their hands through a game of peek-a-boo. The study continued for up to six trials (60 paired stimulations), with participants completing a minimum of four trials (40 paired stimulations).

5.3.5 Data coding

The infants' looking behaviour to the visual and tactile stimuli was coded from the video records. The raters were provided with stimulus onset and offset information only. A second rater coded a proportion of the total trials across all participants, with inter-rater reliability at 89% [$\underline{r}(15) = .89$, $\underline{p} < .001$].

5.4 Results

As the participants in the former study (Freier et al., in prep.) managed to complete 2 trials of the Incongruent condition (20 stimulations), I decided that only 2 trials (so also 20 stimulations) from the current experiment would be analysed. These trials corresponded to the order of those in Freier et al. (in prep.). For example, if Trials 1 and 3 were summed in Freier et al. to compute an average of a condition, Trials 1 and 3 in the current study were summed to compute an average of the control condition.

With the aim to assess infants' looking behaviour in response to pairs of stimuli that were presented to two hands, an ANOVA was performed with Condition (Congruent/Incongruent/Control) as a factor, with the data from Freier et al. contributing to the Congruent and Incongruent conditions and the data from the current experiment contributing to the Control condition. Infant's durations of looking from 2 trials were summed to produce a total duration of looking time and then compared across condition.

The ANOVA showed a main effect of Condition [$\underline{F}(2, 22) = 6.89$, $\underline{p} = .005$, $\eta_{\underline{p}}^2 = .39$]. This main effect was investigated with two post-hoc comparisons. To correct for Type 1 error, the alpha value was Bonferroni corrected to $\underline{p} = .025$. A comparison looking at the duration of looking between the Control and Congruent conditions revealed no significant effect [$\underline{t}(11) = .08$, n.s]. However, a comparison between the Incongruent and the Control conditions found a significant difference [$\underline{t}(11) = 2.77$, $\underline{p} = .018$] with means indicating that infants looked at the Incongruent display much more than the Control display (see Figure 5.3).

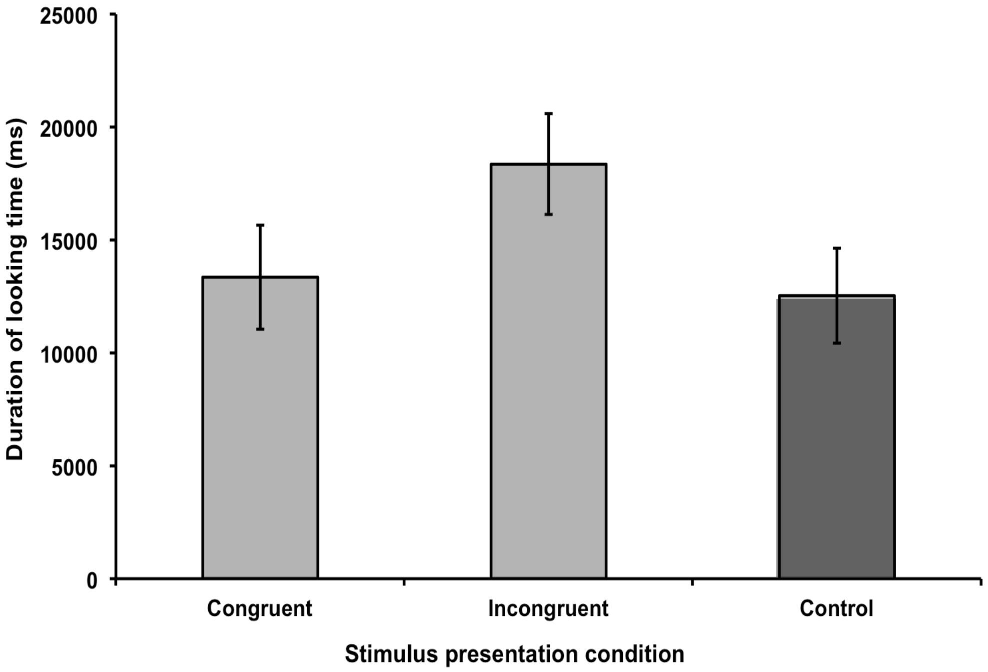


Figure 5.3: Mean looking duration (at the hands) of 6-month-olds across stimulus presentation conditions. Data in the "Control" condition (dark grey bar) were collected from a different set of infants than the data contributing to the "Congruent" and "Incongruent" conditions (light grey bars).

5.5 Discussion

The current study attempted to resolve a potential criticism of a previous experiment (conducted by Freier et al., in prep.) in which it was found that infants as young as 6 months of age were able to perceive visual and tactile information, to the body, within a common spatial location. A possible explanation for this ability (in that 6-month-old infants showed a visual preference for visual-tactile stimuli that occurred in different locations, as opposed to the same location); is that this preference could be the result of infants preferring to view stimuli that occupy a larger spatial distribution. In order to address this alternative explanation, I conducted a study in which 6-month-olds were presented with visual or tactile stimuli that occurred concurrently on both hands. Thus the stimuli shared the same spatial distribution but the stimuli were within one sensory modality, rather than crossmodal as in Freier et al. (in prep.).

Infants' looking behaviour in the current study (Experiment 6a) was compared to infants' looking duration in the study conducted by Freier et al. (in prep.). As predicted, it was found that the infants in the Control condition (Experiment 6a) looked significantly less at their hands than infants in the Incongruent condition in Freier et al. (in prep.). This indicates that that 6-month-old infants demonstrated a preference for stimuli occurring on the hands, not as a result of the spatial distribution of the stimuli, but rather the stimuli occurred concurrently in two sensory modalities. Thus, it seems the alternative explanation of the findings of Freier et al. (in prep.) does not account for the preference for incongruent over congruent stimulus presentations in their study.

Whilst the results from the current study illustrate that the infants were looking at the spatially separate visual or tactile display significantly less than the Incongruent condition in the study conducted by Freier et al., (in prep.), one could argue that it is not entirely correct to conduct these comparisons across different datasets in this way. There are several reasons for this, which I outline below.

The first concern is that different researchers implemented the Control condition to the Congruent and Incongruent conditions. This could potentially be an important limitation in this type of procedure in which behaviour differences between researchers could quite easily affect an infant's co-operation (e.g. how engaged they are with a study, how many trials they complete).

As we are comparing infant behaviour in one condition (a study run by myself) with that of a group of infants who took part in different conditions (conducted by Freier et al., in prep.), there may be systematic differences in researcher behaviour which could then impact infant's co-operation. For example, if a researcher played 'peek-a-boo' in a particularly engaging manner, this may reduce infants' looking at their hands and increase looking for the hidden researcher. This would not be a problem if the researcher tested infants in all conditions of the study, as this reduction in infants' looking at their hands would be reflected in all conditions. However, considering that different researchers conducted different conditions of the study, a direct comparison of these three conditions may not be entirely accurate. Additionally, this is a valid concern for this study in particular as infants were able to complete approximately 6 blocks of trials (60 stimulus pairs) in this study as opposed to an average of 2 blocks of trials (40 stimulus pairs) in Freier et al. (in prep). An increased rate of trial completion could indicate that infants in the Control condition (Experiment 6a) were more engaged with the task compared to the Congruent and Incongruent conditions (conducted by Freier et al., in prep.). However, this concern is alleviated somewhat as although participants in Experiment 6a took part in more trials, they still demonstrated significantly less looking at their hands than the infants in Freier et al. (in prep).

Secondly, a different set of infants took part in this study with only the control condition. Due to the high variability between infants, this was not ideal; although given the significant results, in the anticipated direction (much less looking in the Control condition compared to the Incongruent condition) this was not especially problematic. However, considering the different attrition rates between this study (2 participants excluded due to equipment errors out of 16 infants) and that of Freier et al., who reported a 37% participant exclusion rate due to infant fussiness, one could argue that the 6-month-olds who took part in this study may have been different in temperament, which could then impact on their attentiveness to the task.

A further criticism of the way the current study was run is the fact that different infants were exposed to the experimental conditions in different orders. As a result of this, a direct comparison of looking duration across conditions may not be entirely appropriate. In the study conducted by Freier et al. (in prep.), infants completed two different conditions in sequence; with the Congruent condition preceding the Incongruent condition (or vice versa). As such, the previous condition the infant had been presented with may well impact looking behaviour in the subsequent condition. It is possible for instance that the greater complexity inherent in alternating between conditions rather than presenting a single condition could have led to a greater looking in the incongruent condition conducted by Freier et al. (in prep.) compared to the control condition conducted in this experiment

Overall, there were several concerns with the design of this study. Thus, I decided that in order to tackle adequately the alternate explanations for the findings of Freier et al. (in prep.) and Experiment 6a, a further study was required which incorporated all three stimuli conditions (Congruent, Incongruent and Control); Experiment 6b.

5.6 Experiment 6b: Visual-tactile co-location in 4- and 6-month-olds

As discussed above, Experiment 6b was conducted in order to address potential alternative explanations for 6-month-old infants being able co-locate visual-tactile information on the body i.e. that this group of infants preferred to look at the Incongruent display as the stimuli were occurring on both hands. In addition to addressing these alternative hypotheses, I also included an additional age group of 4-month-olds. This was done to investigate whether infants younger than 6 months are able to co-locate vision and touch. The comparison between 4 and 6-month-old infants is particularly interesting a 4-month-olds infants are typically pre-reaching and will therefore have little active experience of picking up objects; and by extension, less experience than 6-month-olds of visual and tactile correspondences in their environments.

Pilot testing with the youngest age group indicated that 4-month-olds became fussy when they had their hands restricted. However they were much happier when the tactors and lights were placed on their feet. Therefore, the LEDs and the tactors were placed on the feet of infants in both age groups.

5.7 Method

5.7.1 Participants

Fifteen 4-month-olds (9 males), aged between 102 and 104 days (M = 120 days; SD = 14 days) took part in this study. One female participant was excluded from the final analyses due to equipment errors. The older age group included twelve 6-month-olds (5 male), aged between 182 and 231 days (M = 196 days; SD = 14 days). Informed consent was obtained from the parents before commencing the study. The testing took place only if the infant was awake and appeared to be in an alert and content state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London.

5.7.2 Design

Infants were presented with trials in which 10 pairs of stimulation were delivered sequentially across both feet. These 10 stimulus pairs comprised visual flashes and vibrotactile stimuli presented synchronously for 700 ms with 1500 ms interstimulus interval between each pair. Each trial containing 10 stimulus pairs thus lasted for 20.5 seconds in total.

There were three conditions: Congruent, Incongruent and Control. During Congruent trials, the visual and tactile stimuli were presented simultaneously on the same foot, thus they shared the same spatial location on the body. In comparison, for Incongruent trials, the visual and tactile stimuli were presented simultaneously on *different* feet (and did not share the same spatial location). Finally, for Control trials, one pair of stimuli from a single modality (either visual or tactile) were presented to both feet (see Figure 5.4). Each trial consisted of 10 distinct events (of which pairs of visual and/or tactile stimuli were delivered to the feet). The pairs of stimuli were presented in randomized sequences. Infant's overall looking behaviour (to the feet) was measured, so how long they spent looking at the feet in each experimental condition.

To be included in the final analyses, participants had to complete one block of each test condition (a total of 30 stimulations). The order of the three test conditions (Congruent / Incongruent / Control) was fully counterbalanced between participants (see Appendix K).

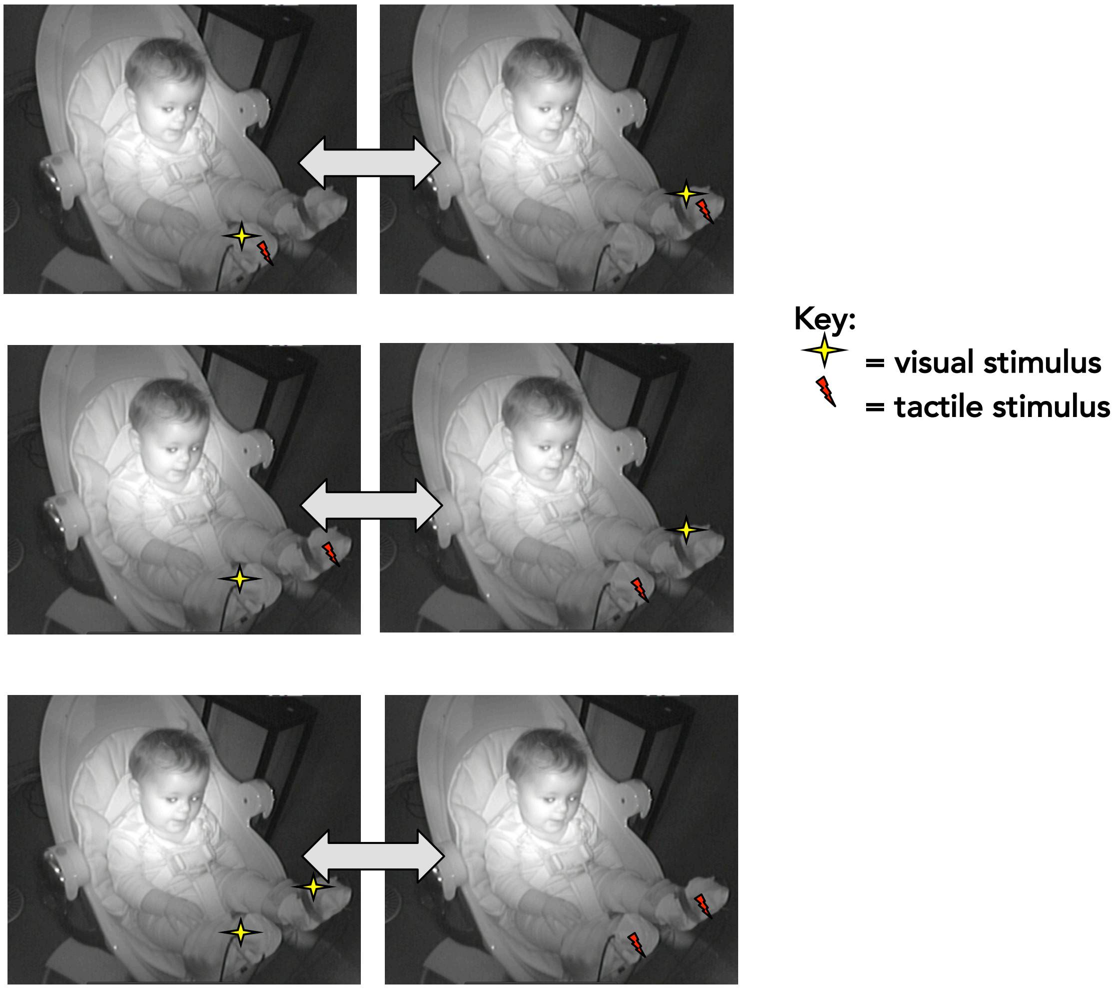


Figure 5.4: Pictures of experimental set up in which an infant has received a visual stimulus (flash of light) and a vibrotactile stimulus to the feet. The infant looks at their feet during, and following, stimulus presentation. Within each trial pairs of stimuli (visual and tactile) were administered to the feet in 10 different synchronous events (each event was 700 ms in duration with an inter-event interval of 1500 ms). Between each event the stimuli moved to the other foot.

5.7.3 Stimulus and apparatus

Infants were seated in a specialist baby chair. The seat was reclined in a horizontal position with the back-rest parallel to the floor. Adjustable straps secured the infant in the seat. Cotton padding and a head-rest were used to secure the posture of the infant's trunk. All testing took place in a dimly lit room, to discourage infants from looking at their surroundings. An infrared video camera located 80 cm in front of the chair and 60 cm above the torso of the infant recorded each infant's looking behaviour. Video data were recorded for offline coding.

The vibrotactile stimuli were delivered by two voice coil tactors (the experimenter placed these on the soles of the infant's feet, securing them in place with cohesive bandage) driven by a 220 Hz sine wave and controlled by custom software scripted in E-Prime. Additionally, the EPrime script sent signals that were time-locked to the onset and offset of the vibrotactile stimuli to a video titler so that the infants' stimulus-locked behaviour could be observed and coded. Any noise emitted by the tactors was masked with grey noise played from a centrally placed loudspeaker. This masked sound cues for both the infant and experimenter.

5.7.4 Procedure

Infants were secured into the baby seat. Following this, the tactors were positioned on the soles of their feet and secured with cohesive bandage before white cotton scratch mittens were placed over the feet. The scratch mittens contained LED assemblies which were positioned (and sewn into the mittens) so that lights could be presented from the top of the infant's feet. The scratch mittens were secured in place with Velcro straps.

On each trial, the experimenter held onto the infant's legs maintaining approximately 10 cm between the feet. The experimenter then engaged in a game of peek-a-boo with the infant's legs (using infant's feet to cover the experimenter's eyes and part of the face whilst 'hiding' and separating the legs to reveal their face. This was carried out so as to engage the infant and direct their gaze to their feet. After three 'peek-a-boos', the experimenter would move out of sight, still holding the infant's legs in place. If the infant remained looking at their feet at this time, a second experimenter initiated a trial. If the infant was not looking at their feet, the second experimenter signaled (via an intercom) for the first experimenter to continue engaging with the infant. Once again, this researcher would engage in a series of three peek-a-boos (one set comprised of three peek-a-boos) before moving out of sight. The second experimenter would then initiate the program. On all trials, two sets of peek-a-boo (six peek-a-boos) was sufficient to direct the infant's gaze to their feet to begin a trial.

In the time during a trial (each trials comprised a series of 10 stimulus pairs) the experimenter stayed out of sight and oriented her face to the floor in order not to distract the infant. Once a trial had reached its completion, the second experimenter signaled via intercom for the first experimenter to redirect the infant's attention to their feet through a game of peek-a-boo. If the infant became fussy, they were entertained with songs or games of peek-a-boo between trials until they were settled enough to continue with the study. Participants completed a minimum of one trial for each condition (30 paired stimulations) and maximum of three trials per condition (90 paired stimulations).

5.7.5 Data coding

The infants' looking behaviour to the visual and tactile stimuli was coded from the video records in Quicktime 7 Player for Macintosh (using frame onset and offset times, calculating the difference before converting to milliseconds). Both raters were blind to the condition, but were provided with stimulus onset and offset information.

5.8 Results

As all infants were able to complete the first block of trials (10 stimulations in each condition), it was decided that all analyses would include only these three trials. As I wanted to look at the developmental trajectory of the ability to co-locate visual-tactile stimuli on the body, I decided to compare the data from the 4-month-olds with those of the 6-month-olds.

A 3 x 2 mixed measures ANOVA of looking time with the within-participants factor of Condition (Congruent / Incongruent / Control) and the between-participants factor of Age (4-month-olds / 6-month-olds) was conducted. This revealed a significant main effect of Condition [$\underline{F}(2, 50) = 8.18$, $\underline{p} = .001$, $\eta_p^2 = .25$] (M = 12.45 s, SD = 1.2 s, M = 12.81 s, SD = 1.04 s, M = 9.86 s, SD = 4.91 s for Congruent, Incongruent and Control conditions respectively). Additionally, a significant interaction of Condition x Age was seen [F(2, 50) = 11.67, $p < .001$, $\eta_p^2 = .32$]. Finally, a main effect of Age approached significance [F(2, 50) = 3.27, $p = .08$, $\eta_p^2 = .17$] (M = 13.12 s, SD = 5.64 s and M = 9.94, SD = 2.54 for the 4- and 6-month-olds respectively); indicating that 4-month-olds tended to look longer at their feet across all conditions.

To further explore the significant main effect of Condition, and the significant interaction of Condition x Age, six post-hoc comparisons and three planned comparisons were conducted (the alpha level was Bonferroni corrected to $p = .008$ to adjust for Type I error).

Three unplanned comparisons were conducted across age group, comparing each of the experimental conditions with each other, to further investigate the significant main effect of Condition. Comparing looking duration in the Congruent and Incongruent conditions revealed no significant findings [t(26) = .34, n.s d = .3]. However, pairwise comparisons between the Congruent and Control conditions [t(26) = 2.86, $p = .008$, d = 2.5] and the Incongruent and Control conditions [t(26) = 3.2, $p = .004$, d = 3.0] revealed significant effects.

To explore the significant interaction of Condition x Age, three comparisons were conducted in each age group, comparing each of the experimental conditions to each other. As I did not have any hypotheses regarding the results of the 4-month-olds, the tests run in this group were unplanned comparisons. In the 4-month-olds group, a comparison of infant's total looking time when they received visual-tactile stimuli on the same foot (Congruent condition) to when they received visual-tactile stimuli on different feet (Incongruent condition) revealed longer at the Congruent display of stimuli [t(14) = 3.13, p = .007, d = .5]. The 4-month-olds also looked for longer at the Congruent than the Control condition [t(14) = 4.37, p = .001, d = .76]. No reliable difference in looking time was observed between the Incongruent and Control conditions [t(14) = 1.02, n.s., d = .2].

The above comparisons were also conducted in the 6-month-old age group, however as I expected to replicate the findings of Freier et al. (in prep.) and the findings from Experiment 6a of this thesis, these were planned comparisons. As expected, the 6-month-olds looked longer on Incongruent than Congruent trials [t(11) = 4.66, p < .001, d = 1.26]. Additionally, as expected infants spent more time looking at the stimuli in the Incongruent condition than the Control condition [t(11) = 4.67, p < .001, d = 1.64]. There was no significant difference in 6-month-olds' looking times between the Congruent and Control conditions [t(11) = .2, n.s, d = .08].

Three more post-hoc comparisons were conducted to inspect any differences between age-groups within each experimental condition (Congruent / Incongruent / Control). Only a significant difference in age-group was found within the Congruent condition [t(25) = 3.61, p = .001, d = 1.4], with means indicating that the 4-month-olds looked longer in this condition compared to the 6-month-olds (see Figure 5.5). No other significant effects were found (all ts < 2).

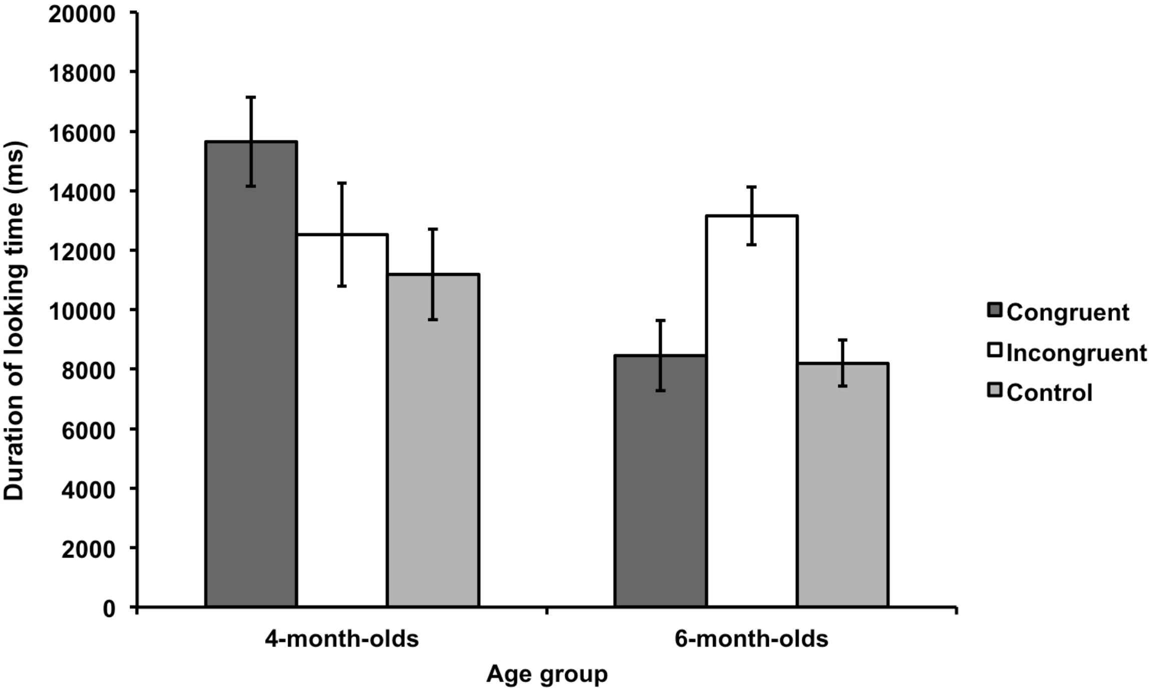


Figure 5.5: Mean looking duration (at the feet) of 4 and 6-month-olds across stimulus presentation conditions. Errors bars indicate the standard error of the mean.

5.9 Discussion

The current study investigated whether 4- and 6-month-old infants perceive visual and tactile stimuli on the body within a common spatial framework (i.e. whether infants of this age perceive co-location between stimuli from these two sensory modalities). Furthermore, this study built on findings from a previous study investigating visual-tactile co-location in the first year of life (Freier et al., in prep), attempting to determine what underlay looking preferences demonstrated in that study.

In terms of answering queries regarding the development of the ability to co-locate stimuli which are disparate in space, this study has unequivocally shown that 6-month-old infants can reliably distinguish between situations in which bimodal stimuli are presented in the same region of space (visual-tactile stimuli that are co-located) versus when they are presented across different locations. Further to this, the data from this study are consistent with the view that 4-month-old infants can distinguish between co-located and dislocated visual-tactile stimuli.

It was found that 6-month-old infants much preferred to fixate on stimuli from different sensory modalities (vision and touch), when the stimuli occurred in separate spatial locations (6-month-olds) as compared to when the stimuli were separate in space. Although there has been much research to demonstrate that infants within the first year of life are sensitive to co-location of audio-visual stimuli (e.g. Fenwick & Chance, 1998; Fenwick & Morrongiello, 1998; Morrongiello, Fenwick & Nutley, 1998; Bahrick & Lickliter, 2001) even from as early as 2 months (Bremner, Slater & Johnson 2007), the current study is one of the first to demonstrate a sensitivity to co-location across visual and tactile inputs. Further to this, the control condition in this study rules out an explanation in terms of the spatial extent of the 6-month-olds (i.e. that they simply preferred to look at the dislocated presentation of stimuli because it occupied a larger spread in space).

The 4-month-old infants in this study demonstrated a preference for viewing the Congruent condition (when the visual and the tactile stimuli occurred on the same foot) relative to when the stimuli occurred across both feet (Incongruent condition) or when stimuli from the same modality were presented separately in space (Control condition). From these results, it could be argued that infants of this age can reliably distinguish between stimuli presented in the same spatial location versus separate regions of space. However, as they show a preference for the condition in which the visual-tactile stimuli occurred on the same foot and were thus co-located, it is possible that infants of this young age show a preference for this condition because two stimuli are occurring on the same foot; an explanation that is not explicitly ruled out by the control condition in this study. Further experiments will thus be needed to determine whether 4 month olds are differentiating congruent and incongruent conditions on the basis of crossmodal co-location or other lower level factors.

If we are to assume that 4-month-old infants could distinguish between co-location and dislocated visual-tactile stimuli, the current study has also shown that between 4 months of age and 6 months of age, infants shift from a visual preference for co-located stimuli to a preference for dislocated bimodal visual tactile stimuli. In contrast to the preferential looking patterns of 6-month-olds, younger infants (those aged 4 months) illustrated a spontaneous preference for visual-tactile stimuli that were not separated in space (i.e., looking significantly longer at their feet when the visual-tactile stimuli occurred on the same foot). Why might this be? I propose that developmental differences in patterns of looking behaviour may relate to the emergence of a preference for novel over familiar perceptual stimuli.

Whilst visual preference techniques have often used the principle that infants tend to look reliably longer at stimuli that is novel, there is also evidence of young infants preferring to look at stimuli that are *familiar* to them (Hunter & Ames, 1988). For example, in a study conducted by Rose, Melloy-Carminar, Gottfried & Bridger (1982), infants aged 3.5 and 6.5 months were presented with a visual stimulus repeatedly. Following this, the visual stimulus was then presented with a novel stimulus. It was found that the younger infants demonstrated a strong preference for the familiar stimulus, whereas the older infants looked longer at the novel stimulus. This pattern of preference has been shown with both visual (Hunter, Ames & Koopman, 1983; Röder, Bushnell & Sasseville, 2000) and auditory stimuli (Columbo & Bundy, 1983; Spence, 1996).

Hunter and Ames (1988) proposed a multifactor model of infant's preferences for novel or familiar stimuli that incorporated both stimulus complexity and familiarization factors. The researchers argued that, initially, exposure to a stimulus is extremely important, with infants preferring to view a familiar stimulus after short intervals of familiarization. Preference then shifts to novel stimuli after longer periods of familiarization. According to Hunter and Ames (1988), this preference shift from familiar to novel is very much dependent on the complexity of the stimuli and infant's processing speed in that it occurs once encoding of the presented stimuli is complete. The most relevant point from this model, in terms of the current study, is the fact that younger infants are more likely to display a preference for familiar stimuli, whilst older infants display a preference for novel stimuli (for recent detailed reviews of the familiarity-novel preference see Houston-Price & Nakai, 2004 and Mather, 2013).

So, how does this explanation affect the findings from the current study? If the younger age group were showing a familiarity preference for visual-tactile stimuli occurring in the same spatial location, the findings could support the conclusions that an ability to co-locate within the visual-tactile domain occurs earlier in infancy; in the first four months of life. As mentioned earlier however, an alternative explanation and one that is not ruled out by the control condition in this study, is that infants at 4 months prefer the Congruent condition as there are two stimuli occurring on the same foot rather than separate feet, regardless of the modality of the input. This is a plausible explanation, and as the current study did not explicitly test this hypothesis, it makes it difficult to conclude that infants at 4 months are able to co-locate visual and tactile stimuli to the body.

Thus, as infants are co-locating visual-tactile stimuli to the body between 4 and 6 months of age, could one argue that they are representing the spatial locations (of the stimuli) within an external reference frame? Arriving to this conclusion is not straightforward as previous research has reliably shown that an external reference frame for touch does not emerge until 6 months of age (Bremner et al., 2008; Experiment 3 in this thesis).

However, given that the ability to co-locate stimuli across two modalities is different than coding touch within external co-ordinates, there are some ways in which we can reconcile these somewhat contradictory findings.

A potential explanation for these conflicting findings could be that the stimuli used in the different experiments were dissimilar in nature. In previous studies investigating the emergence of an external reference frame in infancy (Bremner et al., 2008b; Experiment 3 in this thesis), a single vibrotactile stimulus was delivered to the hand or foot. In this current study, tactile stimuli were presented concurrently with visual stimuli. It could be argued that the infants in this particular study were captured by the visual flash of light, rather than the felt vibrotactile stimulation. Therefore, perhaps, the fact that infants as young as 4 months of age are demonstrating the ability to co-locate visual-tactile stimuli may be evidence of their ability to use a *visually dominated* multisensory reference frame (which is external in nature), rather than an external reference frame for *touch* alone.

If we accept that the younger infants in this study, the 4-month-olds, were demonstrating perception of visual-tactile co-location, it is possible that they were achieving this because the visual stimuli are presented concurrently with the tactile stimulus supporting *visually dominated* spatial coding of the tactile stimulus. Indeed, the ability to use the visual reference frame in this way may be a precursor to locating a touch in external space when the touch is presented alone (rather than with a visual stimulus which could act as a scaffold). This developmental relationship could be indicative of how external spatial reference for touch might originate: external spatial coding under multisensory conditions might lead to a later ability to code tactile stimuli externally when presented in isolation.

In previous chapters, I have outlined how vision of the body (both previous visual experience and current vision) is particularly important in the development and emergence of an external reference frame for touch. Therefore, if we take the position that the 4-month-old infants in this study are able to distinguish between co-located and dislocated visual-tactile stimuli, it could be argued that the visual reference frame could potentially impact how (and when) touches on the body are coded within an external frame of reference. After all, the visual reference frame and the external reference frame for touch have different developmental trajectories; with researchers arguing that the visual reference frame emerges very early in life at approximately 3.5 months of age (e.g., Kauffman & Needham, 2011), whereas the external reference frame for touch emerges at 6 months of age (Bremner et al., 2008; Experiment 3 of this thesis). Considering that these reference frames emerge at different points in development, this could suggest that they are underpinned by different processes.

This study is the first to establish that, from at least 6 months of age (and perhaps even earlier), infants are able to locate visual and tactile stimuli, on the body, within a common spatial framework. Infants aged 4-

and 6-months were able to reliably distinguish between visual-tactile stimuli that occurred on either the same, or different, feet.

In this study, the 6-month-olds demonstrated a novelty preference for when the stimuli was separated in space, whereas the 4-month-olds showed a familiarity preference when the stimuli shared spatial co-ordinates. From the 6-month-old findings, it can be concluded that infants of this age are able to co-locate visual-tactile stimuli in everyday life. In comparison, the findings of the 4-month-old infants are more ambiguous and further studies are required before firm conclusions regarding their co-location abilities can be drawn.

I have attempted to detail how the findings of the current study may be assimilated within the larger body of research in the ability to locate touches to the body within external co-ordinates, which is evident within the first half year of life, but continues developing beyond this age and throughout infancy.

Chapter 6

Visual-tactile links in crossmodal attention in infancy:

6.1 Experiment 7: Crossmodal cueing

In previous chapters, I have investigated how infants locate touches to their hands and feet across different postures (Chapters 3 and 4) and how infants in the first year of life begin to locate visual and tactile stimuli within a common spatial framework (Chapter 5). The following study was borne out of the findings from these previous research findings; namely the findings of Experiment 6b in which it was found that it is by 6 months of age (or perhaps even earlier in development) infants are able to co-locate visual and tactile stimuli occurring on the body. Much of the research in this thesis has investigated how vision and touch are involved in perceiving and locating a touch on the body, whether that is through calibration (Experiment 1 and 2, Chapter 1) or co-location (Experiments 6a and 6b, Chapter 5). In Experiment 6b infants demonstrated that, by 6 months of age, they are able to co-locate visual and tactile stimuli that occurs on the body. If infants of this age are able to co-locate visual and tactile events in space, these sensory cues could also interact in other ways. One particular theme in crossmodal research in adults has been to investigate how information in one modality can effect attentional orienting in another modality (crossmodal spatial attention; see Driver &

Spence, 1998a; Spence & Driver, 2004). The ability to co-locate visual and tactile events at 6 months begs the question of whether there are visual-tactile crossmodal links in attention in early infancy also.

In this chapter, I investigate whether visual spatial cues affect attention to events occurring in touch. I ask whether a visual event can lead to an enhanced processing of somatosensory information at the same location. Before I discuss the ways in which attention to a tactile event can be exogenously cued by a visual event at the same location, I will discuss more general research investigating selective attention in infancy and crossmodal selective attention in adults.

6.1.1 Selective attention

William James (1842-1910) broadly defined attention as “the taking possession of the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought” (James, 1890, pp 403-404). This definition encapsulates the two facets of attention research: i) the selection of information, and ii) arousal (i.e. achieving a state of physiological arousal to a level of alertness that allows sustained contact with, or processing of, a stimulus).

In terms of this thesis, the most relevant aspect of attention is selective attention (i.e., isolating a specific piece of information in the environment and attending to it accordingly), specifically in relation to the role of visual stimuli in cueing attention. Therefore, in the following section I will present research relating to selective attention.

One aspect of selective attention is spatial orienting. Spatial orienting refers to the process by which individuals shift their attention to a specific spatial locus or a stimulus occurring in that spatial location (Posner, 1978, 1980). In order for an attentional shift to occur, there are several processes that need to be completed. First, individuals attend to a stimulus in one spatial location; they then disengage from this stimulus before shifting their vision to another stimulus in a different location; thereby shifting their visual attention (Posner, 1978, 1980). This shifting of attention can occur either covertly (i.e. a shift in attention occurs without individuals moving their eyes to the specific spatial location) or overtly, with the eyes, head or hands moving to the spatial location concurrently with one's attention (Posner & Rothbart, 1998). Research spanning over six decades has yielded an extensive body of research investigating selective attention in adults (both human and primates), a selection of which I will outline below.

6.1.2 Spatial attention in adults

The spatial cueing paradigm (e.g. Eriksen & Hoffner, 1972; Posner, 1978) has been used to investigate spatial attention. Here, individuals are presented with a visual cue that directs participants' attention in one particular spatial direction or location. On any given trial a target subsequently appears in either the cued location (on "valid" cue trials), an uncued location ("invalid" cue trials) or at the centre during "neutral cue" trials. Using this method it has been found that participants are better at discriminating a wide range of features of this target at the cued location, relative to the uncued or neutral location (e.g., Posner, 1978, 1980; Jonides, 1981; Spence & Driver, 1996).

Other studies using the spatial cueing paradigm, or variations of it, have investigated attention within the auditory and tactile domains (Spence & Driver, 1994; 1996; 1997, for a review of this literature see Driver & Spence, 1998 and Spence & Santangelo, 2009). Of course, the research described above is unisensory and as stated many a time previously, infants (and adults alike) reside in a multisensory environment. So, one must ask how attention works in a multisensory perceptual situation.

6.1.3 Crossmodal links in attention (adult literature)

In previous chapters presented in this thesis (specifically Chapters 1 and 3), I have discussed the modulatory effect of vision of a limb on tactile localization. For example, it has been found that viewing a limb being touched modulates processing in the somatosensory cortex (Longo, Pernigo & Haggard, 2011; Taylor-Clark, Kennett & Haggard, 2002; Cardini, Longo & Haggard, 2011), improves tactile acuity (Longo, Cardozo & Haggard, 2008; Press, Taylor-Clark, Kennett & Haggard, 2004), and can even reduce the intensity of acute pain (Longo, Iannetti, Mancini, Driver & Haggard, 2012). Indeed, even when the vision of the limbs is non-informative and participants do not see the limb being touched, it appears that the modulatory effect of vision on somatosensory processing persists (Cardini, Longo, Driver & Haggard, 2012). Further to this, vision of a stimulated limb can also inform individuals about limb posture and location (Graziano, 1999), and change the ways in which limb position is represented in the brain (Lloyd, Shore, Spence & Calvert, 2003; Rigato et al., 2013).

The above research has demonstrated that processing information from one sensory modality affects the processing of information from a different modality, specifically vision and touch. Indeed, these particular sense modalities senses appear to have strong links between them, with viewing a limb receiving a tactile stimulus influencing the processing of this tactile stimulus (Driver & Grossenbacher, 1996; Ernst & Banks, 2002; Cardini et al., 2011, 2012; Longo et al., 2008, 2011, 2012). Further to this, neuroimaging, and neurophysiological studies have found that visual receptive fields and tactile receptive fields show spatial overlap (Graziano, Yap & Gross, 1994; Graziano & Cooke, 2006; Avillac, Deneve, Olivier, Pouget & Duhamel, 2005; Stein & Meredith, 1993).

Given the strong spatial links between visual and tactile sensory modalities, there is surprisingly little research investigating this link within the domain of selective attention and the shifting of attention. Audiovisual crossmodal links in attention have been investigated extensively (e.g., Reisberg, 1978; Ward, 1994; Spence & Driver, 1994, 1996, 1997; Lebib et al., 2004), with researchers even investigating audio-tactile crossmodal links (Foxe, Morocz, Murray, Higgins, Javitt & Schroeder, 2000). I now describe findings regarding visual-tactile links in exogenous attention.

Several studies have now shown that when a tactile stimulus on the body precedes a visual stimulus in the same side of space, participants' demonstrate shorter response times to the visual stimulus (e.g., Spence, Nicholls, Gillespie & Driver, 1998) when compared with response times when the tactile cue and visual target appeared in different sides of space. The same pattern of results has been shown in a variety of spatial tasks, such as those involving speeded discrimination of tactile stimuli in which participants were asked to discriminate between continuous or pulsed tactile presentations as quickly and as accurate as possible (Spence et al., 1998). Additionally, this effect persists when a visual stimulus cues a tactile target (Kennett, Eimer, Spence & Driver, 2001; Kennett, Spence & Driver, 2002).

Neuroimaging research has also shown that attending to a visual stimulus has a facilitating effect on the subsequent processing of a tactile stimulus, by way of the enhancement of the N140 SEP component (e.g., Eimer & Forster, 2003; Kida, Nishihira, Wasaka, Nakata & Sakamoto, 2004; Ku, Ohara, Wang, Lenz, Hsiao, Bodner, Hong & Zhou, 2007; Eimer & Driver, 2000; Van Velzen, Forster & Eimer, 2002). This enhancement of the N140 persists in the absence of a visual cue, but with participants simply attending to the hand that received a tactile stimulus (Desmedt & Robertson, 1977; García-Larrea, Lukaszewicz & Maugière, 1995; Michie, 1984; Michie, Bearparic, Crawford & Glue, 1987). Additionally, there is some evidence that even earlier components of the SEP waveforms are affected when participants' are visually cued to the site of the touch, such as the N80 (Eimer & Forster, 2003; Michie et al., 1987). So visual cues to the location of a tactile stimulus on the body have been shown to affect early somatosensory processing.

Exogenous effects of visual cues on tactile processing would be interesting to examine in infants. Considering that previous research in this thesis has shown that infants are able to co-locate visual and tactile events in space (Experiment 6b, Chapter 5), it may be that there are other links between vision and touch. Indeed, the ability to co-locate visual and tactile events by 6 months generates the question of whether crossmodal links in attention are also present by this age.

6.1.4 Selective attention in infancy

The research described above has been conducted with adult participants. In the following section, I will give a brief overview of the research conducted within the field of infant attention. As with attention in the adult literature, there has been much research conducted with infants (Colombo, 2002; Richards & Casey, 1992; Colombo, 2001). This surge in interest from developmental psychologists is attributable partly to attention being viewed as a predictive measure of cognitive ability and development in early childhood (Colombo, 2001; Colombo, 1997; Colombo & Mitchell, 1990; Rose & Feldman, 1990).

Selective unimodal attention in infancy has been investigated using largely similar paradigms as those used with adults. These studies have used a spatial cueing paradigm where infants' speed of visual orienting to a cue and target were measured. Alternatively, spatial cueing paradigms with infants have also measured infants' neural responses to cues and targets. Using a spatial cueing paradigm where infants were presented with a visual cue, followed (after 200 or 700 ms) by a target in either the same (valid) or different (invalid) location. In addition to this, the study also included control conditions in which a target or a cue was not presented. The speeds of 3- and 6-month-olds' visual orienting responses to the visual target were examined. It was found that at 3 months of age, infants did not demonstrate any differences in reaction times between looking at the valid or invalid locations, nor was there any effect of the time interval between the cue and target. In comparison, the 6-month-old infants displayed shorter reaction times to the visual target during valid trials (relative to invalid and control trials) when the interval between the cue and target was 200 ms. However, when this interval was increased to 700 ms, infants were slower in their reaction times when the visual cue and target appeared in the same side of space (Hood & Atkinson, 1991; Hood, 1993, Hood 1995). Therefore, these studies have demonstrated that by 6 months of age, infants' demonstrate facilitatory effects when a cue and target are presented in the same side of space. However, this is affected by the interval between the two stimuli.

A similar pattern of results was also found by Johnson and Tucker (1996). Here, infants were presented with a visual cue before two visual targets appeared on the screen, one target that was in the same side of space to the cue and one target in the opposite side of space. At 6 months of age, when the cue-target onset asynchrony was relatively short (133 to 200 ms), infants were not only more likely to look towards the visual target that was ipsilateral to the cue, but were also quicker in doing so compared to when the target was in the contralateral side of space of the cue. However, when the delay between cue-target onset increased to 700 ms, this resulted in 6-month-olds looking much less at the ipsilateral target and taking longer to do so. Again, this demonstrates that the interval between the cue and target needs to be relatively short for infants to demonstrate a facilitation effect when both stimuli occur in the same side of space.

In addition to behavioural methodologies, researchers have investigated attentional cueing in infants using neural measures. Richards (2000) recorded ERPs whilst also examining infants' visual reaction times to a visual cue and target. In this study, 14-, 20- and 26-week-old infants took part in a spatial cueing paradigm where a visual cue and target were presented on a screen. It was found that when the interval between the cue and target was 350 ms, infants in all age groups showed shorter reaction times to the target when both stimuli were on the same side of space. If, however, the cue-target interval increased beyond 700 ms, infants took longer to visually orient to the target when both stimuli were on the same side of space. These results are very similar to, and support, the findings of the previously mentioned behavioural studies (Hood & Atkinson, 1991; Hood, 1993, 1995; Johnson & Tucker, 1996).

During this task, Richards (2000) also took recordings of infants' neural activity over occipital areas. Using this measure, infants demonstrated a larger P1 response on valid trials (trials in which the cue and the target shared the same spatial location), which occurred approximately 135 ms after the onset of the visual target.

The above research has demonstrated that, by 6 months of age, infants can be cued towards a location in space. However, the current research has been limited to investigations within one sensory modality. As yet, no research has investigated the origins of crossmodal links in attention in early development, with specific emphasis on the role of using a visual cue to modulate somatosensory perception. In the next section, I will detail Experiment 7, which explores visual-tactile links in exogenous attention in infants in the second half year of life. This age group was chosen due to the fact that attentional cueing effects (within a sensory modality) can be observed at 26 weeks. As such, 7 months of age (28 to 32 weeks) seemed appropriate when investigating attention cueing across two sensory modalities (vision and touch).

In this study, infants were presented with a visual stimulus (on the hand) that acted as a cue to the location of a tactile probe that followed this cue. The tactile probe either occurred on the same or opposite hand to that which received the visual cue. In accordance with the literature on adult crossmodal attentional cuing and unimodal visual cueing in infants, it was expected that the infants in the current study would demonstrate a larger SEP waveform when the visual cue and tactile probe occurred on the same hand, relative to when the stimuli occurred on different hands.

6.2 Methods

6.2.1 Participants

Ten 7-month-olds (5 males), aged between 216 and 241 days (M = 229 days; SD = 8 days) took part in this study. An additional 4 participants were excluded from the final analyses due to fussy behavior in the testing session (1 participant) and excessive movement throughout the testing session resulting in particularly noisy data (3 participants).

Informed consent was obtained from the parents before commencing the study. The testing took place only if the infant was awake and appeared to be in an alert and content state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London.

6.2.2 Apparatus and Materials

The vibrotactile stimuli were delivered by two voice coil tactors (the experimenter placed these on the palms of the infants' hands, securing them with cohesive bandage) and covering their hands with white mittens. The mittens were then secured in place with a length of Velcro around the wrist of the infant. Small LEDs were sewn into the top of the mittens, and once secured, the LEDs were positioned so that they sat on the back of infants' hands. The tactors were driven by a 220 Hz sine wave and both the tactors and the LEDs were controlled by custom software scripted in E-Prime.

Two infrared video cameras (placed 70 cm, 60° and 60 cm, 45°) from the infant recorded the infant's looking behavior. The E-Prime script was also set up to control a serial-controlled video titler. Signals that were time-locked to the onset and offset of each trial were sent to the video titler so that the infants' stimulus-locked looking behaviour could be observed (for offline trial exclusion purposes).

One trial involved a visual cue, which was followed by a tactile probe (both were delivered to infants' hands). Infants' neural activity to the probe (with specific attention to the effect of the cue on the probe) was recorded. Each visual stimulus (a flash of light acting as the 'cue') lasted for 100 ms and each tactile stimulus (acting as the 'probe') lasted for 200 ms. The interstimulus interval between the Cue and the Probe was 50 ms and the inter-trial interval ranged from 800 ms to 1200 ms (see Figure

6.1). Any noise emitted by the tactors was masked with grey noise played from a centrally placed loudspeaker. This masking prevented detection of sound cues for both the infant and experimenter.

6.2.3 Design

The experiment comprised six conditions. In trials in the Congruent condition, the Cue and Probe stimuli occurred on the *same* hand (either right hand or left hand). In trials in the Incongruent condition, the Cue and Probe stimuli occurred on *different* hands (either the cue was on the left and probe on the right, or the cue was on the right and the probe on the left). In trials in the Cue only condition, only the cue was presented (either on the right hand or the left hand). The Congruent, Incongruent and Cue only trials were presented an equal number of times to the left and the right hands, which resulted in six conditions.

Infants were presented with a maximum of sixty blocks of experimental trials. Each block contained four trials, each of which was Congruent, Incongruent or Cue only delivered to each hand. These trials were presented in a random order over the entire sequence of 240 trials. Therefore, if infants completed all sixty blocks, they would have received 40 trials per condition.

In order to maximize the number of trials presented, the vibrotactile stimuli were presented in rapid succession (see Figure 6.1 for details). A higher number of trials would make the evoked responses more resilient to artefacts and noise. Further to this, behavioural studies have indicated that infants' visual orienting latencies towards a touch occurs at approximately 3.5 seconds following stimulus onset (Bremner et al., 2008a) for infants ages 6.5 months, much later than the stimuli duration (100 ms for the visual Cue and 200 ms for the tactile Probe). Given these design considerations, it was not possible to record behavioural measures (orienting responses) during this study.

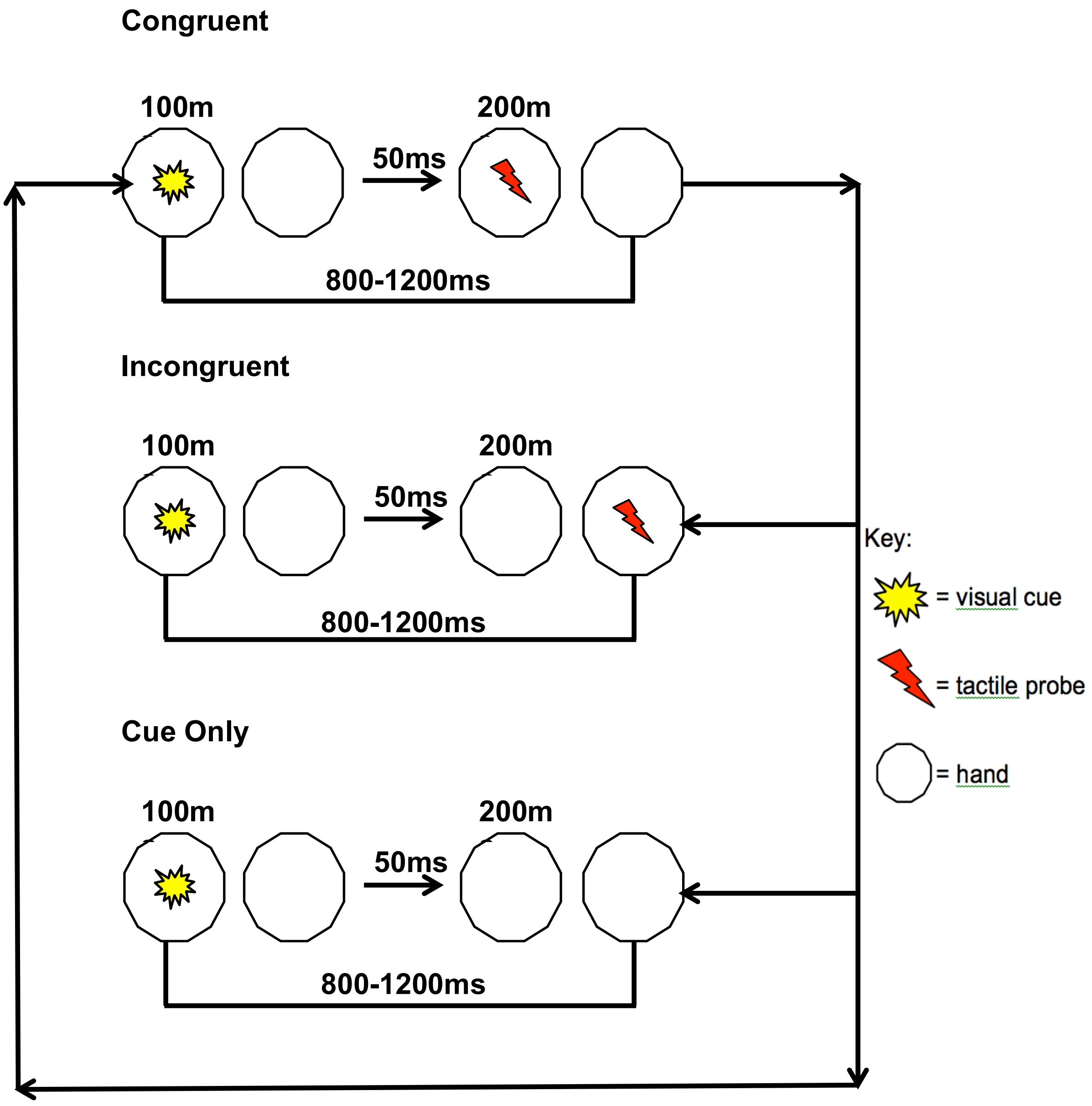


Figure 6.1: Figure depicting stimulus presentation in the three experimental conditions. The Cue (flash of light) lasting 100ms was followed by a 200ms Probe (vibrotactile stimulus) in the Congruent and Incongruent conditions. Note that this figure depicts stimulation occurring on one hand only, throughout the experiment, both hands received an equal number of visual and tactile stimuli.

6.2.4 Procedure

Testing took place in a dimly lit room. Infants were held on a parent’s lap in an upright, seated position. The experimenter gently took hold of the infant’s arms and held them approximately 10 cm apart. At the beginning of the study, the experimenter engaged the infant in a short game of ‘peek-a-boo’. After this game, the experimenter remained in sight of the infant, the infant’s hands now positioned close to the experimenter’s face. Only when infants’ were looking at their hands did a second experimenter (located in a different room) initiate the E-Prime program.

A direct eye gaze and softly spoken nursery rhymes and songs were used to maintain the infant’s attention towards their hands, with the experimenter’s face essentially acting as a fixation point. This also acted as a means of controlling the infants’ eye movements. The second experimenter only initiated blocks of trials when infants were looking in the direction of their hands with a central fixation. The study continued for as long as the infant was willing to co-operate, or until infants had completed the maximum number of trials (240).

6.2.5 Exclusion criteria for experimental trials

The video recordings of the testing session were examined offline at a later date. From these recordings, I was able to see whether the infant was looking in the direction of their hands across all trials. Any trials in which the infant was turned away, or was not looking at their hands with a central gaze, were excluded from the EEG data and not considered in the final analyses. This was, of course, in addition to the general rules of EEG data cleaning, which involved removing artefacts in the data (see Chapter 2, Section 2.5.4 for a more detailed description of such artefacts).

6.3 Results

Infants were presented with an average of 189 trials, of which an average of 122 trials were retained for analysis. After visually inspecting topographic plots of the data, hotspots of neural activity were identified in C3/C4 (electrodes: 7, 13, 29 and 30 in the left hemisphere and 104, 105, 111 and 112 in the right hemisphere).

6 conditions were examined: Congruent Left (the Cue and the Probe occurred on the left hand), Congruent Right (the Cue and the Probe occurred on the right hand), Incongruent Left (the Cue occurred on the right hand, the Probe occurred on the left hand), Incongruent Right (the Cue occurred on the left hand, the Probe occurred on the right hand), Cue only Left (the Cue was presented on the left hand) and Cue only Right (the Cue was presented on the right hand). ERPs for these conditions were extracted for both the contralateral and ipsilateral hemispheres (to the Probe in the first 4 conditions, and the No Probe in the Cue only conditions).

The Cue only conditions were subtracted from the corresponding Congruent and Incongruent conditions to remove any effect of the Cue in somatosensory areas, leaving neural activity that was only as a result of the somatosensory Probe. This was done for both the contralateral and ipsilateral hemispheres.

Monte Carlo simulations (see Chapter 2, section 2.6.2 for details) were conducted on the data to determine at which time point the difference in the waveforms significantly differed from zero. First, I examined whether there were any significant differences between conditions in which infants received a tactile probe to the right and left hands across cueing conditions. The Monte Carlo analysis did not find any significant main effects or interactions of hand and Condition. As such, the data was collapsed across hands, leaving the two conditions: Congruent and Incongruent.

Following this, using the Monte Carlo analysis once again, I compared the amplitude of the ERP waveforms from the two different cueing conditions (Congruent and Incongruent). A significant difference was found at contralateral sites (to the hand which received the Probe) starting at 174 ms and ending at 318 ms, $\underline{p} < .05$ (see Panel A of Figure 6.2), with the amplitude of the SEP waveform indicating a greater neural response in the Incongruent condition, relative to the Congruent condition. The Monte Carlo analysis was also conducted on the ipsilateral (to the probe) hemisphere; no significant differences were found (see Panel B of Figure 6.2).

Additionally, ERP mean amplitudes were computed within time-windows based on the latencies of the somatosensory components observed. Mean amplitudes for effects of cueing (Congruent vs. Incongruent) were tested with t-tests separately for contralateral and ipsilateral sites and for components in which we expected effects (namely the N140 and the P2). When examining the N140, I computed a mean amplitude of the time interval 100-150 ms. For the P2 component, the mean amplitude was computed from the time interval 200-300 ms. As these were the 2 time windows of interest, I used a Bonferroni corrected alpha value of $p = .025$. Furthermore, the data was pooled across 'left' and 'right' hands. No significant effects of cueing were observed for the N140 component at either contralateral or ipsilateral sites. However, a significant effect of the P2 component was found at contralateral sites: [200-300 ms: [$\underline{t}(9) = 2.94$, $\underline{p} = .017$] (congruent: M = 4.1 μV; incongruent: M = 6.85 μV], but not at ipsilateral sites.

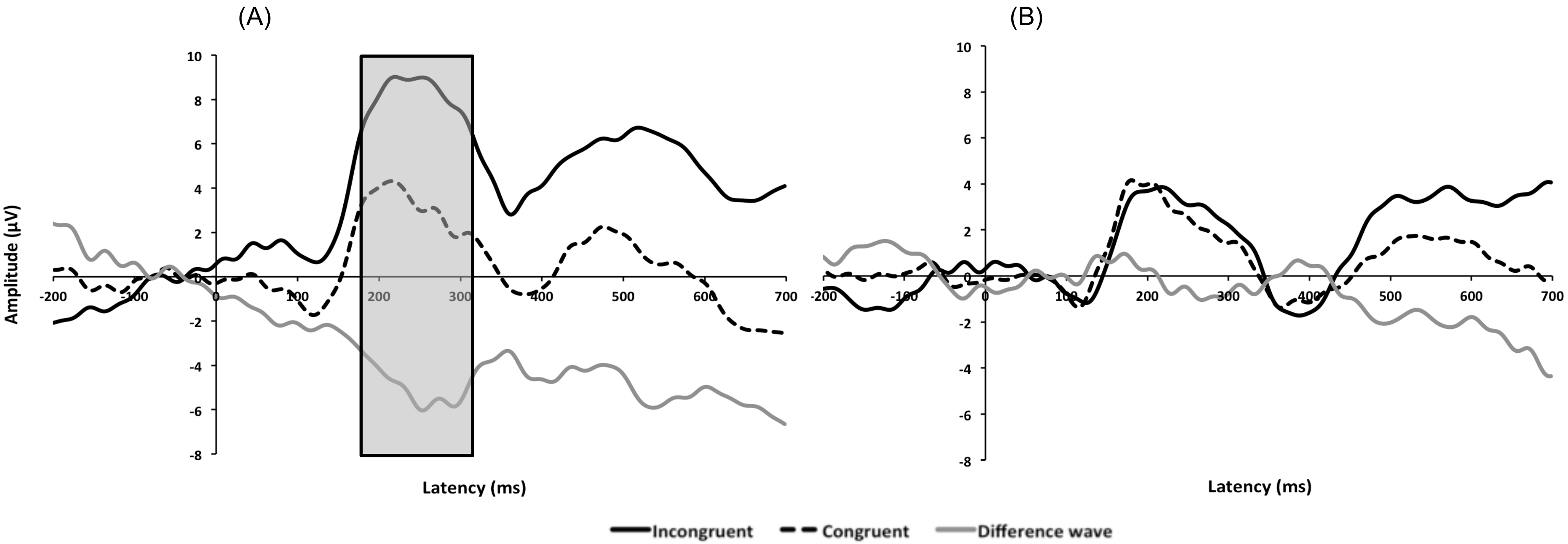


Figure 6.2: Grand averaged somatosensory evoked potentials in the Congruent and Incongruent stimulus conditions from central electrodes (C3/C4) contralateral (Panel A) and ipsilateral (Panel B) to the hand where the tactile Probe occurred. The shaded area in Panel A indicates the beginning and the end of the significant difference between the two conditions at contralateral sites. There were no significant differences found between conditions at ipsilateral sites (Panel B).

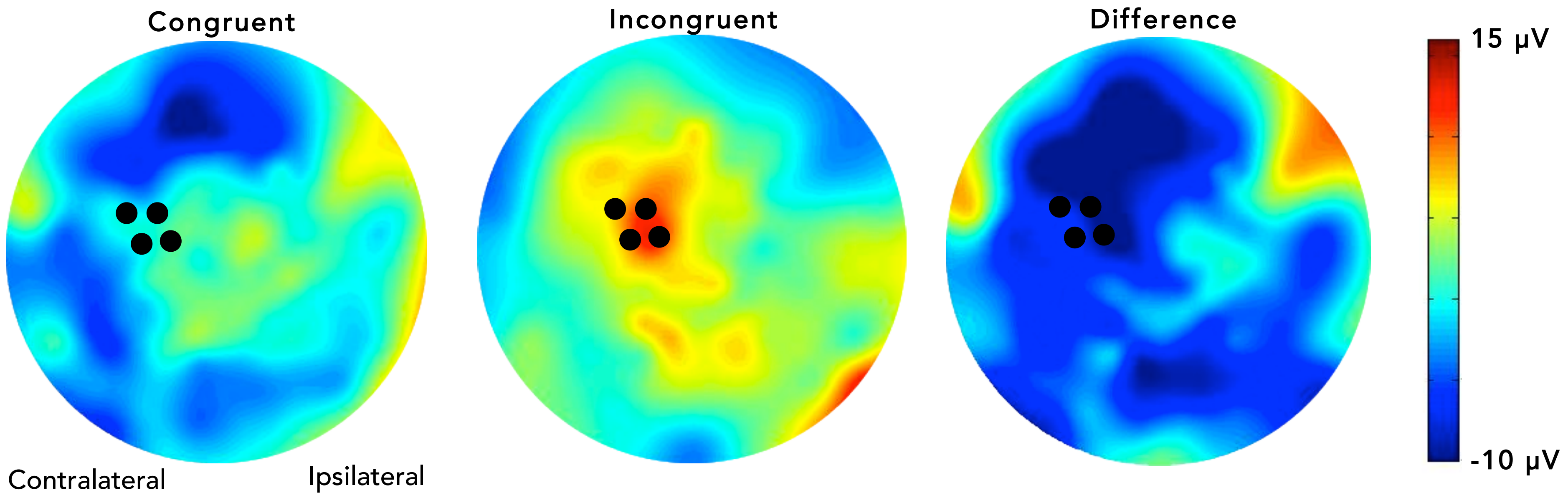


Figure 6.3: Topographical representations of the voltage distribution over the scalp in 7-month-olds from 200-250 ms following the tactile stimulus on trials in which the right hand was stimulated (contralateral effects are on the left of the maps). The map on the far right shows the effect of Cueing (Congruent - Incongruent) over contralateral (left hemisphere) somatosensory sites. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

6.4 Discussion

This study investigated the origins of crossmodal links in attention in early development, with respect to the visual and somatosensory domains. I did this by examining the neural response elicited by a tactile stimulus to the hands when the location of the touch was, or was not, cued by a preceding visual stimulus. Although, previous work with adults has shown that processing of a tactile stimulus at a cued location was enhanced (by way of greater amplitude of the cued probe), our results have shown that infants at 7 months of age demonstrate an enhanced SEP waveform when the cue and the probe occurred on different hands (i.e. at the uncued location of the probe), illustrating effects in the opposite direction to the pattern of effects which is seen in adults (Eimer & Forster, 2003; Kida et al., 2004; Ku et al., 2007; Eimer & Driver, 2000; Van Velzen et al., 2002). This effect began at 174 ms following presentation of the tactile stimuli and ended at 318 ms. This time-window seems likely to encompass the P2 component seen in adults (as evidenced by the significant pairwise comparison of cueing condition within the 200-300 ms time window).

In terms of the infant literature on unimodal visual attentional cueing, it has been found that infants in the first half year of life demonstrate a greater neural response to a visual target (specifically P1 component, which occurred approximately 135 ms after target onset) on trials in which the cue and the target shared the same spatial location (Richards, 2000). This is a similar latency to that observed in the current study, where infants demonstrated a greater neural response at 174 ms following probe onset. However, once again, the pattern of results is in the opposite direction as infants in the current study had a larger SEP for trials in which the cue and probe occurred in different sides of space. Additionally, it must be noted that Richards' experiment involved visual stimuli, whereas the current experiment involved applying tactile stimuli to the hands. Therefore, it may not be entirely accurate to directly compare the findings from the current experiment with Richards (2000). However, the study does provide us with information regarding the latency of infant attentional components.

Although the current study did not find significant differences around the N140 (between the cued and uncued probe locations), this is not too surprising. Indeed, in studies investigating unimodal cueing in infants, early components (such as the N1) are not seen until 260 ms following the onset of the target stimulus (Richards, 2000).

An important issue to deal with here is that the data in the current study demonstrated the opposite cuing effect to that which has been documented within the adult crossmodal and infant unimodal cueing literature. The infants showed a greater amplitude of the waveform to uncued as opposed to cued probes. I put forward a number of potential explanations for this finding.

One potential explanation for the greater amplitude when presented with stimuli on different hands is that of inhibition of return (IOR). IOR (Posner & Cohen, 1984) refers to an attentional orienting response in which there is enhanced processing of stimuli that occurs close to a preceding stimulus. For example, if a flash of light is seen in peripheral vision, other stimuli close to the locus of the flash of light benefits from enhanced processing. After processing is complete at this location and attention removed from it, there is now a delayed response to, and processing of, any stimuli that occurs in this same location (Posner, Rafal, Choate & Vaughan, 1985). Ultimately, as information in this location had already been processed, the brain is discouraged from expending resources to re-orient to this location and re-process stimuli (either previously attended or novel) at this attended location.

This could possibly explain our findings in this study; infants' attention may have been drawn to the flash of light on one hand and processed the proceeding tactile stimulus that occurred on the same hand. However, it may be that attention returning to the site of the cued stimulus was inhibited on subsequent trials, therefore resulting in facilitating the processing of stimuli that occurred at uncued locations, across both hands.

Of course, before we can conclude that our findings are the result of IOR, we must consider the specific characteristics of the IOR phenomenon. First, we must consider the temporal characteristics of IOR. Many researchers have investigated the onset, and time course, of IOR, with similar results. For example, Posner and Cohen (1984) found that IOR occurred when the time difference between the onset of the cue and target was 225 ms. However, other researchers have found that this is task dependent, with inhibitory effects occurring later for tasks which required greater processing (e.g., discrimination as opposed to detection tasks; Lupiáñez, Milán, Tornay, Madrid & Tudela, 1997) or earlier when the task required a saccadic, as opposed to a motor, response (Briand, Larrison & Soreno, 2000). Ultimately, it has been found that the time point in which attentional facilitation becomes inhibition occurs when the cue stimulus is presented 100-200 ms before the target stimulus (see Klein, 1999 for a review of this). However, it must be noted that this is specific to paradigms in which a saccade was made towards the cued and/or uncued locations (Dorris, Taylor & Klein, 1999; Maylor, 1985; Briand et al., 2000; Rafal, Egly & Rhodes, 1994; Abrams & Dobkin, 1994, 1995).

Of course, the studies investigating IOR (addressed above) have been conducted using a sample of adults. Due to the fact that adult and infant ERP waveforms differ in both latency of components and the morphology of the waveform, it is difficult to directly compare adult and infant ERP waveforms and components. As such, I will now discuss the literature that has investigated the time course of the facilitatory and inhibitory effects of IOR in infants.

In a number of infant studies using a spatial cueing paradigm (where a visual cue and target were presented on a screen), it has been found that when the interval between the cue and target varied between 133 to 350 ms, infants at 6 months of age showed shorter reaction times to the target when both stimuli were on the same side of space; facilitation effects. If, however, the cue-target interval increased beyond 700 ms, infants took longer to visually orient to the target when both stimuli were on the same side of space; IOR (Richards, 2000; Johnson & Tucker, 2006; Hood & Atkinson, 1991; Hood, 1993; Hood, 1995).

To this end, IOR does not seem to explain the results in this experiment, given that the interval between the cue and target was only 50 ms. According to this interval, we should have observed attentional facilitation effects at the cued location of the visual-tactile stimuli and only when the interval is beyond 700 ms should we have observed inhibitory effects. As such, IOR alone does not sufficiently explain our findings.

An alternative explanation of our findings, and the one which we think is the most plausible, could be related to sensory (specifically crossmodal) gating. Sensory gating describes a neural process by which the brain is able to modulate its sensitivity to sensory stimuli (e.g., Braff & Geyer, 1990; Adler, Olincy, Waldo, Harris & Griffith et al., 1998). Therefore, sensory gating can result in either enhanced or reduced processing of incoming sensory stimuli (with this information being viewed as either novel or irrelevant respectively; Boutros, Zouridakis & Overall, 1991). In terms of the current study, crossmodal gating refers to the suppression of 'irrelevant' stimuli; specifically in the congruent condition where the visual and the tactile stimuli are occurring on the same hand (i.e. in the same region of space). As such, I will be focusing on literature that demonstrates this suppression effect.

Sensory gating has been observed in a number of studies, both using a unimodal or a crossmodal design. These studies have illustrated the specific characteristics of the sensory gating mechanism. For example, it has been found that sensory gating can occur when the interval between the two presented stimuli is as little as 75 ms or as long as 500 ms (Nagamoto, Adler, Waldo & Freedman, 1989). In the current experiment, the interval between the offset of the Cue and the onset of the Probe was 50 ms. Additionally, sensory gating has been observed neurally at early components such as the P50 (roughly between 40 and 75 ms) or later components such as the N100 (Smith, Boutros & Schwarzkopf, 1994) or even between 160 ms to 200 ms after stimulus onset (Boutros et al., 1991).

Considering that the above studies were conducted with adult participants within a unimodal paradigm (the presentation of two auditory clicks), and the study we conducted involved infants at 7 months of age who were presented with a visual and a tactile stimulus, we must consider that the observed results from these studies are likely to differ. For example, although our cueing effects (as a consequence of sensory gating) occurred at 174 ms after stimulus onset, this is extremely close to the 160 ms demonstrated by Boutros et al. (1991). In addition this, several studies have now found that the latency and morphology of neural waveforms change dramatically in the first two years of life (e.g., Pihko et al., 2009) and infant neural waveforms significantly differ in amplitude, direction, latency and morphology to that of adults (e.g., De Haan, 2007; De Haan, Pascalis & Johnson, 2002). Therefore, it is expected that infant waveforms will not be identical in latency and morphology to adult ERP waveforms.

There has been some research investigating sensory gating in infants (using paired auditory clicks), which has found evidence of suppression at approximately P50 (Hutchinson, Hunter, Wagner, Calvin, Zerbe & Ross, 2013; Kisley, Polks, Ross, Levisogn & Freedman, 2003; Hunter, Corral, Ponicsan & Ross, 2007). However, it must be noted that these studies were conducted when infants were asleep. Considering that infants may not have been processing information from a multitude of sensory modalities whilst sleeping, perhaps their attention was more focused on the salient auditory stimuli they were presented with, thus resulting in effects at early latencies. In comparison, in our study, the infant was awake and in a state of alertness, consciously processing information from several sensory modalities.

Indeed, a further factor that may be related to the differences in the latency of the effects is the fact that this current study used a crossmodal paradigm. It may be that sensory gating takes place later across modalities, as opposed to within a modality, as information from the visual and somatosensory cortices (in different parts of the brain) must intervene and this may take some time.

In terms of the adult literature in crossmodal sensory gating, it has been found that the early P50 component is attenuated when processing congruent, redundant stimuli across audition and touch (Foxe, Morocz, Murray, Higgins, Javitt & Schroeder, 2000; Kisley & Cornwell, 2006) and audition and vision (Lebib, Papo, Bode & Baudonniere, 2003). However, as yet, there is no research concerning vision and touch, so it is difficult to conclude that the longer latency observed in the current study is not a result of crossmodal gating. Indeed, considering the differences between paradigms (stimuli presentation and the intervals between these, the populations used; adults versus infants), the greater latency of the ERP waveform may well be expected.

Ultimately, the current study has found that, at 7 months of age, visual cues to the hand modulate processing of a subsequent tactile stimulus on that same hand but not generally across the hands (the cuing effect was restricted to contralateral sites). This provides further evidence of crossmodal spatial links between touch and vision (see Chapter 5, and also Bahrick & Lickliter, 2012), and we believe this to be the first demonstration of crossmodal attentional cuing effects in infancy. Somewhat surprisingly the cuing effect observed here was manifest as a reduction in somatosensory signal when preceded by a visual cue at the same location. We believe that this is a result of crossmodal sensory gating, with infants demonstrating an attenuated neural response to congruent (redundant) stimuli that occurred on the same hand.

Chapter 7:

General discussion

In this chapter I will summarise the findings from Experiments 1 to 7 and discuss the implications of these results within the wider literature of body representations and multisensory processing in development. First, I will summarise the key findings of Experiments 1 – 3, discussing such findings with respect to the emergence of an external reference frame for touch. Following this, I will go on to summarise the findings of Experiment 4 and 5 and discuss how these findings relate to the development of an ability to neurally remap touches on the body across changes in limb posture. I then go on to address the findings of Experiment 6 and 7 within the wider literature concerning the development of visual-tactile spatial relationships. Finally, I discuss the implications of the findings from this body of research for various accounts of multisensory development.

7.1 Summary of key findings

As discussed in the introductory chapter (Chapter 1), there were originally two avenues of questions that comprise this thesis: how infants and children locate touches on the body in space (through the emergence of an ability to refer touches to an external reference frame) and how infants are able to keep track of touches on their limbs across changes in posture (somatosensory remapping).

First, I will tackle the ability to locate a touch in external space. As discussed throughout this thesis, this is no easy feat, especially when considering that the body does not lie static, but engages in movements that dynamically change the spatial location of the limbs. When considering this, the human infant (and child and adult) must not only locate touches on the body anatomically (so, simply locating the touch on the skin's surface), but must also locate it in the external environment.

In order to examine this, crossed hand studies are used as an index of external localisation of touch, with poorer tactile localisation accuracy in the crossed hands posture (relative to the uncrossed posture) indicating that an external reference frame for touch is employed. In Experiment 1, I attempted to resolve seemingly conflicting findings regarding when an external reference frame for touch emerges in early life. Pagel et al. (2009) found that it was only after 5.5 years that children are able to locate their limbs with respect to this external reference frame, whereas Bremner et al. (2008b) demonstrated that this ability emerged within the first half year of life.

By using a less demanding task (discussed in Chapter 3, Section 3.1), rather than the tactile TOJ task employed by Pagel et al. (2009), I was able to find that children aged 4 years were worse at locating which hand had been stimulated when the hands were crossed over, compared to when the hands were in an uncrossed posture. Such posture effects indicate the ability to use an external reference frame to locate touches. Interestingly, I found that this crossed hands effect occurred only when children did not have current vision of their arms and hands. When children have vision of the stimulated limb, they performed to the same degree of tactile localisation accuracy across the uncrossed and crossed hands postures. However, this comparable performance was driven by children's poor tactile localization accuracy in the *un*crossed posture (rather than an increased accuracy in the crossed posture when hands were visible). Performance in the uncrossed-hands posture was enhanced when the children's hands were hidden; i.e., when only proprioceptive cues to posture were available, with accuracy decreasing in the uncrossed-hands posture when children had sight of their hands.

As proposed by Röder et al. (2004), the crossed hands effect arises due to an increased tactile localisation accuracy in the uncrossed-hands posture, rather than due to poorer performance in the crossed-hands posture. When using the external reference frame, in canonical postures, this would usually provide a benefit in tactile localisation accuracy (as both the current and the usual postures of the limbs are aligned). In the case of this study, when children have vision of limb posture, it seems that they do not benefit from using an external reference frame with uncrossed hands. Rather, having vision of the limb actually disrupts tactile localisation accuracy, which I have argued is the result of children's difficulty in integrating current visual information about the body into the body schema.

This was an avenue of research I further investigated in Experiment 2. Here it was found that viewing artificial hands in a posture that was either congruent or incongruent with that adopted by children aged 4 years (i.e. either uncrossed or crossed) modulated tactile localisation accuracy. When children viewed uncrossed rubber hands, this alleviated the crossed hands deficit. However, this was a consequence of a reduced tactile localisation accuracy in the uncrossed hands posture when the children had vision of uncrossed rubber hands. It seems that viewing artificial hands placed in the uncrossed posture disrupts the advantage children would usually have when their hands are in anatomical locations in space. Thus, providing further support for the assertion that children at 4 years find it difficult to incorporate visual information regarding the current posture of their limbs within their body schema.

In Experiment 3, I set out to trace the developmental trajectory of the crossed hands effect (and the emergence of an external reference frame for touch) within the first half year of life. Röder et al. (2004) and Ley et al. (2013) had argued that an external reference frame emerged as a consequence of visual experience in early life, specifically the first two years of life. These findings conflict somewhat with previous evidence of the external reference frame emerging earlier than this, with 6.5-month-olds demonstrating a crossed-hands effect (Bremner et al., 2008b). Therefore, in order to unequivocally determine when infants begin to use this reference frame, I tested 4- and 6-month-old infants on a tactile localisation task (a “crossed feet” task).

In this study, it was found that 6-, but not 4-month-olds, demonstrated a deficit in tactile localisation accuracy when their legs were crossed over and in the contralateral side of space to their usual placement. I argued that this is due to the fact that, at 4 months of age, infants are simply locating touches in anatomical (somatotopic) spatial coordinates, whereas, by 6 months of age, they attempt to code touches with respect to their external environment. Experiment 3 also demonstrated that the 6-month-olds were significantly slower in their foot responses to the tactile stimulus (in comparison to the 4-month-olds) across all conditions. I proposed that this was the result of the more complex processes required to locating the touch in external space. Ultimately, Experiment 3 was able to determine that the external reference frame in which touches are coded emerged between 4 and 6 months of age.

Of course, as mentioned above, our bodies are in constant motion and in order to accurately locate a touch on limbs that move around in space, we need to be able to keep track of changes in posture of our limbs. This concern sets the framing of the second aspect of my thesis in which I addressed the ways in which the somatosensory remapping of touch develops in early life. Previous research within this area had indicated that somatosensory remapping emerged between 6.5 and 10 months of age (Bremner et al., 2008; Rigato et al., 2014). These studies have demonstrated that at 6.5-months-old, infants do not show somatosensory remapping, however this is evident by 10 months of age. It is this developmental progression that I attempted to explain in terms of sensorimotor experience.

I conducted one pilot study (Experiment 4a) and two research studies (Experiments 4b and 5) that investigated the role of sensorimotor experience in the ability to remap touch across somatosensory changes. In terms of motor experience, I looked at a specific reaching behaviour; midline crossing, in which infants would reach into the contralateral side of space, thus crossing their midlines, to contact a toy. The hypothesis driving this investigation of the relationship between sensorimotor experience and somatosensory remapping was that perhaps the more experience the infant had of the postures their body was able to adopt, the more likely the would be able to take into consideration these changes in posture when locating touches to the limbs.

In Experiments 4b, 8-month-old infants took part in a behavioural task which assessed their ability to engage in reaches that crossed their midline and placed their hand in the contralateral side of space. Following this, infants' neural activity in response to tactile stimuli on the hands, across different arm postures (uncrossed and crossed hands) was recorded. Depending on their performance in the reaching task, infants were categorised as 'Non-crossers' (those who only engaged in ipsilateral reaches) or 'Crossers' (those infants that produced at least one reach that involved crossing the midline). Within each group, infants' neural activity in response to the touches on their hand, across different arm postures, was compared. This showed that whilst there were no reliable differences in posture for the group of ‘Non-crossers’, the ‘Crossers’ group demonstrated a significantly greater neural response to the tactile stimuli in the crossed-hands posture, relative to the uncrossed-hands posture.

Although, there was not a significant relationship between crossing group and somatosensory remapping, the fact that only those infants that crossed the midline during a reaching task demonstrated somatosensory remapping abilities is consistent with the idea that sensorimotor experience might drive the development of somatosensory remapping. This certainly warrants further investigation. As Experiment 4b was correlational in nature, in order to investigate the causal relationship between sensorimotor behaviours and somatosensory remapping, a sensorimotor training study was required: Experiment 5.

In Experiment 5, 6-month-old infants were trained to reach into the contralateral side of space via an at home sensorimotor training study, for a period of two weeks. Infants’ contralateral reaching abilities and neural responses to tactile stimuli to the hands, across changes in posture, were recorded before and after they engaged in the reaching training. No reliable effects of arm posture were found before or after the sensorimotor training. As such, I was unable to obtain evidence for sensorimotor experience being a causal driver of somatosensory remapping.

In Chapter 3 of this thesis, I addressed the question of how infants and children map touches in external space (through the use of an external frame of reference for touch) in Experiments 1, 2 and 3. Considering the role that vision plays in the use and development of the external spatial reference for touch, a question that posed itself was whether infants within the first half year of life are able to perceive touch and vision within the same space. To investigate this question, I conducted studies (Experiment 6a and 6b) in which visual and tactile stimuli were presented concurrently to infants' bodies, either on the same or different limb, and their preferential looking behaviour was assessed.

Using a measure of visual preference, it was found that both 4- and 6-month-old infants were able to distinguish between the visual-tactile stimuli occurring in the same location in space (the same foot) and the stimuli occurring in different spatial locations (different feet). However, the 4-month-old infants demonstrated a preference for the stimuli occurring in the same space, whereas the older infants showed a preference for the stimuli occurring in different regions of space (relative to the control condition where unisensory stimuli was presented across both feet). Additionally, I presented results suggesting that infants as young as 4 months of age may also be able to co-locate visual and tactile inputs within a common spatial framework (however, there may be alternative explanations for this result; which I discuss in more depth in the section below). Ultimately, from these studies, it was found that the ability to co-locate visual and tactile stimuli to the body was present by 6 months of age, with Experiment 6b demonstrating tentative evidence that this ability may emerge even earlier in development.

I continued investigating the early origins of crossmodal links between tactile and visual perception in infancy with a further infant EEG study. In this study (Experiment 7) reported in Chapter 6 examined cross-modal links in attention in 7-month-old infants. Specifically, I examined the extent to which a visual stimulus (a flash of light) could cue somatosensory in the same location. 7-month-old infants were presented with a visual cue to their hands that preceded a tactile stimulus (the probe) on either the same (cued), or different (uncued), hand. The findings of this study (Experiment 7) demonstrated an enhanced SEP waveform when the cue and the probe occurred on different hands (i.e. at the uncued location of the probe). This is a somewhat surprising finding, given that this is a reversal of the effect typically seen adults (Kennett et al., 2001; Kennett et al., 2002). However, I have explained the pattern of results within the context of sensory gating, which describes a neural process by which the brain is able to modulate its sensitivity to sensory stimuli. For example, in the case of this study, sensory gating refers to the suppression of 'irrelevant' stimuli; specifically in the congruent condition where the visual and the tactile stimuli are occurring on the same hand (i.e. in the same region of space).

From the studies described in this thesis, there are a number of conclusions that can be drawn from the findings. The first is related to the how infants and children locate touches in space; they do this by using an external reference frame for touch and this can be seen in children as young as 4 years of age. In addition to this, the external reference frame for touch emerges in the first half year of life; namely between 4 and 6 months. Secondly, I have investigated the relationship between sensorimotor experience and somatosensory remapping; considering the null finding of the relationship between sensorimotor experience (midline crossing ability) and somatosensory remapping, it is difficult to conclude that sensorimotor experience is or is not a causal driver of somatosensory remapping. Indeed, I discuss several potential reasons for these null findings in greater depth in the section below.

Thirdly, I have presented evidence regarding visual-tactile spatial relationships in the first year of life. Specifically, that it is between 4 and 6 months of age that infants are able to map visual and tactile stimuli within common spatial co-ordinates. Additionally, I have provided evidence of early acquired crossmodal links between vision and touch via crossmodal attentional cuing effects in infancy. These key findings are discussed in greater depth below.

7.2 The emergence of an external reference frame for touch

Findings from studies in this thesis have demonstrated that it is not until 6 months of age that infants coded touch in space. The younger age group tested (4-month-olds) seemed to be coding touch in anatomical frame of reference. So, how do the findings from this study relate to the way in which infants and children perceive touch in space, or indeed their understanding and perception of the world?

If, as I am claiming, infants prior to 6 months code touches in an anatomical frame of reference only, this would suggest that tactile perception is quite disjointed from a representation of the external world arriving from other sense modalities. Touches on the body could be felt, but the infant would be unable to relate this felt touch to the visual or external world. Indeed, this idea of a developmental progression from perceiving touch relative to itself only, but later in relation to the external world chimes somewhat with Piaget's (1952) 'organisation of reciprocal assimilation'; in that, to begin with, the sensory schemas are conceived of as separate but become through development integrated to form a more objective view of the world (I discuss this in greater depth in Section 7.4 of this chapter).

Other studies in this thesis have investigated how children locate touches in space using a 'crossed hands task', and the role of current visual information of the limb on tactile localisation. From these studies, it was found that when children saw either their own, or artificial, limbs in the uncrossed hands posture, this interfered with their tactile localisation accuracy. However, this interference was limited to when the children's arms were in the more usual, uncrossed posture. In previous sections of this thesis (Chapter 3, Sections 3.4 and 3.8), I have proposed that 4-year-olds have difficulty integrating current visual information of limb position with prior information regarding the body schema, and are thus unable to derive the benefit they would normally gain when their limbs are in a canonical posture. To extend this theory, it could be argued that whilst children at 4 years are able to locate touches with reference to the allocentric environment, children of this age are still refining the ways in which sensory cues to the body help them to locate touches in the world; there is the continued integration of touch in a multisensory body representation.

Whilst conducting the studies in this thesis, a recurring theme that began to emerge related to the relationship between vision and touch within space. Considering that vision is a requisite for the use, and development, of the external spatial reference frame for touch (Röder et al., 2004; Ley et al., 2013; Chapter 3, Section 3.9 of this thesis), this prompted the question of whether infants are able to perceive touch and vision within the same space. Testing 4- and 6-month-old infants, I found that, by 6 months of age, infants are able to co-locate visual and tactile information. Further to this, there was tentative evidence that perhaps even the 4-month-old infants in this study also possessed this ability. However, as discussed earlier, this particular conclusion does not go unqualified. It was found that 4-month-old infants demonstrated a spontaneous novelty preference for the condition in which the visual and tactile stimuli occurred in the same region of space as opposed to when the stimuli (from either one or both modalities) occurred in different regions of space. As such, it could be argued that rather than reliably distinguishing between stimuli presented in the same spatial location versus separate regions of space, infants of this tender age are merely showing a preference for this condition because two stimuli are occurring on the same foot. This is an explanation that is not explicitly ruled out by the control condition used in this study.

As such, an immediate challenge for future research would be to conduct a further study investigating the finding that 4-month-old infants show a familiarity preference for visual-tactile stimuli that occurs in the same region of space in comparison to unisensory stimuli that occurs in the same spatial location. If this visual preference is evident for only the multisensory condition, one could argue that infants at this age expect concurrent visual and tactile inputs to occur in the same location.

A further study could be to conduct the original study (Experiment 6b) with a younger group of infants, perhaps even newborns. Using this population would allow us to examine whether visual-tactile co-location is present at birth, clarifying the developmental trajectory of this ability. If newborn infants are unable to distinguish between conditions when visual-tactile stimuli occurs on the same foot versus different feet (via preferential looking measures), this might suggest that multisensory experience is necessary for learning to perceive visual-tactile co-location. Indeed, perhaps learning about co-location in bimodal presentations scaffolds infants learning of locating touches in external space when such touches are presented alone (as in Experiment 3 of this thesis).

Visual-tactile co-location abilities were found to be present by 6 months of age (with tentative evidence for this emerging earlier). This is a similar trajectory to the emergence of an external frame of reference for touch (with this reference frame also emerging between 4 and 6 months). From this, perhaps it is possible to argue that the infants in this current study (even those at 4 months) are representing the spatial locations of the visual and tactile stimuli within an external reference frame for touch? However, considering that Bremner et al. (2008b) found that infants in the first half year of life do not tend to look towards the site of a touch on the body (before a manual movement), it seems more plausible to argue that the infants in the visual-tactile study, their perceptions of the tactile event are captured by the visual flash of light. This visual stimulus scaffolds the infant's ability to then orient to, and code, the location of the tactile stimulus. Therefore, rather than using an external reference frame to locate touches on the body, the 4-month-old infant is using the visual frame of reference. Of course, it could be argued that this is the same for the 6-month-old infant. However, our findings from Experiment 3 suggested that infants at 6 months are already using an external reference frame to locate touches in space. Ultimately, it may be that the visual reference frame also impacts how (and when) the external frame of reference for touch develops in the first half year of life.

A further line of investigation was borne out of the findings from the research described above. Experiment 7 also examined the spatial links between visual-tactile events. In this study, infant's were presented with a visual cue, followed by a tactile probe to the hands. The cue and the probe occurred on either the same, or different, hands. In this study, infants' demonstrated a greater neural response when the cue and the probe were presented to different hands. I have explained this finding in terms of sensory gating; infants are suppressing stimuli where the visual and the tactile stimuli are occurring on the same hand (i.e. as the stimuli are occurring in the same region of space, this area of space is processed as 'familiar' and attention is directed to the more novel area of space; the uncued hand).

Considering that this study did not find enhanced neural activity when the cue and the probe occurred on the same hand, a question that remains to be answered is whether infants' demonstrate this cueing effect and under which conditions exogenous cueing occurs. Perhaps by varying the interstimulus interval between the cue and the probe (by increasing it), we are likely to see exogenous cueing effects. Additionally, it may be fruitful to investigate this in younger infants, especially considering the tentative evidence of crossmodal spatial links at 4 months of age that have been found (Experiment 6b, Chapter 5 of this thesis).

The results of this study (as well as those of Experiments 6a and 6b) have demonstrated the spatial links between the visual and tactile modalities. A potential study that could be conducted to further investigate the links (in terms of both co-location and crossmodal attention) between these sensory modalities and spatial attention would be to manipulate the posture of the infant's arms (i.e. by crossing the hands at the forearms). In this less usual, crossed hands posture, the visual and tactile receptive fields are no longer aligned and the remapping process between vision and touch can be examined. This experiment would inform us of whether infants expect visual-tactile events to occur in the same spatial location, and whether they can update the location of the visual-tactile stimulus across changes in posture.

The above section has dealt with how infants (and children, alike) locate touches in space, mapping touches in external co-ordinates. However, the question of how the location of these touches is updated across changes in posture remains. I address this question in the following section.

7.3 Sensorimotor drivers of somatosensory remapping

In Chapter 4, I described a series of studies that explored the relationship between sensorimotor experience (specifically reaches that involved crossing the midline) and somatosensory remapping. Experiment 4b depicted a correlation study in which a non-significant interaction between somatosensory remapping and midline crossing reaching (sensorimotor experience) was found. In addition to this, Experiment 5 (which involved measuring somatosensory remapping before and after infants were trained to reach across the midline) also demonstrated null findings. So what does this mean in terms of the relationship between sensorimotor experience and somatosensory remapping?

For one, these null findings could suggest that there is not a relationship between sensorimotor experience (specifically midline crossing reaching) and somatosensory remapping. It may be that it is not sensorimotor experience that is a causal driver of somatosensory remapping, but, for instance, brain maturation. For example, it may be that between the ages of 6 and 8 months, there is an increase in both intra and inter-hemispheric connections in the brain, with particular emphasis on increased connections within the somatosensory network (see Nevalainen, Lauronen & Pihko, 2014). Additionally, the maturation of the corpus callosum may be of importance (Ballesteros et al., 1993; Teicher et al., 2004; Barkovich & Kjos, 1988). When the hands are crossed, and in the contralateral side of space to their usual placement, the anatomical location of a touch on the hand conflicts with the location of the touch in *visual* space. It may be that increased neural connections within the somatosensory network and corpus callosum are required to initiate, or more efficiently, integrate inputs from vision and touch (so that these spatial reference frames are aligned) to then dynamically update the spatial location of the touch across changes in posture.

This increase in neural connections could be a contributing factor to, not only the somatosensory remapping process, but may also be involved in the range of motoric and limb movements and postures the developing infant is capable of adopting. Though, of course, this explanation is not necessarily independent of sensorimotor experience explanations as it is entirely possible that experiential and maturational factors could interact.

Another potential explanation for this null finding may have been the result of methodological choices. I present the methodology used in the current studies, as well as potential alternatives that could be used in future studies. Firstly, Experiment 5 used a passive reaching training task where parents would initiate and guide the infant's contralateral reaching behaviour. It may be that infants need to engage in active sensorimotor experience for this to impact somatosensory remapping. Therefore, for future research, a motor training study in which infants take part in active contralateral reaching (where the infant initiates and guides their reaching behaviour) could be conducted to assess this hypothesis.

In addition to this, as a few parents in my sample reported that infants lost interest and were bored of the training toys towards the end of the two weeks of training, for future studies I would include a number of contralateral reaching tasks for the infant to perform throughout the two weeks, so as to maximise the infant's interest in the tasks and keep them fully engaged throughout the fourteen training sessions. I would also include toys that were more interactive and provided infants with visual or auditory feedback whilst the infant engaged with them, and stopped when they did not. Another possible training activity I could introduce is one that includes the 'sticky mittens' (as described in Chapter 4, Section 4.4), this would encourage infants to make reaches, and would also allow them to manipulate objects not only in their initial placement (in the contralateral side of space), but also on retrieval into ipsilateral space.

Parents could then remove the toy and place it back, eliciting further reaching attempts from the infants. It may be that these changes would encourage infants to continue playing with the toys and completing the reaching training protocol.

Finally, the reaching task employed in this series of studies to examine midline crossing reaching, may have not been a sensitive enough measure to investigate this reaching behaviour successfully. It is at approximately 6 months of age that infants are weaned from a purely liquid diet to include solids. With the increasing popularity of baby led weaning, perhaps a more successful and naturalistic method of measuring midline crossing frequency would have been to present infants with food items (real or toys) laid out on a high chair tray, on either side of the midline. This may have been more familiar for the infants and may have encouraged more midline crossing reaching behaviours.

Whilst I was unable to conclude that sensorimotor experience was a causal driver of somatosensory remapping, in Experiment 4b I found that a group of 8-month-olds demonstrated somatosensory remapping. A point of note is the fact that these 8-month-olds began to spatially remap touches across posture changes at 298 ms following a touch on their hands. This is later than that found by Rigato et al., (2014) in 10-month-old infants. They found this process to begin at 58 ms following a tactile stimulus to the hand. There are a number of potential explanations for this delay in latency. For example, given the differences in maturation of the somatosensory areas of the brain in these two age groups (Pihko et al., 2005; Pihko & Lauronen, 2004, discussed in Chapter 4, section 4.3.4), this difference in latency is not surprising. Alternatively, a suggestion put forward by Rigato et al. (2014) asserts that at earlier stages of development (i.e. in younger infants), posture is taken into account at somewhat more post-perceptual stages of processing. In comparison, by 10 months of age, posture is accounted for more automatically and at earlier stages of somatosensory perception.

Ultimately, this series of studies (Experiments 4a, 4b and 5) has established that it was possible to observe somatosensory remapping in infants aged 8 months (albeit in a group of infants that exhibited midline crossing reaching behaviours). Whereas, previous research asserted that somatosensory remapping abilities emerged between 6.5 and 10 months of age, the findings from Experiment 4b narrowed this interval to between 6.5 and 8 months. In addition to this, the null finding of a relationship between sensorimotor experience and somatosensory remapping suggests that this is not a straightforward relationship, with other potential factors (such as brain maturation) to consider. An immediate challenge for future research is to disentangle this relationship.

7.4 Findings in context: What does this mean for accounts of multisensory development?

The findings from Experiment 3 (in which it is not until 6 months of age that infants code touches in external co-ordinates) are especially problematic for established theories of multisensory development, particularly the Intersensory Redundancy Hypothesis (IRH; Bahrick and Lickliter, 2000). The IRH argues that the human infant attends to various properties of a stimulus, some of which are redundant. For example, when visually and haptically exploring an object, the shape of the stimulus would be redundant (as both the visual and tactile sensory modalities would be capable of determining this property). If the infant attends to this redundant information, it is able to distinguish sensory information that unifies a stimulus in their environment.

Further to this, the IRH asserts that this ability to detect amodal stimulation across the senses is present in early life, suggesting that the senses are aligned in early infancy before becoming differentiated in later life. However, considering the results of Experiment 3 of this thesis, this may not be entirely applicable to locating touches in space. Indeed, this pattern of results suggests that, at first, the sensory modalities (in this case vision and touch) work in isolation and through experience of the environment do these senses become integrated. If, in early life, the senses are separate, how does this integration occur? Piaget (1952) proposed that separate sensory schemas interact to form objective representations of the world ('organisation of reciprocal assimilation'); at first a toy that can be grasped is moved into view and becomes a toy that can be both seen and grasped, thus producing a reciprocal relationship. In terms of the localization of touch in space, in early life, a touch on the body is not related to a visual event, rather simply felt. However, perhaps fortuitously, the infant observes an impinging touch and learns to relate a felt touch with the visual event of this impinging touch. So, where the the visual and tactile modalities were previously separated, they are now integrated.

However, whilst Piaget's theory of integration elegantly explains the findings of Experiment 3, the studies regarding the co-location of vision and touch in this thesis (Experiments 6a and 6b) provide cautious support for the IRH. In these studies, there was tentative evidence of 4-month-old infants expecting visual and tactile stimuli to occur in a common spatial location. As such, demonstrating support for the IRH. So how does this reconcile with the findings of Experiment 3 and Piaget's view of integration over differentiation (the IRH)? Perhaps in order to address and resolve this concern, a study in which newborn infants' abilities to co-locate visual-tactile information could be measured. If it was found that newborns are able to co-locate visual-tactile information, this would support the IRH. If, however, newborns do not have the capability for this, it may lend support for Piaget's theory of constructionism. Ultimately, the findings from the various studies of this thesis have raised potential queries of established accounts of multisensory development, with scope to address these queries in future studies.

7.5 Conclusion

From the studies conducted in this thesis, I have found that, in early life, touch is quite separate from the other senses. It is not until 6 months that infants begin to consider the allocentric environment when locating touches in space, which suggests an extended trajectory of development in which touch is gradually linked with other senses. This then allows infants and children a more coherent and objective perception of themselves in relation to the world around them.

The conclusions drawn from the series of studies conducted in this thesis raise some important questions in terms of the current theories of multisensory development. Initially, in early life, touch is coded without reference to external co-ordinates and is quite disjointed from the other senses. It is only at 6 months that infants begin to consider the external environment when locating touches. This developmental trajectory lends support to Piaget's 'organisation of reciprocal assimilation' theory, but is quite problematic for the IRH; although, studies in this thesis have also shown tentative evidence in support of the IRH. A potential resolution for this contradiction may lie in the fact that, initially, the human infant requires information from multiple sensory sources to locate touches in space (i.e. from the visual and tactile modalities; with the visual stimulus scaffolding the tactile stimulus). As the infant continues to develop, they no longer require the visual stimulus to scaffold their localisation of the touch and are then able to code the location of this touch in external co-ordinates. Finally, after infants are able to use the external reference frame for touch, they then are able to update the location of this touch via somatosensory remapping; which may occur as a result of maturation of hemispheric connections in the brain or through sensorimotor experience.

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Appendices

Appendix A

Counterbalancing order for Experiment 1

1	Unseen Unx	Unseen X	Seen Unx	Seen X
2	Unseen Unx	Unseen X	Seen X	Seen Unx
3	Unseen X	Unseen Unx	Seen X	Seen Unx
4	Unseen X	Unseen Unx	Seen Unx	Seen X
5	Seen Unx	Seen X	Unseen Unx	Unseen X
6	Seen Unx	Seen X	Unseen X	Unseen Unx
7	Seen X	Seen Unx	Unseen X	Unseen Unx
8	Seen X	Seen Unx	Unseen Unx	Unseen X
9	Unseen Unx	Seen Unx	Unseen X	Seen X
10	Unseen X	Seen X	Unseen Unx	Seen Unx
11	Unseen Unx	Seen X	Unseen X	Seen Unx
12	Unseen X	Seen Unx	Unseen Unx	Seen X
13	Seen Unx	Unseen Unx	Seen X	Unseen X
14	Seen X	Unseen X	Seen Unx	Unseen Unx
15	Seen Unx	Unseen X	Seen X	Unseen Unx
16	Seen X	Unseen Unx	Seen Unx	Unseen X
17	Unseen Unx	Seen X	Seen Unx	Unseen X
18	Unseen X	Seen X	Seen Unx	Unseen Unx
19	Unseen Unx	Seen Unx	Seen X	Unseen X
20	Unseen X	Seen Unx	Seen X	Unseen Unx
21	Seen Unx	UnSeen X	UnSeen Unx	Seen X
22	Seen X	UnSeen X	UnSeen Unx	Seen Unx
23	Seen Unx	UnSeen Unx	UnSeen X	Seen X
24	Seen X	UnSeen Unx	UnSeen X	Seen Unx

Appendix B

Counterbalancing order for Experiment 2

1	No RH, Hands Unx	No RH, Hands X	RH Unx, Hands Unx	RH Unx, Hands X	RH X, Hands Unx	RH X, Hands X
2	RH Unx, Hands Unx	RH Unx, Hands X	RH X, Hands Unx	RH X, Hands X	No RH, Hands Unx	No RH, Hands X
3	RH X, Hands Unx	RH X, Hands X	No RH, Hands Unx	No RH, Hands X	RH Unx, Hands Unx	RH Unx, Hands X
4	No RH, Hands Unx	No RH, Hands X	RH X, Hands Unx	RH X, Hands X	RH Unx, Hands Unx	RH Unx, Hands X
5	RH Unx, Hands Unx	RH Unx, Hands X	No RH, Hands Unx	No RH, Hands X	RH X, Hands Unx	RH X, Hands X
6	RH X, Hands Unx	RH X, Hands X	RH Unx, Hands Unx	RH Unx, Hands X	No RH, Hands Unx	No RH, Hands X
7	No RH, Hands X	No RH, Hands Unx	RH Unx, Hands X	RH Unx, Hands Unx	RH X, Hands X	RH X, Hands Unx
8	RH Unx, Hands X	RH Unx, Hands Unx	RH X, Hands X	RH X, Hands Unx	No RH, Hands X	No RH, Hands Unx
9	RH X, Hands X	RH X, Hands Unx	No RH, Hands X	No RH, Hands Unx	RH Unx, Hands X	RH Unx, Hands Unx
10	No RH, Hands X	No RH, Hands Unx	RH X, Hands X	RH X, Hands Unx	RH Unx, Hands X	RH Unx, Hands Unx
11	RH Unx, Hands X	RH Unx, Hands Unx	No RH, Hands X	No RH, Hands Unx	RH X, Hands X	RH X, Hands Unx
12	RH X, Hands X	RH X, Hands Unx	RH Unx, Hands X	RH Unx, Hands Unx	No RH, Hands X	No RH, Unx

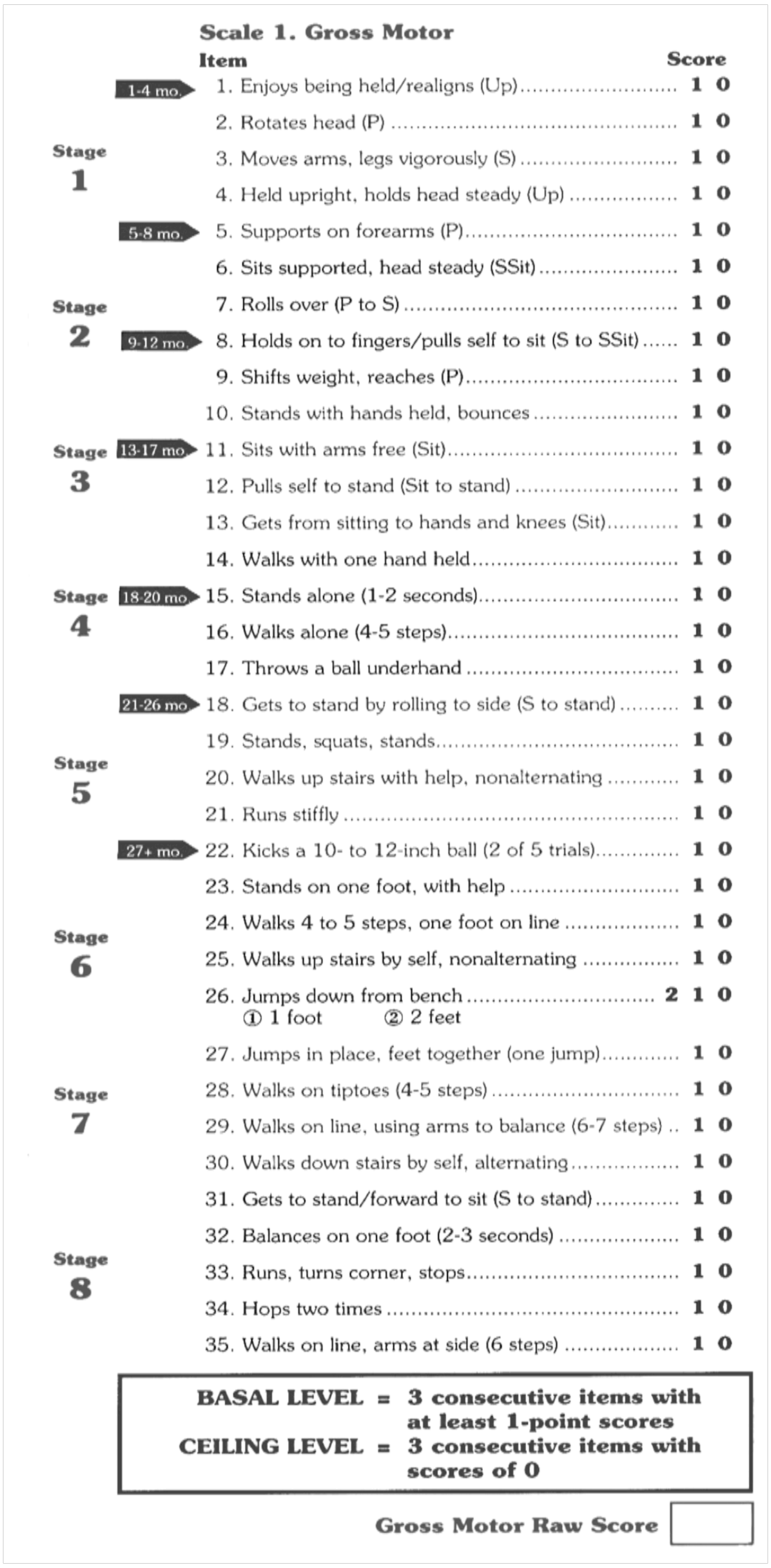
Appendix C

Counterbalancing order for midline crossing reaching task in Experiments 4a, 4b and 5

1	Left shoulder	Right shoulder	Midline
2	Right shoulder	Left shoulder	Midline
3	Midline	Left shoulder	Right shoulder
4	Midline	Right shoulder	Left shoulder
5	Right shoulder	Midline	Left shoulder
6	Left shoulder	Midline	Right shoulder

Appendix D

Mullen scales of early learning: Gross motor scale used in Experiments 4b and 5



Scale 1. Gross Motor

Stage	Age	Item	Score
Stage 1	1-4 mo.	1. Enjoys being held/realigns (Up)	1 0
		2. Rotates head (P)	1 0
		3. Moves arms, legs vigorously (S)	1 0
		4. Held upright, holds head steady (Up)	1 0
Stage 2	5-8 mo.	5. Supports on forearms (P)	1 0
		6. Sits supported, head steady (SSit)	1 0
		7. Rolls over (P to S)	1 0
	9-12 mo.	8. Holds on to fingers/pulls self to sit (S to SSit)	1 0
		9. Shifts weight, reaches (P)	1 0
Stage 3		10. Stands with hands held, bounces	1 0
	13-17 mo.	11. Sits with arms free (Sit)	1 0
		12. Pulls self to stand (Sit to stand)	1 0
		13. Gets from sitting to hands and knees (Sit)	1 0
Stage 4		14. Walks with one hand held	1 0
	18-20 mo.	15. Stands alone (1-2 seconds)	1 0
		16. Walks alone (4-5 steps)	1 0
		17. Throws a ball underhand	1 0
Stage 5	21-26 mo.	18. Gets to stand by rolling to side (S to stand)	1 0
		19. Stands, squats, stands	1 0
		20. Walks up stairs with help, nonalternating	1 0
		21. Runs stiffly	1 0
Stage 6	27+ mo.	22. Kicks a 10- to 12-inch ball (2 of 5 trials)	1 0
		23. Stands on one foot, with help	1 0
		24. Walks 4 to 5 steps, one foot on line	1 0
		25. Walks up stairs by self, nonalternating	1 0
		26. Jumps down from bench ① 1 foot ② 2 feet	2 1 0
Stage 7		27. Jumps in place, feet together (one jump)	1 0
		28. Walks on tiptoes (4-5 steps)	1 0
		29. Walks on line, using arms to balance (6-7 steps)	1 0
		30. Walks down stairs by self, alternating	1 0
Stage 8		31. Gets to stand/forward to sit (S to stand)	1 0
		32. Balances on one foot (2-3 seconds)	1 0
		33. Runs, turns corner, stops	1 0
		34. Hops two times	1 0
		35. Walks on line, arms at side (6 steps)	1 0

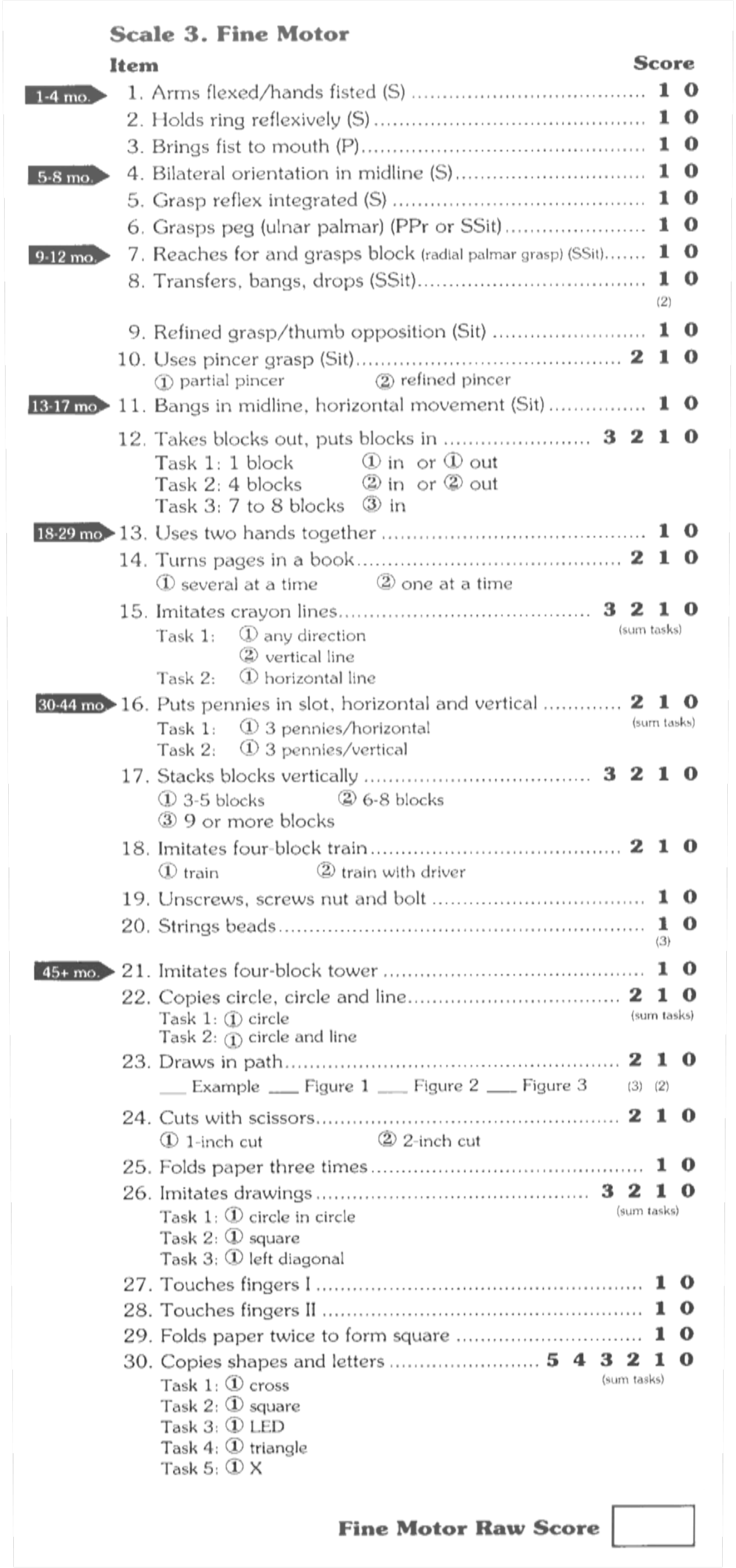
BASAL LEVEL = 3 consecutive items with at least 1-point scores

CEILING LEVEL = 3 consecutive items with scores of 0

Gross Motor Raw Score ☐

Appendix E

Mullen scales of early learning: Fine motor scale used in Experiments 4b and 5



Scale 3. Fine Motor

Item **Score**

1-4 mo. 1. Arms flexed/hands fisted (S) **1 0**
2. Holds ring reflexively (S) **1 0**
3. Brings fist to mouth (P).. **1 0**
5-8 mo. 4. Bilateral orientation in midline (S).............................. **1 0**
5. Grasp reflex integrated (S) **1 0**
6. Grasps peg (ulnar palmar) (PPr or SSit)...................... **1 0**
9-12 mo. 7. Reaches for and grasps block (radial palmar grasp) (SSit)....... **1 0**
8. Transfers, bangs, drops (SSit)................................... **1 0**
(2)

9. Refined grasp/thumb opposition (Sit) **1 0**
10. Uses pincer grasp (Sit)... **2 1 0**
① partial pincer ② refined pincer
13-17 mo 11. Bangs in midline, horizontal movement (Sit) **1 0**

12. Takes blocks out, puts blocks in **3 2 1 0**
Task 1: 1 block ① in or ① out
Task 2: 4 blocks ② in or ② out
Task 3: 7 to 8 blocks ③ in
18-29 mo 13. Uses two hands together **1 0**
14. Turns pages in a book... **2 1 0**
① several at a time ② one at a time
15. Imitates crayon lines.. **3 2 1 0**
(sum tasks)
Task 1: ① any direction
② vertical line
Task 2: ① horizontal line
30-44 mo 16. Puts pennies in slot, horizontal and vertical **2 1 0**
(sum tasks)
Task 1: ① 3 pennies/horizontal
Task 2: ① 3 pennies/vertical
17. Stacks blocks vertically **3 2 1 0**
① 3-5 blocks ② 6-8 blocks
③ 9 or more blocks
18. Imitates four-block train.. **2 1 0**
① train ② train with driver
19. Unscrews, screws nut and bolt **1 0**
20. Strings beads.. **1 0**
(3)

45+ mo. 21. Imitates four-block tower **1 0**
22. Copies circle, circle and line.................................. **2 1 0**
(sum tasks)
Task 1: ① circle
Task 2: ① circle and line
23. Draws in path... **2 1 0**
___ Example ___ Figure 1 ___ Figure 2 ___ Figure 3 (3) (2)

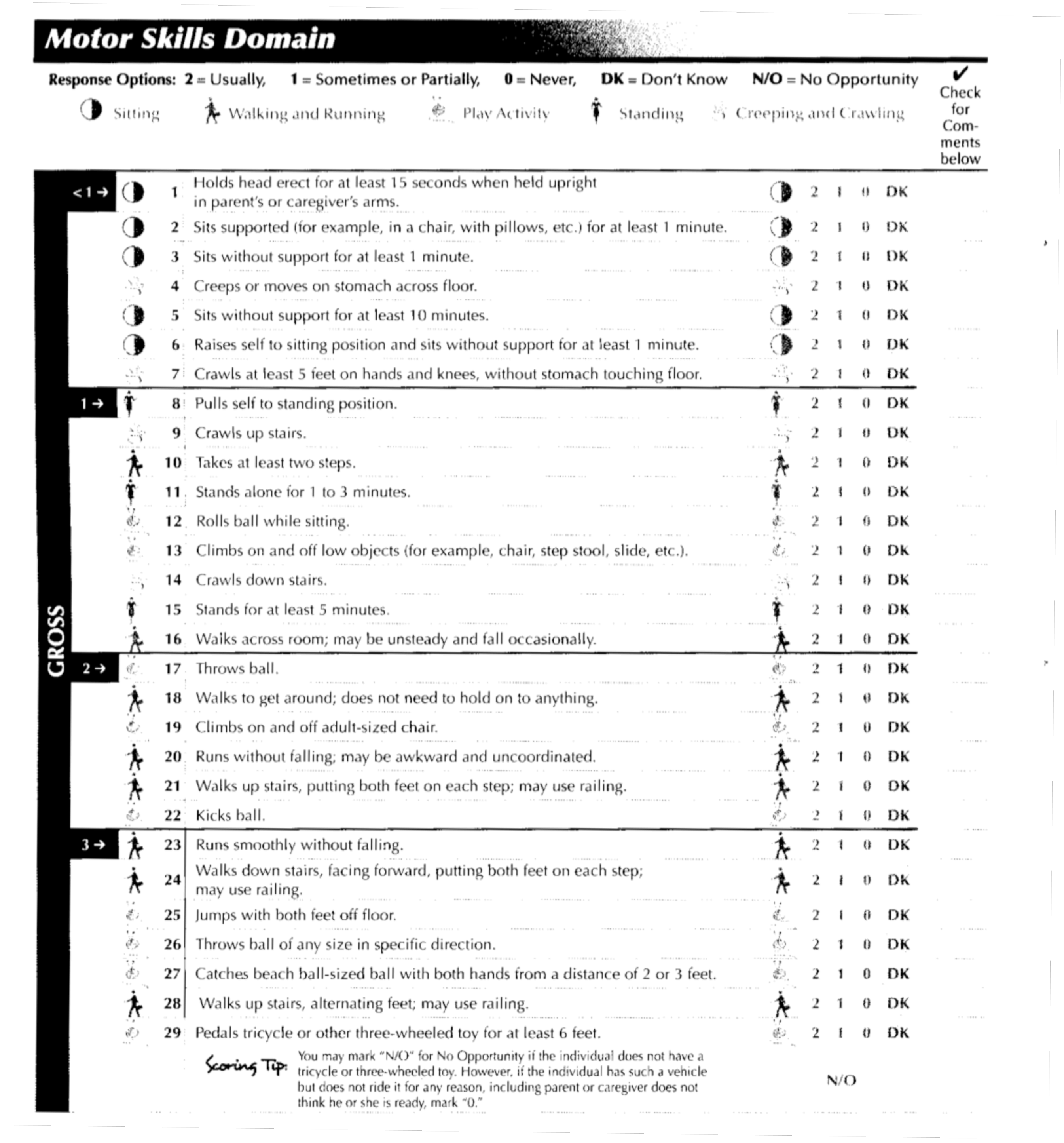
24. Cuts with scissors... **2 1 0**
① 1-inch cut ② 2-inch cut
25. Folds paper three times **1 0**
26. Imitates drawings **3 2 1 0**
(sum tasks)
Task 1: ① circle in circle
Task 2: ① square
Task 3: ① left diagonal
27. Touches fingers I **1 0**
28. Touches fingers II **1 0**
29. Folds paper twice to form square **1 0**
30. Copies shapes and letters **5 4 3 2 1 0**
(sum tasks)
Task 1: ① cross
Task 2: ① square
Task 3: ① LED
Task 4: ① triangle
Task 5: ① X

Fine Motor Raw Score ☐

Appendix F

Vineland adaptive behaviour scales: Gross motor scale used in Experiments 4b and 5

Appendix G



Motor Skills Domain

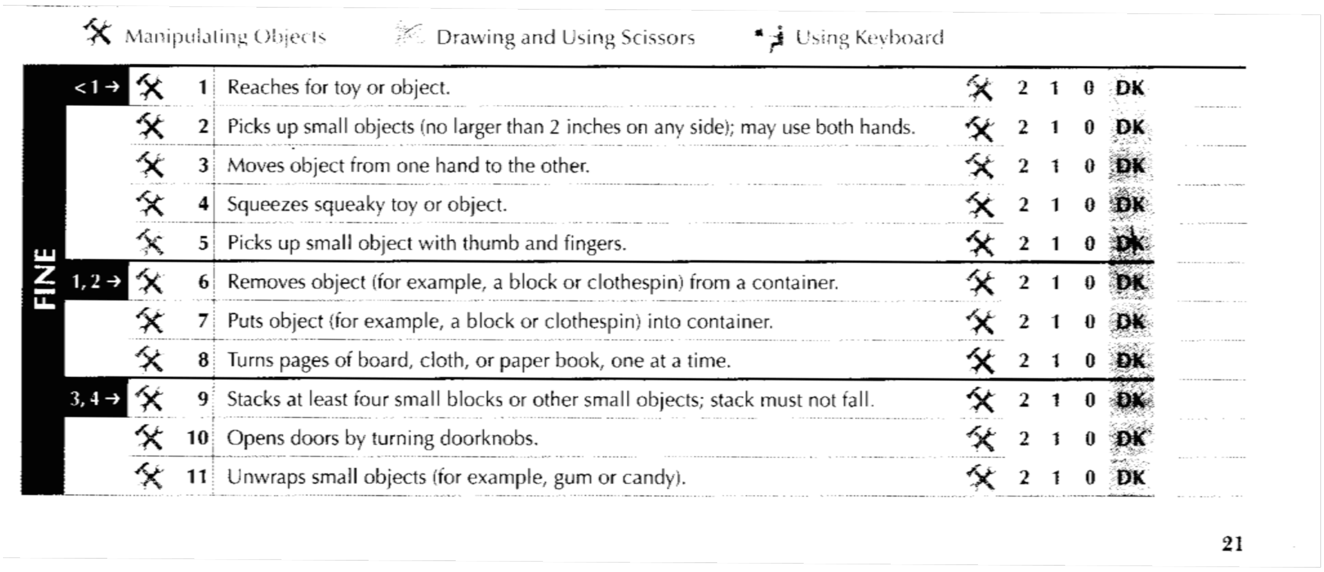
Response Options: 2 = Usually, **1** = Sometimes or Partially, **0** = Never, **DK** = Don't Know **N/O** = No Opportunity

◑ Sitting 🚶 Walking and Running ⚽ Play Activity 🧍 Standing 🐾 Creeping and Crawling

						✔ Check for Comments below
GROSS <1 →	◑	1	Holds head erect for at least 15 seconds when held upright in parent's or caregiver's arms.	◑	2 1 0 DK	
	◑	2	Sits supported (for example, in a chair, with pillows, etc.) for at least 1 minute.	◑	2 1 0 DK	
	◑	3	Sits without support for at least 1 minute.	◑	2 1 0 DK	
	🐾	4	Creeps or moves on stomach across floor.	🐾	2 1 0 DK	
	◑	5	Sits without support for at least 10 minutes.	◑	2 1 0 DK	
	◑	6	Raises self to sitting position and sits without support for at least 1 minute.	◑	2 1 0 DK	
	🐾	7	Crawls at least 5 feet on hands and knees, without stomach touching floor.	🐾	2 1 0 DK	
1 →	🧍	8	Pulls self to standing position.	🧍	2 1 0 DK	
	🐾	9	Crawls up stairs.	🐾	2 1 0 DK	
	🚶	10	Takes at least two steps.	🚶	2 1 0 DK	
	🧍	11	Stands alone for 1 to 3 minutes.	🧍	2 1 0 DK	
	⚽	12	Rolls ball while sitting.	⚽	2 1 0 DK	
	⚽	13	Climbs on and off low objects (for example, chair, step stool, slide, etc.).	⚽	2 1 0 DK	
	🐾	14	Crawls down stairs.	🐾	2 1 0 DK	
	🧍	15	Stands for at least 5 minutes.	🧍	2 1 0 DK	
	🚶	16	Walks across room; may be unsteady and fall occasionally.	🚶	2 1 0 DK	
2 →	⚽	17	Throws ball.	⚽	2 1 0 DK	
	🚶	18	Walks to get around; does not need to hold on to anything.	🚶	2 1 0 DK	
	⚽	19	Climbs on and off adult-sized chair.	⚽	2 1 0 DK	
	🚶	20	Runs without falling; may be awkward and uncoordinated.	🚶	2 1 0 DK	
	🚶	21	Walks up stairs, putting both feet on each step; may use railing.	🚶	2 1 0 DK	
	⚽	22	Kicks ball.	⚽	2 1 0 DK	
3 →	🚶	23	Runs smoothly without falling.	🚶	2 1 0 DK	
	🚶	24	Walks down stairs, facing forward, putting both feet on each step; may use railing.	🚶	2 1 0 DK	
	⚽	25	Jumps with both feet off floor.	⚽	2 1 0 DK	
	⚽	26	Throws ball of any size in specific direction.	⚽	2 1 0 DK	
	⚽	27	Catches beach ball-sized ball with both hands from a distance of 2 or 3 feet.	⚽	2 1 0 DK	
	🚶	28	Walks up stairs, alternating feet; may use railing.	🚶	2 1 0 DK	
	⚽	29	Pedals tricycle or other three-wheeled toy for at least 6 feet.	⚽	2 1 0 DK N/O	

Scoring Tip: You may mark "N/O" for No Opportunity if the individual does not have a tricycle or three-wheeled toy. However, if the individual has such a vehicle but does not ride it for any reason, including parent or caregiver does not think he or she is ready, mark "0."

Vineland adaptive behaviour scales: Fine motor scale used in Experiments 4b and 5



Manipulating Objects Drawing and Using Scissors Using Keyboard

FINE	<1 →	1	Reaches for toy or object.	2 1 0 DK
		2	Picks up small objects (no larger than 2 inches on any side); may use both hands.	2 1 0 DK
		3	Moves object from one hand to the other.	2 1 0 DK
		4	Squeezes squeaky toy or object.	2 1 0 DK
		5	Picks up small object with thumb and fingers.	2 1 0 DK
	1, 2 →	6	Removes object (for example, a block or clothespin) from a container.	2 1 0 DK
		7	Puts object (for example, a block or clothespin) into container.	2 1 0 DK
		8	Turns pages of board, cloth, or paper book, one at a time.	2 1 0 DK
	3, 4 →	9	Stacks at least four small blocks or other small objects; stack must not fall.	2 1 0 DK
		10	Opens doors by turning doorknobs.	2 1 0 DK
		11	Unwraps small objects (for example, gum or candy).	2 1 0 DK

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Appendix H

Motor milestones (parent report) questionnaire used in Experiment 5

My baby can:	**Not sure**	**Not yet**	**Yes**	**Age of acquisition**
roll from front to back				
roll from back to front				
sit with support (on lap)				
sit with support (in baby chair)				
sit with support (cushions/pillows)				
sit without support				
when lying on front, can they push themselves up with their hands?				
If ‘yes’ – can they support themselves with just one hand?				
If ‘yes’ – with the free hand, do they reach/grasp for things?				
stay on hands and knees in crawling posture?				
If ‘yes’ – can they support themselves with just one hand?				
If ‘yes’ – with the free hand, do they reach/grasp for things?				
go from sitting to lying (on front)				
go from sitting to lying (on back)				
pull self up from lying (on back) with help (i.e. holding onto fingers)				
crawl (shuffling)				
crawl (commando crawling)				
rock back and forth when in crawling position				
crawl (alternating hands and knees)				
can go from sitting to crawling				
pull self to stand from sitting (holding onto parent’s hands)				
pull self to stand from sitting (with furniture)				

Appendix I

Motor training protocol given to parents in Experiment 5

What you will need:

- Pen/pencil
- Clock/timer
- Special toy board

Note down the time you start in the learning journal!

1) Put baby on your lap

- It might be easiest to sit on the floor with your legs crossed and have baby nestled in your lap
- Place your left arm around your baby's middle, with their left arm secured by yours
- Make sure their back is close to your chest and that one of their arms is free

2) Place toy board so that the middle of it is in line with your baby's midline, making sure your baby can reach the toys without difficulty:

- This should be across their knees and close to their body, so they can reach it with ease

3) With your right hand, take hold of your baby's right arm. Keeping the other arm secure beneath yours, place their right hand on the toy that is opposite to this hand (i.e. on the left hand side of the board).

4) Allow them to play with and explore the toy with the opposite hand.

5) After 1 minute of playing, remove your child's right hand from the toy. Remove the toy from their lap (place the toy beside you)

6) Now, with the baby still on your lap, place your right arm around their middle, with their right arm secured beneath yours.

- Make sure their back is close to your chest and that their left arm is free
- Then place the toy board back on baby's lap, making sure that the middle of the board is in line with your baby's middle

7) Taking your child's left hand, place this on the toy that is opposite to it (i.e. on the right side of the board). Allow them to play with and explore the toy with their left hand only for 1 minute.

8) Repeat the above steps 3 times – so baby has a total play time of 6 minutes (3 minutes for each hand)

9) After the 6 minutes of play, release your baby's arms so that it can play freely with the toy, in any way they like, with both hands for as long as they want to (until they seem to get bored).

Remember to fill in the rest of your baby's learning journal for today!

Tidy away the special toy! This is so that the toy is still appealing and exciting for your child every time they play with it.

Frequently Asked Questions

Should I sit my baby at a table to do the training?

It's actually better to have them on your lap. This way they can use your chest to support their backs more securely. Also, they are able to reach and play with the toys with ease

Does it matter what time of day we do the training?

Not at all. Whatever time is convenient for you, when your baby is in an active and happy mood. Although it would be preferable if you did the training at approximately the same time of day, we understand that's not entirely possible with a young baby

What if we miss a training session?

If possible, try to do that session as soon as you remember. But if you can't, you can either double up the following day's session or do 2 throughout the next day

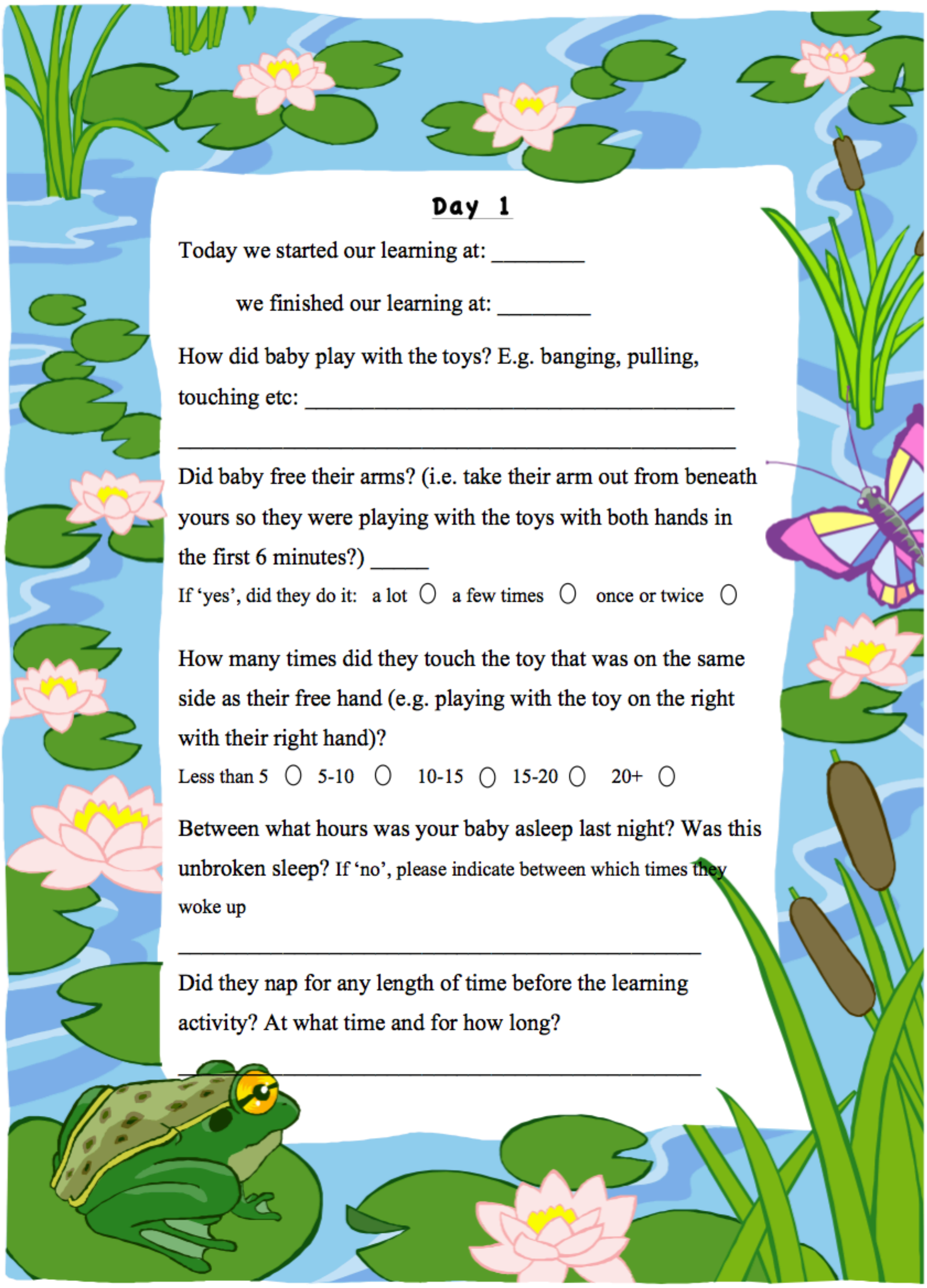
I can't remember a few details about carrying out the training, what should I do?

I will have sent you a link to a video showing how to do the training. If you would like me to resend the link, you can contact me via phone or email

If you have any other questions, please do feel free to contact me on: **020 7717 2983** or **020 7078 5128** or email me at j.begum@gold.ac.uk

Appendix J

Example training log parents completed after motor training in Experiment 5



Day 1

Today we started our learning at: ________

we finished our learning at: ________

How did baby play with the toys? E.g. banging, pulling, touching etc: ______________________________________

____

Did baby free their arms? (i.e. take their arm out from beneath yours so they were playing with the toys with both hands in the first 6 minutes?) _____

If 'yes', did they do it: a lot ○ a few times ○ once or twice ○

How many times did they touch the toy that was on the same side as their free hand (e.g. playing with the toy on the right with their right hand)?

Less than 5 ○ 5-10 ○ 10-15 ○ 15-20 ○ 20+ ○

Between what hours was your baby asleep last night? Was this unbroken sleep? If 'no', please indicate between which times they woke up

____

Did they nap for any length of time before the learning activity? At what time and for how long?

____

Appendix K

Counterbalancing order for Experiment 6b

1	Congruent	Incongruent	Control
2	Incongruent	Congruent	Control
3	Control	Incongruent	Congruent
4	Congruent	Control	Incongruent
5	Control	Congruent	Incongruent
6	Incongruent	Control	Congruent