The development of multisensory integration in autism spectrum disorders

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Thesis submitted to the University of Nottingham for the degree of Doctor of Philosophy

July 2016

General Abstract

In order to understand and interact with the world, our brains must integrate information from multiple sensory modalities to create coherent representations of scenes and events. The integration of visual, tactile and proprioceptive inputs underpins the subjective sense of self and body ownership. This, in turn, underlies the development of social processes including self-awareness, imitation and empathising, which are impaired in autism spectrum disorders (ASD). Evidence suggests that the social functioning deficits characterising ASD could contribute to atypical sensory integration underlying body representation. However, the exact mechanisms underlying sensory integration difficulties have not been specified. Moreover, it is not clear when, and how, visual, tactile and proprioceptive integration matures in typical development. This is important to establish, in order to compare how and why this integration may differ in ASD populations.

This thesis firstly aimed to investigate the typical development of multisensory integration underlying body representation. Experiment One found that the ability to optimally integrate visual and proprioceptive inputs during hand localisation increases with age from very little integration in 4-year-olds to almost adult-like in typically developing 10- to 11-year-olds. Experiments Two and Three showed that sensitivity to the spatial constraints of visuo-proprioceptive integration, and sensitivity to the temporal constraints of visuo-tactile integration, develops with age in 4 to 11-year-olds. Together these studies suggest that the maturation of adult-like multisensory integration for body representation follows a protracted time course over childhood.

The second aim of this thesis was to investigate the evidence for two prominent theories of atypical sensory integration underlying body representation in ASD. These are 1) an over-reliance on proprioception and 2) temporally extended sensory binding.

Experiment Four examined whether trypically developing (TD) adults with a high number of autistic traits exhibit an over-reliance on proprioception. No evidence was found for this, which could indicate that atypical sensory integration is only present in individuals with a clinical diagnosis of ASD. Experiments Five and Six found evidence for temporally extended visuo-tactile integration in children with ASD, compared to TD control participants. Though no evidence was found for a fundamental over-reliance on proprioception, extended binding may have led to reduced processing of temporal synchrony over modality-specific information (i.e. proprioception). Experiment Seven and Eight found no evidence of proprioceptive over-reliance or temporally extended sensory binding in adults with ASD, relative to a TD control group.

I conclude that children with ASD demonstrate temporally extended visuo-tactile binding. This represents a developmental delay rather than a life-long deficit; however, it could have a life-long impact on sensory sensitivities and social processing.

Acknowledgements

Firstly, I would like to thank my supervisors Danielle Ropar, Roger Newport and Ali Smith for their constant encouragement, enthusiasm and advice. I need to thank Roger in particular for creating the amazing MIRAGE - this PhD would not exist without it - and Dani for helping to transport it around Nottinghamshire (and for all the much-needed coffees). I could not have asked for better supervisors!

Thanks, also, to my wonderful fellow PhD students for their time and friendship. In particular Mark Carey, Natasha Ratcliffe, Dani Smith, Hayley Thair and Kristy Themelis for all their help. This would have been a lonely three years without you all!

I am very grateful to all the participants for their time and effort, as well as the schools and organisations that assisted me with participant recruitment. Thanks also to the members of the Autism Social Group, especially Duncan MacGregor, for continually teaching me more about the complex world of autism.

I would like to thank my friends and family, including the amazing diabetes online community (#DOC), for their help and support. In particular, my Dad for the many proofreading tasks I've emailed over at short notice (I promise this is the very last time I return to student life) and my Mum for her continual enthusiasm for my work with 'the creepy hand box'. Lastly, I want to thank Steve for his encouragement, superior hugs and outstanding ability to make excellent cups of tea.

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Chapter One: General Introduction

1.1. General Introduction

In order to understand and interact with the world, our brains must integrate information from multiple sensory modalities to construct unified representations of objects and scenes in the environment. For example, to interact with another person, we combine information from their speech, body language, tone and facial expressions to understand what they are saying.

Autism spectrum disorders (ASD) are characterised by socio-communicative impairments as well as hypo- and hyper-sensitivities to sensory stimuli (American Psychological Association, 2013). A growing body of research demonstrates atypical multisensory integration in ASD but the precise mechanisms underlying this have not been established. This is important to assess since several theories suggest that these integration difficulties could underlie the core features of the disorder. Specifically, a greater understanding of visual, tactile and proprioceptive integration in ASD is needed since this underpins the subjective sense of self and body ownership (Makin, Holmes, & Ehrsson, 2008). This, in turn, underlies the development of self-awareness, imitation and empathising (Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006). These are fundamental social processes that are impaired in ASD. However, it is not clear when and how optimal visual, tactile and proprioceptive integration matures in typical development. This is necessary to establish first, in order to compare how, and why, this integration may differ in ASD populations.

This thesis has two overarching aims. Firstly, I will use novel experimental methods to investigate the development of visual, tactile and proprioceptive integration in typically developing (TD) populations. Through this, I aim to increase our understanding of the mechanisms underlying the development of social behaviours and to provide a comparison point to assess the nature of atypical multisensory integration in ASD. Secondly, I will conduct experiments to assess if and how visual, tactile and proprioceptive integration is atypical in adults on the non-clinical autism spectrum and children and adults with ASD.

In this chapter, I will first explain the concept of multisensory integration and how it provides us with important behavioural and perceptual benefits for understanding and interacting with our environment. I will discuss how it is affected by both bottom-up processes (relating to the nature of the multimodal stimuli in question) and top-down processes (i.e. prior knowledge and experience). Next, I will examine visual, tactile and proprioceptive integration specifically, and how this underlies body representation and social functioning. I will then review the literature on the development of optimal integration of these inputs in TD children before introducing the research on atypical integration in ASD. Lastly, I will outline the central research questions that this thesis aims to answer and how these will be investigated through each of my experiments.

1.2. Multisensory Integration

1.2.1. Advantages of multisensory integration

Multisensory integration (MSI) refers to the process of combining sensory input to construct a comprehensible and unified representation of the world. MSI is required for 1) perception of objects, 2) performing behaviours and 3) understanding others' actions (Calvert, Spence, & Stein, 2004). For example, flavour was believed to be an independent perceptual system. However, increasing evidence demonstrates that our perception of flavour is actually dependent on the integration of tastes and smells as well as tactile, visual and auditory inputs (Auvray & Spence, 2008). Moreover, changing these sensory inputs can dramatically alter the perceived flavour of food (Spence, Levitan, Shankar, & Zampini, 2010; Spence & Shankar, 2010). Effective action execution is also dependent on MSI, for example, when writing an email we need to integrate visual, tactile and proprioceptive inputs to achieve the task. MSI additionally helps us to recognise individuals' actions and cognitions. For instance, when having a conversation we integrate visual information regarding body language and facial expressions, with auditory speech inputs to understand another person and respond appropriately to them.

A wealth of evidence from behavioural and perceptual studies with humans and animals indicates that multisensory information has significant behavioural advantages over unisensory information that is processed separately (Stein, Stanford, & Rowland, 2014). For example, Forster, Cavina-Pratesi, Aglioti, & Berlucchi (2002) instructed observers to press a response key as soon as they perceived a visual and/or a tactile stimulus. Reaction times were significantly shorter for simultaneously presented tactile and visual stimuli compared to a single tactile or visual stimulus. Moreover, reaction times were shorter for simultaneous visuo-tactile stimuli than for two visual stimuli or two tactile stimuli. This suggests that such behavioural advantages are not simply due to the multisensory stimuli containing more sensory information than unimodal stimuli. Indeed, across studies, multisensory enhancement effects are consistently greater than the summed average of the unimodal inputs (Laurienti, Kraft, Maldjian, Burdette, & Wallace, 2004).

As well as speeded reaction times (Forster et al., 2002; Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994; Schröger & Widmann, 1998), multisensory stimuli has been found to reduce the latency of eye movements (Frens & Van Opstal, 1998; Harrington & Peck, 1998; Hughes et al., 1994), lower thresholds for stimuli detection (Frassinetti et al., 2002; Lovelace et al., 2003) and lead to more accurate target localisation (Nelson et al., 1998; Wilkinson, Meredith, & Stein, 1996). Significantly, other studies show that MSI also has facilitative effects on higher order cognitive processes including heightening attention, enhancing speech processing abilities and improving memory (Dionne-Dostie, Paquette, Lassonde, & Gallagher, 2015). For example, Bishop & Miller (2008) found that speech signals within noisy environments were more intelligible when presented in a multisensory context, demonstrating that these facilitation effects can have important consequences for how we interact with and understand our environment.

1.2.2. Bottom-up and top-down influences on multisensory integration

The changes in behaviour observed when multisensory as opposed to unimodal stimuli are presented (e.g. speeded reaction times) are believed to occur because inputs from different sensory modalities converge onto single neurons or structures, which then exhibit heightened responses (Perrault, Vaughan, Stein, & Wallace, 2003). This occurs in a number of brain areas, in particular, the superior colliculus. Indeed, single cell recordings of certain neurones in the superior colliculus of cats and primates reveal that neuronal response to multisensory stimuli can be between 38 and over 1000 times greater than the sum of the neuronal response to the separate unimodal stimuli (Hicks, Molotchnikoff, & Ono, 1993). Studies using local field potential recordings, E-cog recordings, MEG and EEG have also found evidence of cross-modal influences in low level cortical areas such as the primary visual cortex and primary auditory cortex (Bell, Corneil, Alex, & Munoz, 2001; Binns & Salt, 1996; Frens & Van Opstal, 1998). Together these findings indicate that, instead of dedicated processing streams for unimodal inputs that only converge in higher cortical areas, inputs from multimodal stimuli are actively integrated even within the central nervous system.

MSI, and thus multisensory facilitation effects, are dependent on a number of factors relating to the nature of the sensory inputs being combined. In particular, the spatial and temporal structures of multisensory stimuli dramatically affect the likelihood that sensory integration will occur (Wallace et al., 2004).

Specifically, researchers have proposed a spatial rule of MSI whereby sensory inputs are more likely to be integrated together, and thus produce multisensory performance gains, if they are presented in close spatial proximity (Soto-Faraco, Kingstone, & Spence, 2003; Stein, Scott Huneycutt, & Alex Meredith, 1988). This concept stems from findings from neurophysiological animal studies, which demonstrate that stimuli in the same location will stimulate cells with overlapping receptive fields. This leads to a greater overall neuronal response compared to stimuli that are presented far apart from each other (Meredith & Stein, 1986, 1996). Thus, these differences in neuronal firings appear to aid us in integrating inputs originating from the same event and distinguishing them from unrelated sensory information. In support of this, the strength of the classic ventriloquism effect, (in which seeing a hand puppet move at the same time as hearing a person speaking creates the illusion that the puppet is talking) reduces as the distance between the auditory and visual stimuli increases (Jackson, 1953; Lewald, Ehrenstein, & Guski, 2001; Slutsky & Recanzone, 2001).

A large number of human perceptual and behavioural studies demonstrate that this spatial rule is particularly robust across visuo-auditory, visuo-tactile and tactile-auditory interactions, provided that tasks involve a spatial component (Lin & Otaduy, 2008; Ro, Hsu, Yasar, Elmore, & Beauchamp, 2009; Simon & Craft, 1970; Soto-Faraco et al., 2003). For example, in a spatial cueing experiment, a spatially non-informative stimulus in one sensory modality precedes a target stimulus in a different modality. When the cue and target are presented from the same rather than different locations (Wickelgren, 1971), observers typically discriminate the target more rapidly and show enhanced perceptual sensitivity.

However, a recent review by Spence (2013) cautions that the spatial rule may not be a universal finding and may, in fact, be relatively task- and modality- dependant. Indeed, non-spatial discrimination studies do not find robust evidence of a spatial rule for MSI, as demonstrated by tasks employing the McGurk effect (Mcgurk & Macdonald, 1976). In this illusion, participants hear a spoken syllable (e.g. 'ba') but see someone saying a different syllable (e.g. 'ga') and will typically integrate the two to perceive a third sound (e.g. 'da'). While Tiippana, Puharinen, Möttönen, & Sams (2011) found that the location of the auditory and visual stimuli affected the strength of the illusion, studies by Jones & Munhill (1997) and Jones & Jarick (2006) did not show this.

There is, however, stronger evidence that MSI follows a temporal rule, even when tasks do not directly test temporal discrimination. Animal studies show that the largest neuronal response enhancements are seen when stimuli occur in close temporal proximity while no enhancement or a depressed neuronal response is found when multisensory stimuli are clearly temporally asynchronous (Wallace, Wilkinson, & Stein, 1996). Moreover, even if two or more stimuli do not occur at exactly the same time, there is a narrow window of time within which the brain will integrate temporally asynchronous sensory inputs and perceive them as originating from the same multimodal event (Wallace et al., 2004). This is evidenced by behavioural and perceptual studies with animals and humans demonstrating that multisensory mediated performance gains are greatest when the temporal offset between sensory stimuli is short. These gains are then reduced and ultimately extinguished when stimuli are considerably temporally incongruent (Corneil & Munoz, 1996; Frassinetti et al., 2002).

The period of time during which MSI is very likely to occur has been referred to as the temporal binding window (TBW) of multisensory integration (Colonius & Diederich, 2004; Hairston, Hodges, Burdette, & Wallace, 2006; Hillock, Powers, &

Wallace, 2011). It has been suggested that the TBW is necessary because sensory inputs originating from the same source reach the brain at different speeds, due to variations in travel and processing times. For example, it takes approximately 30 to 40 ms for information from the eye to reach the primary visual cortex while inputs from the ear reach the primary auditory cortex in around 10 ms (Calvert et al., 2004). Thus, a TBW allows multisensory interactions to be flexibly specified.

The TBW can be seen as an approximate gauge for when MSI takes place and has been measured using a number of different tasks (e.g. Dixon & Spitz, 1980; Miller & D'Esposito, 2005; Navarra et al., 2005) such as a visuo-auditory simultaneity judgment task (Stevenson & Wallace, 2013). In this, a visual stimulus and an auditory stimulus are separated by a variable delay and observers are asked if the stimuli occurred simultaneously. The length of the delay within which the stimuli are reported as simultaneous approximately 75% of the time is then commonly used as a proxy measure of the width of the TBW.

Though there are large individual differences in the size of the TBW, within participants it appears to be robust across different statistical criteria (Stevenson & Wallace, 2013). The size of the TBW does, however, vary depending on the task and stimuli used (Stevenson & Wallace, 2013). For instance, the window is typically larger for speech stimuli than simple stimuli, such as a light flash, and non-speech stimuli, for example, an audio-visual video of an object hitting a surface (Stevenson & Wallace, 2013; Vatakis, Navarra, Soto-Faraco, & Spence, 2007). Stevenson & Wallace (2013) suggest that this is because complex stimuli, such as speech, may need more within-modality processing before, or in parallel with, multimodal integration, relative to simple stimuli. Consequently, MSI may be most effective if there is flexibility regarding the timing of sensory inputs. As will be discussed in Sections 1.3.2 and 1.4.5, research suggests that the TBW may narrow gradually throughout typical development and that this narrowing may be delayed or reduced in children with ASD.

While MSI is dependent on neuronal processes, the degree to which multimodal inputs are integrated is also influenced by top-down factors, such as the semantic congruency between different inputs (Laurienti et al., 2004). Evidence suggests that the brain compares incoming sensory information with top-down prior knowledge to make probabilistic judgements regarding the source of sensory inputs i.e. whether they originated from the same or separate sources. For instance, we learn from past experience that the closer in time and space that sensory inputs are presented, the more likely it is that they emanate from the same source (Spence, 2007), and thus that they should be integrated together to accurately perceive our surroundings.

The influence of top-down processes has been demonstrated robustly in studies employing the rubber hand illusion (RHI; Botvinick & Cohen, 1998). In this illusion, temporally congruent seen and felt brushstrokes are applied to a fake hand and a real hand, respectively. This usually leads to embodiment of the fake hand due to the integration of visual, tactile and proprioceptive inputs. The strength of the illusion, and hence the extent that multisensory inputs are integrated, is directly influenced by the degree of visual similarity between the real and fake hand. Tsakiris, Carpenter, James, & Fotopoulou (2010) demonstrated that participants only embody the fake hand when it is a realistic prosthetic limb, not when it is either a wooden hand or a wooden block. This suggests that observers combine prior knowledge about the appearance of their own limbs with incoming information (the synchronous visuo-tactile stimuli) and this determines the degree to which multisensory inputs are integrated.

1.2.3. Optimal Multisensory Integration

Studies (e.g. Alais & Burr, 2004; Trommershauser, Kording, & Landy, 2011) show that the degree to which adults integrate sensory inputs can be quantitatively predicted by a Maximum-Likelihood-Estimate (MLE) model of optimal integration (van Beers, Sittig, & Denier, 1996; Ernst & Banks, 2002). When judging the size of an object, for example, estimates of size derived from each sense are averaged and combined to construct a coherent percept. These estimates are prone to variance (or noise) but, by averaging the estimates, the brain can reduce the variance in the overall percept (Landy, Maloney, Johnston, & Young, 1995). Specifically, a greater weighting will be given to estimates with less variance, since these are deemed as more reliable. The degree of variance in an estimate is dependent on both bottom-up processes (i.e. the incoming sensory information) and top-down processes (derived from prior knowledge and experience).

Support for this model has been found in MSI studies that introduce a conflict between cues from different senses since this procedure allows the weightings given to each sense to be assessed. Ernst and Banks (2002), for example, reported that adults' estimates of object size were more accurate when only visual information was available compared to when only tactile information was present, suggesting that vision is normally a more reliable (i.e. less noisy) information source. When congruent visuo-tactile information was available, estimates were more precise than in unimodal conditions, demonstrating that visual and tactile estimates had been combined to reduce the variance in the overall percept. When visual and tactile inputs were put into conflict, participants relied more heavily on the visual compared to the tactile estimates. However, when vision of the object was blurred, tactile inputs were weighted more heavily. This indicates that adults take into account both prior knowledge and experience (i.e. that vision is usually more reliable than tactile inputs) and changes in the environment (blurred vision leading to increased variance in the visual estimate) to compute a weighted average of sensory inputs that achieves greater precision and less uncertainty than unweighted averages.

Other studies also support the model and demonstrate that, in adults, no single sense totally dominates. Instead, the experimental context predicts which sense is deemed as more reliable and hence given a greater weighting. For example, in a study by Mon-Williams, Wann, Jenkinson, & Rushton (1997), participants rested one hand on a table while the other hand rested, unseen, below the table. Participants wore prism goggles that displaced the perceived location of the hand and were asked to point with their unseen index finger to their seen hand. In passive conditions, participants closed their eyes before pointing and the experimenter moved their seen hand to a new location. In active conditions, participants could move their seen hand and, thus, gain awareness of the prism-induced visual displacement. The authors found that proprioceptive inputs were weighted more strongly in active than passive conditions since active movement yields more reliable sensory information regarding limb position. Similarly, while participants relied more on visual cues than proprioceptive information when perceiving limb position, the reverse was found when visual information was limited to a small light attached to one finger (Plooy, Tresilian, Mon-Williams, & Wann, 1998). Together, findings from the adult literature support the idea that we integrate information from multiple modalities in a statistically optimal way by taking into account the precision of inputs in different circumstances (van Beers, Sittig, & Gon, 1999). However, less is known about the *development* of optimal MSI thus, one of the main aims of this thesis was to investigate this.

1.2.4. Multisensory integration in typical development

As discussed in Section 1.2.3, a body of research supports the idea that adult MSI operates in a statistically optimal way by taking into account the reliability of inputs in different circumstances. An initial review of MSI in typical development argues that preschool children, and even infants, are able to integrate multisensory inputs accurately, in an adult-like way (Lewkowicz, 2000). However, as pointed out by

Gori, Del Viva, Sandini, & Burr (2008) the majority of the studies reviewed actually measure the ability to compare information from different sensory modalities (e.g. Klein, 1966; McGurk & Power, 1980; Mjsceo, Hershberger, & Mancini, 1999). In McGurk & Power's (1980) study, for example, children grasped a square while viewing it through a reduced lens that created a conflict between the visual and tactile information. Participants were then asked to select a visual or tactile stimulus from a comparison set that matched the size of the square. The authors propose that the results show a visual dominance in pre-schoolers since they weighted visual information more heavily than tactile inputs, regardless of whether the comparison set of stimuli were visual or tactile. Mjesco et al's (1990) study also found this pattern of results using the same procedure in 6-year-olds while, in contrast, 12-year-olds weighted tactile inputs more heavily when the comparisons were tactile yet the reverse was true when visual comparison stimuli were used. However, this comparison procedure does not assess the degree to which MSI took place or children's ability to flexibly re-weight sensory inputs according to changes in the sensory environment. Indeed, an updated review on the development of MSI abilities concludes that the age at which optimal integration occurs is still unclear (Dionne-Dostie et al., 2015).

A more appropriate assessment of MSI abilities involves measuring the reliability of unimodal sensory estimates separately, before presenting congruent or incongruent multisensory information and assessing whether participants weight the sensory inputs differently, depending on their context-dependent reliability. As discussed in Section 1.2.3, studies using this method show that adults optimally integrate inputs by flexibly up-weighting the more reliable sensory information when inputs are incongruent (Ernst & Banks, 2002). However, few studies have used this method to assess the development of MSI abilities in children. As outlined in Section 1.1, social, cognitive and behavioural processes that are impaired in ASD are dependent on MSI. Thus, it is necessary to assess how MSI abilities mature in typical development to provide a comparison point for assessing how this may be different in children with ASD. In particular, it is important to establish whether adult-like optimal integration of sensory estimates is present from birth or whether it develops with age. For example, it could be that initially information from one sensory modality dominates over other sensory inputs and it is only later in development that children learn to weight input from different inputs depending on prior experience and the current context.

Moreover, as detailed in the following section, the development of visual, tactile and proprioceptive integration is particularly important to establish, yet there is a lack of research in this area, perhaps because it is challenging to tease apart and measure the relative weightings of these inputs. Indeed, the majority of research on MSI in typical development has focused on audio-visual integration (Dionne-Dostie et al., 2015). However, it cannot be assumed that visual, tactile and proprioceptive integration follows the same developmental trajectory.

1.3. Visual-tactile-proprioceptive integration

1.3.1. Body representation

As discussed in the preceding sections, integrating inputs from multiple sensory modalities helps us to make sense of, and interact with, our environment. Specifically, the integration of visual, tactile and proprioceptive inputs underlies our sense of bodily self which includes body localisation - the ability to locate our limbs - and a sense of body ownership (Nava, Steiger, & Röder, 2014) - the awareness and understanding that our body belongs to us (and not someone else) and that we can see, feel and move it (Gallagher, 2000).

Both body localisation and ownership are important for the development of motor skills, which allow us to successfully navigate our environment (Petkova, Khoshnevis, & Ehrsson, 2011; Piaget, 1952). Additionally, body ownership is required for identifying, distinguishing and comparing ourselves with others (Meltzoff, 2007; Schütz-Bosbach et al., 2006). Furthermore, we cannot infer and understand others' perceptions, emotions and intentions without comparing another's actions with our own past or present actions (Meltzoff, 2007). Thus, body ownership is also necessary for higher-order cognitive processes (Chaminade, Meltzoff, & Decety, 2005; Gallese, 2003; Gallese, Keysers, & Rizzolatti, 2004). In support of this, studies with children as young as 12 months showed that they look at a target for longer when an adult orientates towards it with open eyes than closed eyes (Brooks & Meltzoff, 2002, 2005). This indicates that the infants have learnt through their own experience that vision of a target is obscured when their own eyes are closed and, thus, they infer that the same is true for another person (Meltzoff, 2007).

Additionally, body ownership is a foundation for important social processes. For instance, it allows us to imitate novel actions, which requires recognising correspondences between our own movements and other people's (Meltzoff & Moore, 1997; Meltzoff & Moore, 1977; Vinter, 1986). Importantly, a sense of body ownership also enables us to infer others' mental states. For example, infants know that when they desire an object they will reach out and attempt to grasp it. They learn the relationship between their desires and their corresponding bodily movements and they use this information to interpret another person's grasping behaviour (Meltzoff, 2007; Repacholi, Meltzoff, & Olsen, 2008). Studies suggest that, in typical development, these abilities are acquired very early on in life. In Repacholi and Meltzoff's (2007) study, for example, infants aged 18 months observed an adult expressing anger after seeing someone else perform a specific action. Interestingly, infants were then less likely to perform the act if this adult was watching them, compared to when the adult's back was turned. This indicates that the infants had firstly compared the second adult's past actions with their own present actions, secondly, they had inferred that the first adult would be angry if the act was performed and thirdly they understood that the second adult could not perceive the act with their back turned. All of these inferences require the ability to detect others mental states from their actions, which depends on having a sense of body ownership. Lastly, many researchers have argued that the ability to detect similarities between someone else's movements and our own is a foundation for developing empathy for others and 'mentally standing in their shoes' (Husserl, 2012; Smith 2010). This, again, is not possible without a sense of body ownership.

Thus, body localisation and ownership are important for the development of behavioural, cognitive and social processes. A large number of studies indicate that, by the first year of life, infants recognise and distinguish their own body and actions from those of other people (Geangu, 2008; Rochat, 1998), indicating that body localisation and ownership start to develop at a very early age in TD populations. Bahrick & Watson (1985), for example, found that 5-month-olds looked longer at a video image displaying delayed feedback of their own leg movements compared to a video without a delay, while Schmuckler (1996) also found this pattern of results when videos of the infants' hand and arm movements were used. Additionally, infants of less than 6 months looked longer at a video of their legs in which visuo-proprioceptive conflict was created (e.g. by reversing the way the legs move in relation to each other) compared to a video of their legs as they would be sensed via direct visuo-proprioceptive feedback (Morgan & Rochat, 1997; Rochat & Morgan, 1995; Schmuckler, 1996). However, it is not clear when and how children show adult-like MSI underlying body representation since preferential looking studies cannot assess the relative weighting given to different senses or determine whether weightings are flexibly re-weighted depending on changing environments. This is important to establish since ASD are characterised by deficits in social processes purported to depend on accurate body representation, including inferring others' mental states, empathising and imitation. A greater understanding of the processes underlying the development of body representation in typical development can inform us on how and why this may be atypical in ASD. Since body representation is dependent on visual-proprioceptive, visual-tactile and visual-tactile-proprioceptive integration, I will now review the literature on the development of these processes in children with and without ASD.

1.3.2. Visual-tactile-proprioceptive integration in typical development

Pagel, Heed, & Röder (2009) used a tactile temporal order judgment (TOJ) task to investigate visuo-tactile-proprioceptive integration in 4- to 7-year-olds, who were divided posthoc into three age groups (4:10-5:05 years, 5:06-5:11 years and 6:00-7:06 years) In the task, children located touches to their hand in a crossed hand condition and an uncrossed hand condition. In a typical TOJ task, two stimuli are presented, separated by a variable delay, and observers judge which one appeared first. When the stimuli are in the form of touches to the left and right hand, participants are slower to localise the touches when their hands are crossed over the midline compared to when they are uncrossed (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). This suggests that, in this task, adults weight visual estimates more strongly than tactile estimates when the two are in conflict, since, if tactile inputs dominated, then changing the visual information (i.e. from a crossed to an uncrossed posture) would not alter detection speeds. This finding also coheres with other studies (e.g. Ernst & Banks, 2002) demonstrating that visual estimates are usually less variable than tactile estimates and thus, according to an optimal integration model, we should weight them more strongly. Moreover, it supports findings of top-down influences on MSI (Tsakiris et al., 2010). In this case, we use our prior knowledge that observing a touch on the left side of the body normally corresponds to a touch on the left and vice versa. This then impacts on the speed at which we determine the location of a touch when the hands are crossed at the midline. Pagel et al., (2009) reported that only the older two groups (children aged over 5 years 5 months) exhibited significantly slower touch localisation in a crossed, compared to an uncrossed, hand posture. Children aged between 4 years 10 months and 5 years 5 months did not show the crossed hand effect. This indicates that, unlike adults and older children, younger children do not seem to weight visual inputs more strongly than tactile inputs when localising touches. Instead, they may lack the experience necessary to learn that visual inputs are usually more accurate and so should normally be relied on more than tactile information in this task.

Cowie, Makin, & Bremner (2013) and Cowie, Stirling, & Bremner (2016) investigated visuo-tactile-proprioceptive integration in TD children using the rubber hand illusion (RHI), in which a fake hand is embodied following synchronous seen and felt touch applied to an individual's unseen hand and a fake hand respectively. The degree to which the fake hand is embodied can inform us on the relative influence of visual, tactile and proprioceptive inputs. Thus, this is arguably a valuable tool for assessing sensory integration underlying body localisation and ownership specifically. The authors reported that, when visual-tactile inputs were synchronous, both adults and children aged 4 to 13 years estimated the location of their unseen hand to be closer to the fake hand than in pre-touch baseline conditions, indicating that MSI had occurred. Unlike adults and children aged 10 years and over, though, even when visual-tactile inputs were asynchronous, 4- to 9-year-olds' estimates were also closer to the fake hand than in baseline conditions. The authors thus propose that visual inputs dominate proprioceptive information in determining hand position in these children since, regardless of incongruent proprioceptive and tactile signals, they showed signs of embodying the fake hand purely on the basis of sight. Visual inputs are normally more reliable than proprioception when localising a passive limb (Mon-Williams et al., 1997). However, in this task, proprioceptive inputs came from the actual, unseen hand whereas visual information was in the form of a fake hand. Consequently, older children and adults may have discounted the visual inputs in asynchronous conditions because they were deemed less reliable in this situation than proprioception, while younger children were less able to re-weight the sensory inputs depending on their context-specific reliability.

An additional, but complementary explanation for Cowie et al's (2013, 2015) results is that the binding of information from different senses is not as tightly constrained in younger children as it is in adults. A wide body of research demonstrates that young infants and even newborns can detect and attend to cross-modal contingencies between visual, tactile and proprioceptive inputs. For instance, studies show that neonates preferentially attend to synchronous compared to asynchronous visuo-tactile brush strokes, indicating awareness of the difference between the two (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Zmyj, Jank, Schütz-Bosbach, & Daum, 2011). As discussed in Section 1.2.2, inputs occurring in close proximity are likely to have originated from the same source, thus, sensitivity to temporal or spatial congruency aids appropriate integration of inputs from multimodal events. This is an important pre-cursor for adult-like MSI and the development of higher order social and cognitive processes (Bahrick & Watson, 1985). However, it could be that, compared to adults, young children will continue to integrate sensory inputs that are separated by a larger temporal or spatial gap. Thus, in Cowie et al (2013), children aged 4 to 9 years may have perceived the asynchronous brushing as synchronous if sensory binding is less tightly constrained. In support of this, a recent study by Hillock-Dunn & Wallace (2012) indicates that the window of time in which visual and auditory inputs are perceived to be simultaneous (i.e. the temporal binding window; TBW) narrows linearly with age. In this study, 6- to 23-year-old participants completed a simultaneity judgment task in which an audio and a visual stimulus were presented and participants judged whether these occurred at the same or different times. Results showed that, relative to adults, both children aged 6 to 11 years and adolescences aged 12 to 16 years, required a longer time period between the stimuli before they were aware of the delay between them. Interestingly, though the width of the TBW varied between participants, overall it narrowed linearly with age and did not reach adult levels until well into adolescence. As yet, though, no studies have systematically assessed whether temporal binding underlying body representation is similarly extended in childhood and adolescence.

1.3.3. Visuo-tactile integration in typical development

Gori et al's (2008) study assessed the degree to which 5- to 10-year-olds' visuo-tactile integration abilities could be predicted by an MLE model of optimal integration. Children were required to discriminate the height and orientation of 3-D blocks. First, the within-modality variances of visual and tactile estimates were assessed separately. In a tactile-only condition, children judged which of two simultaneously presented unseen ridges were taller, using only touch. In a visual-only condition, children determined by sight which of two blocks were taller, while visual inputs were systematically varied by blurring the image of the blocks. In a third condition, both visual and tactile inputs were available but, again, vision of the blocks was blurred across trials.

Adults integrate inputs in a statistically optimal way in this task, such that, when visual inputs are degraded, accuracy in the visuo-tactile conditions is higher than in the visual-only condition (Helbig & Ernst, 2007). In Gori et al., (2008) this effect was seen in 10-year-olds and, to a lesser extent, in 8-year-olds. However, 5-year-olds' thresholds in the dual-modality condition were as high as their thresholds in the tactile-only condition, indicating a lack of visuo-tactile integration. Thus, these findings suggest that while 8-year-olds show evidence of MSI, it is not until 10 years of age that children appear to combine multimodal information in a statistically optimal way.

The authors also conducted a further size discrimination task, in which incongruous visual and tactile information were presented such that one of the blocks appeared as a single block, yet was actually comprised of a visual block that was taller than the tactile block. Results showed that all age groups had lower visual than tactile thresholds. Consequently, if children integrate inputs in an optimal way, they should weight the visual inputs more than the tactile information when the two are in conflict. However, only the 10-year-olds performance was predicted by an optimal integration model while all 5-year-olds showed clear tactile dominance in the incongruent condition, Indeed, unlike older children, 5-year-olds' thresholds in the incongruent condition were as high as those in the tactile-only condition and significantly higher than thresholds in the visual-only condition. Eight-year-olds' estimates were influenced by both visual and tactile information yet performance was not optimal i.e. they were not as proficient as older children at flexibly re-weighting visuo-tactile information in response to changes in the reliability of these inputs.

Although these results could suggest that 5-year-olds have a bias towards tactile inputs, the reverse was found in a second task with the same children, in which participants discriminated the orientation (instead of the size) of objects. In the incongruent condition for this task, unlike older children, 5-year-olds exhibited a total visual dominance such that orientation judgments were based almost exclusively on visual information, indicating that the 'dominant' sense appears to be task-dependent.

Together these results suggest that visuo-tactile integration for size and orientation estimation is statistically optimal by 10 years of age. However, it is not known if the same applies to MSI underlying body representation specifically. Moreover, this study cannot ascertain whether there is a critical age at which optimal integration develops since only a small number of 5-, 6-, 8- and 10-year-olds were tested and no 7- or 9-year-olds were included. Moreover, the authors did not report between-group analyses for the other age groups (6- and 8-year-olds). Interestingly, these results are in contrast to findings from studies involving audio-visual integration.

Neil, Chee-Ruiter, Scheier, Lewkowicz, & Shimojo (2006), for example, found that 8- to 10-month-old babies, but not younger infants, exhibited significantly faster orientating to a visuo-auditory stimulus compared to either a visual or auditory stimulus and results were in line with an optimal integration model. Gori et al., (2008) suggest that these age differences could be because the haptic modality reaches maturity later than the auditory modality since sensory systems that process tactile information must allow for the continual growth of limbs.

1.3.4. Visuo-proprioceptive integration in typical development

Like research on visuo-tactile integration, visuo-proprioceptive integration in typical development is an under-researched area relative to visuo-auditory research. Nardini, Jones, Bedford, & Braddick (2008) assessed visuo-proprioceptive integration in 4- to 5-year-olds, 7- to 8-year-olds and adults in a task in which participants had to return an object to its original location in an arena. When both visual landmarks regarding the object's starting point and nonvisual proprioceptive inputs gained from self-motion were available, adults' estimates were more reliable than when only visual or proprioceptive information was accessible. However, neither the younger nor older children's estimates reduced in variance when both sensory inputs were available. When visual and proprioceptive inputs were incongruent, a model of optimal integration predicted adults' performance such that they relied on a weighted average of the two sensory inputs while children alternated between using solely visual or solely proprioceptive information. These results mirror those found for visuo-tactile integration in Gori et al's (2008) study, suggesting that, though young children can use unisensory cues, neither visuo-tactile nor visuo-proprioceptive integration is optimal and adult-like in children of 8 years and younger. However, Nardini et al's (2008) study cannot specify whether there is a critical age at which visuo-proprioceptive integration starts to become adult-like since only children in two wide age bands (4- to 5-years and 7- to 8-years) were tested. Furthermore, this task is concerned with extra-personal space and does not relate to body representation specifically.

Hand localisation tasks arguably do assess abilities underlying body representation yet studies using these with children have produced inconsistent results. In Warren & Pick's (1970) study, visuo-proprioceptive conflict was created via prism goggles that displaced the seen location of the participant's left hand. 7- to 8-year-olds, 11- to 12-year-olds and young adults were asked to point with their unseen right hand to the seen position (using only visual information) or felt position (using only proprioceptive information) of their left hand. Though vision biased estimates based on felt hand position in all groups, no effect of age was found. Nonetheless, while this task tests body localisation, it does not assess MSI, but rather the ability to ignore inputs from one sensory modality in favour of another. MSI underlying hand localisation was tested more directly in a study conducted by Nardini, Begus, & Mareschal (2013) with 92 4- to 12-year-olds and 17 adults. The authors found that 7- to 9-year-olds and adults' hand localisation estimates were significantly more accurate when both proprioceptive and visual information was available, compared to when only sensory information from one of the modalities was present. However, interestingly, this variance reduction was not seen in either 4- to 6-year-olds or 10- to 12-year-olds. This could suggest that the development of optimal visuo-proprioceptive integration is not linear but instead follows a 'u-shaped' trajectory. A return to less efficient MSI in 10- to 12-year-olds could be due to rapid changes in the size of developing limbs. The authors suggest that this may lead to a temporary reduction in the accuracy of proprioceptive information, leading to a reduced reliance on this modality.

Bremner, Hill, Pratt, Rigato, & Spence (2013) investigated visuo-proprioceptive integration using a mirror illusion task in 5- to 7-year-olds and adults. The participant's left hand was reflected in a mirror placed between the hands so that it appeared on the right side of the body, but was not in the same actual location as the participant's actual right hand (which was hidden from view). In the task, participants pointed with the unseen right hand to a visual target located to the right of the mirror. Results showed that for children in all age groups (5-, 6- and 7-year-olds) and adults, reaches came from the seen hand location, not the actual hand location. This coheres with previous research using this task with adults (Holmes, Crozier, & Spence, 2004) and supports findings that visual inputs are normally a more reliable source of information regarding body localisation than proprioception (Mon-Williams et al., 1997). Since children, like adults, did not show a total reliance on vision over proprioception, this indicates that the ability to integrate visuo-proprioceptive information for hand localisation is present in children from at least 4 years of age. Although the authors did not report the weighting given to each sense, a correlational analysis involving all participants under 6 years revealed a significant increase in reliance on visual information with age, which could indicate that the ability to flexibly up-weight more reliable inputs develops over childhood.

In support of this, research examining the development of postural control indicates that sensory re-weighting in response to changing sensory environments is seen in children as young as 4 years, yet the magnitude of this re-weighting increases with age (Bair, Kiemel, Jeka, & Clark, 2007; Barela, Jeka, & Clark, 2003; Polastri & Barela, 2013). King, Pangelinan, Kagerer, & Clark (2010) also found a comparable age effect in a study conducted with 7- to 13-year-olds. Children pointed to a visual target, or a proprioceptive target (the unseen finger of their other hand), with or without the addition of a visual marker indicating the target location. As in Bremner et al., (2013), when visual and proprioceptive inputs gave conflicting information regarding hand location, all participants showed evidence of MSI such that no children relied wholly on a 'dominant' sensory channel. Older children, though, tended to weight proprioception more strongly than vision while younger children showed the opposite pattern. This appears to contradict Bremner et al's (2013) results. However, though vision is usually a more reliable information source for body localisation than proprioception, in this task visual information was only in the form of a sticker indicating possible hand location, whereas proprioceptive inputs came from the participant's actual hand. Thus, older children may have deemed the proprioceptive information to be more informative for accurately locating the hand in *this specific situation*. Younger children may have been less able to flexibly re-weight sensory information depending on its context-dependent reliability. Moreover, though this study and postural paradigms suggest that optimal integration underlying body representation develops over childhood, the tasks employed necessitate motor skills that also develop with age. Consequently, it is unclear whether age effects are due to changes in motor adaptation, sensory integration or both (Barkley, Salomonczyk, Cressman, & Henriques, 2014).

1.3.5. Conclusions on visual, tactile and proprioceptive integration in typical development

Overall, the literature suggests that children's ability to use reliable and accurate unimodal sensory estimates improves with age. However, the research investigating when visuo-tactile and visuo-proprioceptive integration becomes adult-like yields inconsistent findings. Results indicate that infants and even neonates can detect cross-modal correspondences such as temporal synchrony, while children as young as 4 years are able to integrate these inputs together. Nevertheless, the capacity for visuo-tactile or visuo-proprioceptive integration seems to mature before the ability to flexibly re-weight these sensory inputs according to changes in the environment.

An RHI study suggests that children aged 4 to 9 years may show temporally extended visuo-tactile binding compared to older children and adults. However, this has not been systematically assessed. Additionally, in adults the accuracy and precision of estimates (of e.g. size, orientation or location) increase when congruent visual-tactile or visual-proprioceptive information are presented, compared to only unimodal information, indicating optimal MSI. However, of the few studies that have directly assessed this in children, most have not found evidence of this before the age of 10 years.

Other research has measured sensory estimates when children are presented with incongruent multisensory information, to assess whether they can flexibly re-weight inputs in response to changes in their perceived reliability. While adults up-weight the more reliable and accurate inputs, some studies show that children appear to rely solely on information from one sense. However, the 'dominant' sense seems to be task dependent. For example, when both visual and tactile information are available, 5-year-olds rely solely on vision in a size discrimination task and only on tactile information in an orientation discrimination task (Gori et al., 2008). Thus, there does not appear to be a fundamental over-reliance on one specific sense, in early development. Other studies find that children's estimates, like adults, are influenced by information from more than one sense. However, younger children seem less able to up-weight inputs depending on their perceived *reliability* in a given context. Results are inconsistent, though, regarding the age at which children can achieve this, which could be due to differences in the tasks employed and the extent that they necessitate body ownership and localisation.

Moreover, a number of the studies in this area have used threshold measures to indicate sensory estimates, but the accuracy of these measurements is susceptible to participants forgetting or misunderstanding the goal of the task. Additionally, the tasks used in studies such as Nardini et al., (2008) and King et al., (2010) dependent on working memory (the mental workspace used to maintain and manipulate information over short periods of time), which improves significantly with age in 4 to 15-year-olds (Gathercole, Pickering, Ambridge, & Wearing, 2004) and could thus be contributing to apparent age differences in sensory integration.

Furthermore, the same task has rarely been used across a broad age range and most studies have used a cross-sectional design, which can mask changes in behaviour at critical developmental periods. Future research would benefit from employing tasks that assess MSI underlying body representation with a wider age range of children and analysing data using developmental trajectory analyses.

1.4. Multisensory Integration in Autism Spectrum Disorders

1.4.1. Autism

Autism spectrum disorders (ASD) are characterised by impairments in social interaction, communication, and imagination (American Psychological Association, 2013). However, as noted by Bogdashina (2003), numerous personal accounts from individuals with ASD also document unusual sensory sensitivities. Temple Grandin, a well-known researcher with ASD, describes how 'sudden loud noises hurt my ears - like a dentist's drill hitting a nerve' (p.107, Grandin, 1992) yet she also 'liked the visual stimulation of watching automatic sliding doors' (p.115, Grandin, 1992). Clinical reports (e.g. Leekam, Nieto, Libby, Wing, & Gould, 2006; Talay-Ongan & Wood, 2000) have documented sensory abnormalities in over 90% of individuals with ASD. Indeed, a review of over 40 empirical studies reported significantly more unusual responses to sensory stimuli in children with ASD compared to TD children (Rogers & Ozonoff, 2005), while clinical, parental and self-reports have consistently documented unusual attention to, or avoidance of, sensory stimuli across modalities in individuals with the disorder (Minshew & Hobson, 2008).

There is lack of research, though, assessing whether individuals with ASD actually perform differently to TD participants on objective tests of sensory acuity and the majority of studies in this area have focused only on visual perception (Marco, Hinkley, Hill, & Nagarajan, 2011a). Though there is some evidence of enhanced visual perception for simple stimuli in ASD (Bertone et al., 2005), much of this research has assessed face processing, which is confounded by differences in the type and complexity of the stimuli used (Klin, 2008) and it is unclear whether performance differences are due to primary cortical abnormalities or higher-order social cognitive deficits. Only a few psychophysical studies have investigated tactile thresholds and sensitivity in ASD yet, again, results are mixed. Adults with ASD, for example, showed lower tactile thresholds for 200 Hz but not 30 Hz, compared to TD participants (Blakemore et al., 2006) but no threshold differences were found in children with ASD compared to a control group for 40 or 250 Hz stimuli (Güçlü, Tanidir, Mukaddes, & Ünal, 2007). These variable findings could be due to the small sample sizes and different designs, diagnoses and age groups involved. Thus it is not clear whether reported sensory sensitivities represent low-level sensory perceptual abnormalities or whether it is the *interpretation* of the sensory signals at a higher level that is different in individuals with ASD. Nonetheless, the latest version of the Diagnostic and Statistical Manual of Mental Disorders (DSM-V; American Psychiatric Association, 2013) has, for the first time, included hypo- and hypersensitivities to sensory stimuli as additional diagnostic criteria, suggesting they are being recognised as core aspects of the disorder.

1.4.2. Traditional Theories of Autism

Many prominent theories of ASD, such as Emotion Processing (Foa, Huppert, & Cahill, 2006), Social Motivation Theory (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012) and the Theory of Mind hypothesis (Baron-Cohen, Leslie, & Frith, 1985), have focused predominantly on explaining social impairments in ASD, without addressing sensory symptoms. Though Weak Central Coherence theory (Happé & Frith, 2006) and Enhanced Perceptual Functioning (Mottron, Dawson, Soulières, Hubert, & Burack, 2006) present a partial explanation for sensory sensitivities, neither theory fully specifies the mechanisms underlying these atypicalities. Weak Central Coherence theory proposes that those with ASD have a detailed focused cognitive style. This leads to an impaired ability to integrate information across different contexts to derive higher-level meaning. In a similar vein, Mottron et al's (2006) Enhanced Perceptual Functioning theory suggests that in ASD bottom-up perceptual processes are 'enhanced,' difficult to control and consequently disrupt the development of higher-level cognitions and behaviours. Both theories purport to explain not only superior abilities in low-level perceptual tasks (such as detail recognition) but also hypersensitivities to sensory stimuli. However, neither theory can fully explain the mechanisms underlying these, or why people with ASD often exhibit *hyposensitivities* to sensory stimuli (Pellicano & Burr, 2012). Furthermore, these theories have focused predominantly on visual and auditory sensory atypicalities and cannot explain the heterogeneity of sensory sensitivities seen within and between individuals (Leekam et al., 2006). For example, one person may be drawn to a specific texture, but only in certain circumstances, while another individual may show no tactile sensitivities but have a strong dislike of specific sounds or pitches.

1.4.3. Theories of atypical sensory processing in ASD

More recent theories have suggested that both sensory and socio-communicative features of ASD could be due, at least in part, to atypical MSI. It could be, for example, that difficulties integrating multisensory inputs leads to an increased processing of inputs from one sensory channel at the expense of others, resulting in hypersensitivities to stimuli from this channel and hyposensitivities to the remaining, neglected sensory stimuli. Furthermore, social stimuli are inherently multisensory, for example, face-to-face communication involves seamlessly integrating speech, tone, facial expressions, and body language (Kwakye, Foss-Feig, Cascio, Stone, & Wallace, 2011). Thus, atypical MSI could lead to problems with social functioning and social interaction.

Most research into unimodal and multimodal sensory processing in ASD has focused on visual and auditory inputs (Iarocci & McDonald, 2006; Marco, Hinkley, Hill, &

Nagarajan, 2011b). The majority of studies suggest that while unimodal processing is intact or even superior in people with ASD, they fail to show the facilitatory benefits of MSI to the same degree as TD populations. Bonnel et al., (2003), for example, found that adults with ASD showed an enhanced ability to differentiate pitches of similar frequency while other studies consistently report enhanced visual processing (Mottron et al., 2006; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005). However, other investigations have found strong evidence of speech processing deficits in this disorder (Magnée, De Gelder, Van Engeland, & Kemner, 2008; Smith & Bennetto, 2007), which could indicate visuo-auditory integration problems. In support of this, EEG studies measuring event-related potentials report that compared with TD children, those with ASD exhibit decreased response amplitude when presented with simultaneous visual and auditory stimuli (Courchesne, Lincoln, Kilman, & Galambos, 1985; Courchesne, Lincoln, Yeung-Courchesne, Elmasian, & Grillon, 1989). Further support for atypical MSI was found in Collignon et al's (2013) study. In this, unimodal visual search performance was more efficient in adults with ASD compared to a matched control group, yet only the TD individuals showed an increase in search efficiency in the presence of concurrent auditory stimuli. This again points to a problem with MSI specifically and suggests that, consequently, multisensory facilitation effects may be reduced or absent in individuals with ASD.

Compared to the visuo-auditory literature, there is far less research regarding visual-tactile-proprioceptive integration in ASD. This is particularly important to investigate since studies have indicated strong correlations between tactile sensitivities and ASD features such as stereotyped behaviours (Baranek, Foster, & Berkson, 1997). Furthermore, as discussed in Section 1.3.1, the capacity to compare and differentiate between the self and others depends on the normal integration of these inputs (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012). This ability and a sense of body ownership underlie the development of social behaviours and skills including self-awareness, imitation and empathising (Schütz-Bosbach et al., 2006), which are compromised in ASD (American Psychological Association, 2013). Therefore, atypical integration of these inputs could underlie both sensory and social deficits observed in the disorder, offering an explanatory mechanism that could account for both low-level and high-level components of the ASD behavioural profile.

Processes underlying visual, tactile and proprioceptive integration in ASD have not been clearly established. However, evidence is growing for two separate, but not necessarily mutually exclusive, theories for atypical integration of these inputs. These are (1) an over-reliance on proprioception and (2) temporally extended visuo-tactile binding. I will now describe these theories in more detail.

1.4.4. Over-reliance on proprioception

Proprioception refers to our sense of the position and movement of our body parts (Sherrington, 1910). We use it in everyday life in order to carry out motor skills and interact successfully with our environment. Several studies have implicated a specific bias for, or over-reliance on, proprioceptive inputs over other sensory inputs in ASD. In Haswell, Izawa, Dowell, Mostofsky, & Shadmehr's (2009) study, 14 children with ASD and 13 TD children learnt to control a robotic arm to capture toy animals. Previous studies have demonstrated that, over training trials, TD brains develop connections between arm movements and the resulting visual and proprioceptive feedback (Shadmehr, 2004). The strength of these connections is measured by assessing the extent that learning to reach to a target in a training phase carries over to a test phase, in which the target is in a new location. Haswell et al., (2009) found no significant differences between groups in the initial rate of learning; deviations away from the target decreased with training across all participants. However, the children with ASD developed a much stronger association between their arm movements and the resulting proprioceptive inputs than the TD children who, in contrast, showed a greater integration of visual and proprioceptive feedback. This then allowed them to generalise learning to targets requiring different hand motions. This finding has ben replicated in studies using similar tasks e.g. (e.g. Gidley Larson & Mostofsky, 2008; Izawa et al., 2012) and suggests that individuals with ASD may have a preference for processing proprioceptive inputs over integrating these with visual information. Moreover, Izawa et al., (2012) found that this atypical sensory processing significantly predicted the level of social and motor impairments in participants with ASD.

More recently, Marco et al., (2015) adapted the robotic arm task to include trials in which reaching actions were perturbed, resulting in movement errors sensed through vision and proprioception. Results showed that sensitivity to proprioceptive error was significantly larger in children with ASD compared to TD controls while the reverse was true for sensitivity to visual error. This could indicate that, compared to TD individuals, those with ASD may be more accurate at body localisation when only proprioceptive inputs are available but less accurate when congruent visual and proprioceptive information is present. This explanation coheres with numerous studies reporting superior performance by participants with ASD in tasks relying on unimodal processing in the visual domain. However, studies have not consistently found evidence for this (e.g. Fuentes, Mostofsky, & Bastian, 2010; Weimer, Schatz, Lincoln, Ballantyne, & Trauner, 2001).

Weimer et al., (2001), for example, reported that children with ASD performed worse than TD children on tasks in which a lack of visual information necessitated dependence on proprioceptive feedback alone, such as one-leg balancing with eyes closed. Moreover, Fuentes et al., (2010) assessed the precision of proprioceptive estimates in 12 adolescents with ASD and 12 TD adolescents. Participants used a joystick in their left hand to move a dot on a screen until they judged it be above their right, unseen index finger. In a further condition, participants moved their unseen elbow until they perceived it to match a line on the screen. Control trials in which the right arm was visible were also included and indicated judgement error that was not due to proprioception. This error was subtracted from judgement error in the experimental trials to give a measure of purely proprioceptive error. Interestingly, results showed no significant difference between the groups on judgment accuracy in any of the tasks. Moreover, electromyography recordings of the right arm monitored movement and trials in which the arm moved were excluded, thus ensuring muscle activity was not underlying differences in the perceived accuracy of proprioceptive estimates. Therefore, perhaps proprioceptive over-reliance does not necessarily equate to superior abilities in using proprioception to localise the body. Indeed, many anecdotal reports indicate impaired ability to use proprioception in day-to-day tasks, such as pointing, and reduced awareness of body position and movements (Biklen & Attfield, 2005).

Palmer, Paton, Kirkovski, Enticott, & Hohwy (2015) advocate an alternative explanation for these somewhat inconsistent findings. As detailed in Section 1.2.3, when integrating sensory inputs, adults' performance can be predicted by a statistical model of optimal integration (Ernst and Bulthoff, 2004). Sensory inputs are perceived as more reliable and thus given a greater weighting when there is little variance (or noise) in the estimate derived from that sense. The degree of variance in the estimate is dependent on prior and contextual information. Palmer et al., (2015) suggest that the influence of top-down processes (i.e. the environmental context) on low-level processing is reduced in individuals with ASD. Thus, according to this theory, when a change in the environmental context deems proprioception to be a less reliable information source, TD individuals, but not those with ASD, should show reduced reliance on proprioception. Hence, performance differences between individuals with and without ASD may not be seen in situations when proprioception is the most reliable, or the only available, sensory source, such as in the studies by Weimer et al., (2001) and Fuentes et al., (2010). However, those with ASD may continue to rely on proprioception regardless of changes in the top-down representation of the environment while TD individuals should alter their weightings depending on this contextual information. Paton et al., (2012) found some support for this theory in an RHI study, however, due to the nature of the task design, alternative explanations for performance differences between ASD and control groups cannot be ruled out (see Section 1.4.5).

In summary, though several studies find evidence of an over-reliance on proprioceptive processing in individuals with ASD, the majority have used similar tasks and have only tested children. Increased proprioceptive accuracy in ASD might be expected if those with the disorder show an inherent over-reliance on this sensory modality, yet evidence for this is limited, with some studies reporting poorer proprioceptive ability in those with ASD. It is thus possible that there is a different explanation for atypical MSI, which manifests itself as proprioceptive over-reliance, but only in certain contexts.

1.4.5. Extended sensory binding in ASD

An alternative leading theory of atypical MSI proposes that sensory binding is atypical in ASD. As discussed in Section 1.3.5, evidence suggests that MSI becomes more sensitive and specific as children develop. Adults integrate sensory inputs separated by a temporal delay, provided that these inputs occur within the temporal binding window (TBW). Hillock-Dunn & Wallace (2012) found that, at least in the visuo-auditory domain, the TBW narrows with age. Thus, older children and adults are less likely to incorrectly bind together inputs that are separated by a temporal delay than younger children. It has been proposed that, in ASD, the ability to specify which inputs should (and should not) be integrated together either does not improve with age, or shows a delayed improvement relative to TD populations, resulting in extended sensory binding across modalities (Foss-Feig et al., 2010; Kwakye et al., 2011; Stevenson et al., 2014).

Temporally extended sensory binding would likely lead to inappropriate integration of information from unrelated events, which could underlie the feelings of sensory overload commonly seen in the disorder (Rogers & Ozonoff, 2005), particularly in environments with a high degree of dynamically changing multimodal inputs, such as a crowded room. Consequently, this might encourage piecemeal processing of events, leading to a preference for processing local over global information as purported by The Weak Central Coherence Theory (Happé & Frith, 2006) and could, in turn, explain findings of enhanced unimodal processing abilities in ASD.

Additionally, extended sensory binding would likely have cascading effects on higher-order social, cognitive and behavioural functioning. For example, communicating with another person necessitates detecting the temporal synchrony between their speech, lip movements and body language and combining this information together. If temporal binding is extended or less precise in ASD then this would lead to problems distinguishing the synchronous sensory information relating to the speaker from sensory inputs that originated from unrelated stimuli (Bahrick & Todd, 2012). In support of this, Stevenson et al., (2014) demonstrated a relationship between temporally extended audio-visual binding and poor speech processing abilities in children with ASD. Furthermore, if individuals with ASD are not guided towards social events to the same degree as TD populations, due to extended binding, this could explain why, unlike TD populations, some people with ASD do not show a preference for social over non-social stimuli (Chevallier et al., 2012).

Evidence for temporally extended sensory binding has been found for both social and non-social visual-auditory integration in ASD (e.g. Foss-Feig et al., 2010; Kwakye et al., 2011; Woynaroski et al., 2013). As discussed in Section 1.2.1, MSI facilitation effects (such as speeded reaction times) occur when inputs from different modalities occur either simultaneously or in close temporal proximity (i.e. within the TBW). In Foss-Feig et al., (2001), a temporal order judgment (TOJ) task was used in which multiple auditory beeps were coupled with one brief visual flash. When this experiment is conducted with TD adults, provided that the delay between visual and auditory inputs is small (<100ms) these inputs are integrated, resulting in the perception of multiple flashes (Shams, Kamitani, & Shimojo, 2002). With a larger delay, this illusion does not occur (Shams et al., 2002). Foss-Feig et al., (2010) reported that when the temporal gap between the beeps and the flash was extended to beyond 150ms, the illusion was disrupted in TD children but preserved in children with ASD, indicating a wider TBW (i.e. less specific multisensory binding).

This finding has been replicated in children with ASD using different tasks. Kwakye et al., (2011), for example, employed a visual-auditory TOJ task in which participants observed a light flash and a tone presented simultaneously. After a variable delay, they were presented with a second light flash followed by a second tone and were asked which light flash occurred first. Studies have consistently shown that the additional auditory stimuli enhance performance even though they give no information about which visual stimulus appeared first (Hairston et al., 2006; Morein-Zamir, Soto-Faraco, & Kingstone, 2003). Kwakye et al., (2011) found that the auditory stimuli enhanced performance for TD children when the delay between the second flash and the second tone was between 50 and 150ms. At smaller or larger delays there was no minimal or no enhancement effect. Importantly, however, the authors found that the auditory enhancement effect was present when the multisensory delay ranged from 0-300ms in children with ASD, again indicating extended temporal binding for visuo-auditory integration.

Though these studies indicate that highly asynchronous stimuli are more likely to be perceived as synchronous in persons with ASD than in TD populations, the majority of the research on this area has been conducted with children. Thus, it is not clear whether these findings represent a delay or a deficit in the proficiency and accuracy of sensory binding. Indeed, Smagt, Engeland, & Kemner (2007) failed to find evidence of extended visuo-auditory binding in adults with ASD relative to a TD control group in a study employing the flash-beep task. Furthermore, a recent study found no evidence for temporally extended visuo-tactile binding in adults with ASD in a cross-modal congruency task, in which participants discriminated between single and double tactile pulses applied to the hand (Poole, Gowen, Warren, & Poliakoff, 2015). For TD participants, when a task-irrelevant light flash occurred 200ms or 400ms after the tactile stimuli, performance was not significantly different to baseline conditions (when no visual stimuli were present). However, significantly faster and more accurate responses were seen when the visual stimuli occurred 30ms before or 100ms after the tactile stimuli. This multisensory enhancement effect indicates that visuo-tactile temporal binding had only occurred in conditions with visuo-tactile stimulus onset asynchronies (SOAs) of 30ms or 100ms. With longer SOAs, the temporal distance between the visual and tactile inputs was wide enough for them to be treated as two separate events. Interestingly, for the ASD group, enhanced performance was only significantly greater than baseline at SOAs of -30ms, indicating that participants with ASD may, in fact, be *more* sensitive to the temporal constraints of visuo-tactile integration than the TD group. Nevertheless, there were no significant differences in the strength of the multisensory enhancement effect between groups - instead, they displayed a similar temporal profile of visuo–tactile integration. This could suggest that the developmental narrowing of the temporal binding window is delayed in children with ASD but, by adulthood, they have either caught up with their peers or employ alternative strategies for determining when inputs should be integrated (and, importantly, when they should not).

1.4.6. Visuo-tactile-proprioceptive integration in ASD

To my knowledge, only three studies have directly investigated visuo-tactile-proprioceptive processing in individuals with ASD (Cascio et al., 2012; Palmer et al., 2015; Paton, Hohwy, & Enticott, 2012) and all have used the rubber hand illusion (RHI; Botvinick & Cohen, 1998). In this procedure, the participant's unseen hand is touched at the same time as they see a rubber hand being touched, leading to embodiment of the fake hand when seen and felt touches are synchronous, but not when they are asynchronous. This finding has been consistently replicated in TD adults (e.g. Botvinick, 2004) and relies on integrating the visual and tactile inputs such that one multisensory event is experienced, as opposed to two separate unimodal events. The RHI is useful since it can indicate how sensory integration may impact on body ownership, but it is limited in its ability to discriminate between alternative explanations for atypical MSI in ASD.

The RHI study conducted by Paton et al., (2012) included an additional condition purported to reveal if over-reliance on proprioception is exhibited in adults with ASD relative to TD individuals. The classic RHI was conducted with and without the participant wearing video goggles that showed the fake hand in the same spatial location as the real, hidden hand. The goggles expedite illusion onset in TD adults (Hohwy & Paton, 2010) by minimising proprioceptive incongruity between the real and fake hand. Both groups reported a greater embodiment of the fake hand in synchronous compared to asynchronous conditions. Interestingly, TD adults showed a greater embodiment of the fake hand in the goggles compared to the no-goggles condition whereas the ASD group showed no significant difference between the conditions. The authors suggest that the TD group attempted to integrate visuo-tactile and proprioceptive inputs together and thus experienced proprioceptive discrepancy interference in the no-goggles condition, which was attenuated via the goggles. In contrast, the ASD group may have weighted proprioceptive inputs more heavily than visuo-tactile inputs in all conditions and thus may not have integrated the multisensory inputs to the same degree as the TD adults. Thus, they were less affected by whether or not the proprioceptive inputs concurred with the visuo-tactile information.

Visuo-tactile-proprioceptive integration was also measured by assessing proprioceptive drift in the direction of the fake hand. This is the change in distance between the perceived location of the hidden hand pre- and post-brushing. If participants have integrated visuo-tactile inputs and embodied the fake hand then they should exhibit proprioceptive drift after synchronous, but not asynchronous, conditions. Interestingly, a difference in drift between these conditions was not found in either group, yet drift across conditions was significantly greater in the TD compared to the ASD group. The authors suggest that the individuals with ASD focused more on the proprioceptive inputs rather than integrating these with the visuo-tactile events, leading to a more accurate estimation of hand location. Yet as no baseline measure of drift was taken it cannot be ruled out that hand localisation ability was contributing to group differences in drift, especially since impaired motor functioning is common in ASD (Nazarali, Glazebrook, & Elliott, 2009) which could affect the reliability of drift as a measure of MSI. Additionally, there was a wide variability in drift in the ASD group, with some participants displaying drift *away* from the real hand, which would not be expected if the ASD group was indeed more accurate in localising their hand.

Moreover, a significant difference in proprioceptive drift between adults with ASD and TD controls was not seen in a more recent RHI study (Palmer et al., 2015). Nonetheless, this study did reveal group differences in the extent that synchronous visuo-tactile inputs influenced subsequent reach-to-grasp movements (in which participants grasped a cylinder located in front of their hidden hand). Compared to TD individuals with few autistic traits (as assessed by the Autism Quotient Questionnaire; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) the ASD group appeared to show a reduced influence of context such that movements were similar across synchronous and asynchronous conditions. In contrast, TD individuals seemed to show a conflict between proprioceptive input and illusory expectations for arm position, leading to on-line corrections to their movements in the synchronous condition only. Nevertheless, these findings and interpretation do not fit with the lack of group differences in proprioceptive drift seen in this study.

In the RHI study by Cascio et al. (2012), synchronous and asynchronous conditions were conducted over two 3-minute blocks with 21 participants with ASD and 28 TD participants. Children with ASD exhibited similar drift across the conditions after the first block but considerably more drift after the second block, in the synchronous condition only. The authors interpret this finding as a delay in the experience of the illusion, and thus a delay in MSI, which could be due to extended temporal binding for visuo-tactile inputs. Thus, the ASD group may have perceived the asynchronous brushing as synchronous in the first block if the 500ms offset between the visual and tactile inputs was not large enough to be outside their TBW.

Since drift was no longer exhibited after six minutes of asynchronous stroking, the authors suggest that the TBW may have narrowed with continued visual-tactile stimulation such that the asynchronous events are no longer perceived as synchronous. This coheres with findings by Stevenson, Wilson, Powers, & Wallace (2013) showing that the audio-visual binding window can narrow with training in TD adults (via repeated exposure to temporally asynchronous sensory inputs). Nonetheless, this cannot explain why the ASD group only exhibited drift after the second block of synchronous stroking, not the first. An enlarged TBW should have no effect on drift in the synchronous condition at all. Alternatively, the authors propose that the ASD group was focusing preferentially on proprioceptive signals over visuo-tactile inputs, which would thus reduce illusion susceptibility. Yet, this cannot explain why drift then increased after the second block of synchronous stroking but decreased after the second block of asynchronous stroking.

Together the findings from Cascio et al. (2012), Palmer et al., (2015) and Paton et al. (2012) point to atypical visual-tactile-proprioceptive integration in children and adults with ASD. However, the classic RHI paradigm cannot distinguish evidence for an over-reliance on proprioceptive processing over temporally extended visuo-tactile binding as both accounts predict reduced illusion susceptibility. Moreover, the precise nature of either cause cannot be clearly specified. It should also be noted that group differences might be due to the ASD group not attending to the fake hand for a sustained length of time to induce the illusion. Indeed, attention towards the visual cues was only assessed indirectly based on experimenter impression in Cascio et al. (2012) and Palmer et al., (2015) and Paton et al., (2012) do not report if and how sustained attention was measured. Without looking at the fake hand for at least 11s, MSI of the seen and felt strokes, and hence the illusion, is very unlikely to occur (Ehrsson et al., 2004). Moreover, as reported by Murray (2010), 50% of individuals with ASD meet the criteria for attention deficit hyperactive disorder (ADHD) and problems maintaining visual attention when distractors are present have also been reported in ASD (Burack, 1994). Consequently, the felt strokes could have distracted attention away from the fake hand, particularly because of the heightened sensitivity to touch in ASD commonly seen in those with the disorder (Cascio et al., 2007), thereby preventing the illusion. Furthermore, in order to embody the fake hand in the classic RHI paradigm, participants must overcome discrepancies in physical characteristics between the fake and real hands, such as texture, size, and shape, which influence susceptibility to the illusion (Tsakiris & Haggard, 2005). These differences could be more salient for individuals with ASD since heightened detail-focused processing and imagination deficits characterise the disorder (American Psychological Association, 2013; Baron-Cohen, Ashwin, Ashwin, Tavassoli, & Chakrabarti, 2009; Happé & Frith, 2006) and thus, could also underlie reduced embodiment of the rubber hand.

In addition to these design issues, the number of participants in the ASD group in the RHI studies was small, ranging between 12 and 21 participants and no other studies have yet been published assessing the effect of the RHI on individuals with ASD. Before firm conclusions can be drawn, further studies investigating visual, tactile and proprioceptive integration in ASD with larger sample sizes should be conducted. The studies reported in this thesis use a unique technique that avoided these inherent limitations of the classic RHI design and aim to distinguish evidence for an over-reliance on proprioceptive processing and temporally extended visuo-tactile binding.

1.5. Conclusions and thesis aims

MSI is necessary for us to understand and interact with our environment. It provides us with significant behavioural and perceptual advantages over processing sensory inputs from different modalities separately. The adult brain takes inputs from different sensory modalities and combines them with prior knowledge about the world in a statistically optimal way. It is not clear, however, when this ability reaches maturity in TD children. Collectively the research suggests that, unlike older children and adults, younger children may show a dominance for inputs from one sense (e.g. tactile) over another (e.g. vision), regardless of whether this is the most reliable information source in the given circumstances. Additionally, studies indicate that sensory binding in younger children is less sensitive and specific than in older children, such that inputs originating from different events are more likely to be integrated together. Specifically, research indicates that the visuo-auditory TBW narrows with age, however temporally extended binding of visuo-tactile inputs in younger children has not been systematically assessed.

The typical development of optimal visual-tactile, visual-proprioceptive and visual-tactile-proprioceptive integration is important to understand since these processes underpin body representation. This is needed for the development of fundamental behavioural, cognitive and social processes that are impaired in individuals with ASD. Evidence suggests that these, and the sensory sensitivities characterising the disorder, may be due to atypical MSI. Specifically, there may be a fundamental over-reliance on proprioception and/or temporally extended sensory binding in ASD. As yet, no study has directly tested the evidence for these theories. Moreover, it is not known if atypical MSI is due to a developmental delay (present only in children) or a permanent deficit that continues into adulthood.

In this thesis, I firstly aim to investigate how and when sensory integration underlying body representation becomes optimal in TD children. Secondly, I aim to examine whether this sensory integration is atypical in children with ASD, and in adults on the non-clinical and clinical autism spectrum. Specifically, I test the evidence for 1) an over-reliance on proprioception and 2) extended visuo-tactile temporal binding in ASD.

1.6. Methods

All experiments were conducted using a MIRAGE mediated reality device (Newport, Pearce, & Preston, 2010; see Figure 1.1). The MIRAGE uses a rectangular horizontal mirror, suspended equidistant between the work surface below and a computer screen above. The mirror reflects live camera images of the participant's hands displayed on the computer screen. These video images are viewed in real time as if viewing the hand directly; that is, in the same spatial location and from the same visual perspective. Real-time videos are acquired and manipulated online using a powerful combination of custom-made hardware and software that can control visual presentation with millisecond precision.

As discussed in Section 1.3.2, a useful method of investigating sensory integration involves introducing a conflict between the information from two senses and assessing how this changes the weighting given to each input. King et al., (2010) used this method in their target localisation task. However, this had limitations since information relating to body ownership was only present for proprioceptive inputs but not visual inputs, which were in the form of coloured stickers indicating the location of the unseen hand. The MIRAGE is able to resolve this issue since visual cues of limb localisation originate from vision of the body, as opposed to visual targets signalling body position, thereby giving a more valid measure of the relative contributions of visual and proprioceptive inputs on body ownership.

The RHI has been used to investigate visuo-tactile-proprioceptive integration in children and adults with and without ASD. However, as detailed in Section 1.4.4, the classic RHI is limited in its ability to distinguish between alternative theories for atypical integration. The MIRAGE can again avoid these difficulties. Firstly, the hand in MIRAGE looks exactly as the participants' own hand does and moves in real-time. Secondly, reported illusion onset is reliably quicker in MIRAGE illusions than in the RHI and does not require intensive periods of sustained attention. Thirdly, asynchronous inputs can be precisely defined such that extended visuo-tactile binding can be tested more sensitively. Lastly, unlike the classic RHI, using the MIRAGE, proprioceptive discrepancy between the real and the fake hand can be removed.

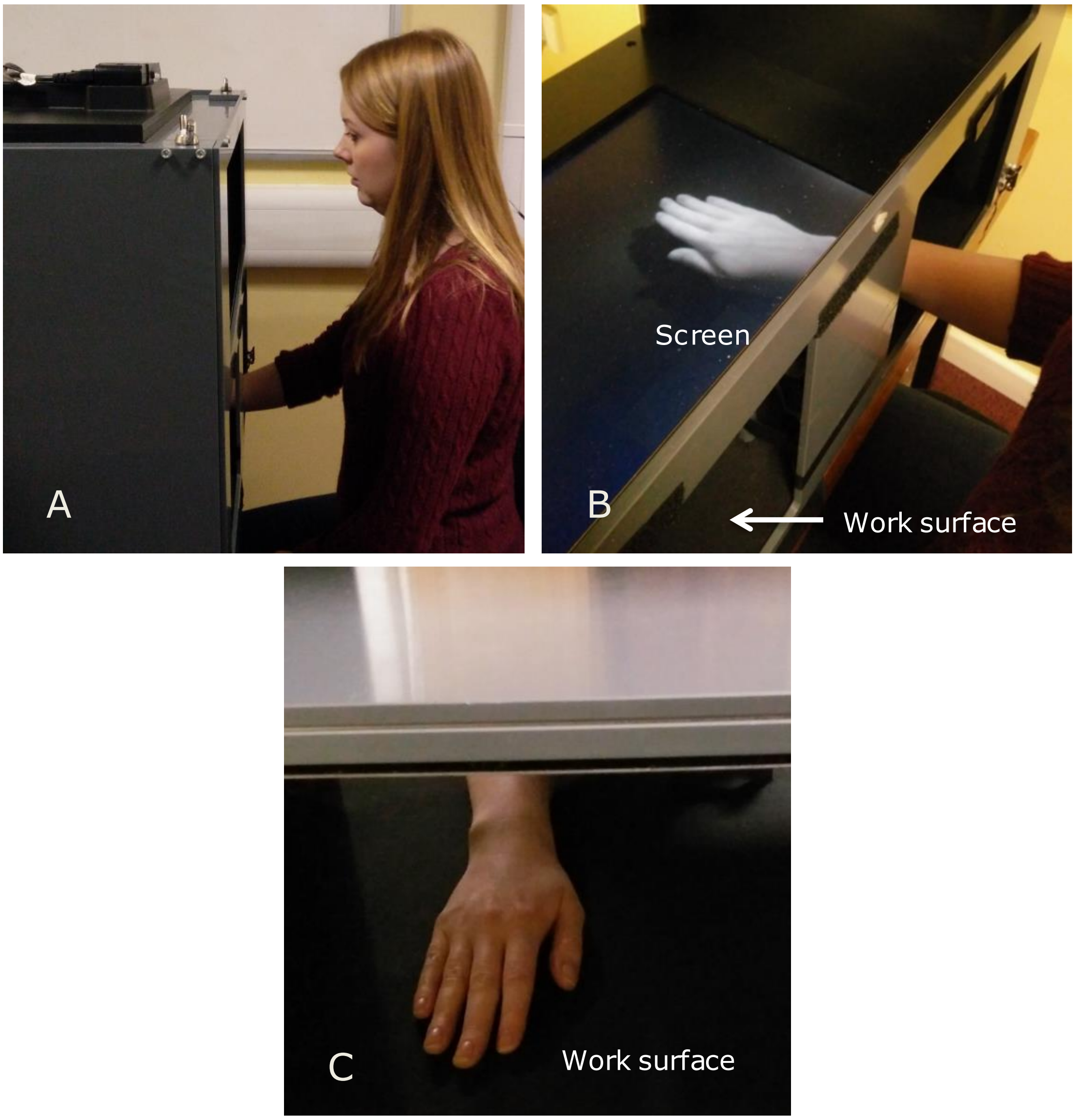


Figure 1.1. MIRAGE set up. A) The participant places his/her hand onto the work surface of MIRAGE and sees it on the screen in the same spatial location, and in the same plane, as his/her actual hand. B) Hand from participant's perspective; C) Hand from experimenter's perspective.
In all experiments, a black bib was tied across the length of the MIRAGE so that the participant could not see the exact relationship between his/her limb and the visual image. The arm is here uncovered for illustrative purposes only.

1.7. Summary of studies

Experiment 1

In this study, I conducted a developmental trajectory analysis of a hand localisation task in TD 4- to 11-year-olds. I found that children of all ages could use unimodal visual and proprioceptive information accurately. However, the age at which children optimally integrate these inputs develops from very little integration in 4-year-olds to almost adult-like abilities in 10- to 11- year-olds.

Experiment 2

This study tested whether younger children's visuo-proprioceptive binding is less specific and sensitive than older children's. Results showed that younger children are more likely to integrate spatially separated visuo-proprioceptive information than older children. Moreover, the findings suggest that the results of Study 1 are not due to superior hand localisation ability in younger children.

Experiment 3

This study tested the hypothesis that visuo-tactile binding underlying body representation is temporally extended in younger compared to older children. Results supported this hypothesis, indicating that, like the visuo-auditory TBW, the visuo-tactile TBW may also narrow with age in typical development.

Experiment 4

This study investigated whether ASD traits in the TD adult population are related to atypical visuo-proprioceptive integration and, specifically, an over-reliance on proprioception. No support was found for this. This could indicate that atypical MSI is seen only in individuals with a clinical diagnosis of ASD.

Experiment 5

In this study, I investigated the evidence for over-reliance on proprioception and extended visuo-tactile binding in children with ASD, using a body ownership task. Results showed evidence for temporally extended visuo-tactile integration. Though no evidence was found for a fundamental over-reliance on proprioception, extended sensory binding may have led to reduced processing of temporal synchrony over modality-specific information (i.e. proprioception).

Experiment 6

This study examined whether evidence of temporally extended visuo-tactile integration is seen in children with ASD when a more objective measure of body ownership is used. Again, results indicated temporally extended sensory binding in children with ASD relative to chronological age-matched control children.

Experiment 7

The penultimate study used the body ownership task employed in Experiment 5 to investigate whether adults with ASD exhibit the same pattern of atypical MSI seen in children with the disorder. I found that adults with ASD do not show evidence of over-reliance on proprioception or extended visuo-tactile binding, relative to a TD adult group. This could suggest that extended sensory binding represents a developmental delay not a deficit in ASD.

Experiment 8

In the final study, I examined whether adults with ASD show atypical MSI in the body representation task used in Experiment 6. Mirroring the findings from Experiment 7, I found no group differences between ASD and TD adults. Again this indicates that extended sensory binding may represent a developmental delay but not a life-long deficit in ASD. Alternative explanations for the findings are also discussed.

Chapter Two: Visuo-proprioceptive integration in typical development

Experiment One: Visuo-proprioceptive integration in typical development

2.1. Abstract

Forming an accurate representation of the body relies on the integration of information from multiple sensory inputs and, in particular, vision and proprioception. Whilst adults have been shown to integrate these sources in an optimal fashion, few studies have investigated how children integrate visual and proprioceptive information when localising the body. In the current study, children were asked to estimate the position of their index finger after viewing congruent or incongruent visuo-proprioceptive information regarding hand position. There was a significant developmental change in the extent to which incongruent sensory information led to mislocalisation of the hand towards the visual representation. Estimates by younger children were closer to the true location of the hand compared to those by older children. This suggests that, throughout early childhood, visual inputs are increasingly integrated with proprioceptive information to determine hand location. Variability in social skills or inattention did not predict task performance.

2.2. Introduction

In chapter one, I summarised the literature on multisensory integration (MSI) in typical development, focusing specifically on visual, tactile and proprioceptive integration. A wide body of research demonstrates that adults integrate sensory information from these modalities in a statistically optimal way. Specifically, a weighted average of multisensory inputs is produced such that sensory cues are weighted more or less strongly depending on bottom-up (incoming sensory inputs) and top-down (prior knowledge) information (van Beers, Wolpert, & Haggard 2002).

However, it is less clear if, and when, children integrate visual, tactile and proprioceptive information in a statistically optimal manner. A wide body of research indicates that young infants and even newborns can detect cross-modal contingencies between these inputs. Preferential looking studies report that neonates attend to synchronous visuo-tactile brushstrokes for a longer time period than asynchronous brushstrokes, indicating awareness of the difference between the two (Filippetti et al., 2013; Zmyj et al., 2011). Young infants also look longer at a video displaying delayed feedback of their leg, hand or arm movements, compared to a video without a delay (Bahrick & Watson, 1985; Schmukler, 1996). Moreover, infants of less than 6 months look longer at a video of their legs that creates visuo-proprioceptive conflict (e.g. by reversing the way the legs move in relation to each other) compared to a video of their legs as they would be sensed via direct visuo-proprioceptive feedback (Morgan & Rochat, 1997; Rochat & Morgan, 1995; Schmuckler, 1996). Together these findings suggest that very young children can detect visuo-tactile and visuo-proprioceptive contingencies yet it is not clear whether they actually derive a sense of bodily self or body ownership from this. As pointed out by Bremner, Lewkowicz, & Spence (2012), the visual cues in the majority of these studies are presented via a video display that is outside peripersonal space, while other studies assess infants' perceptions of contingencies between their movements and the movements of external objects (i.e. a paintbrush), rather than perceptions of body representation specifically. Moreover, though this literature suggests that infants have the capacity to integrate visuo-tactile and visuo-proprioceptive inputs, preferential looking studies cannot assess the relative weighting given to different senses and the extent that MSI is optimal and adult-like.

Though studies with older children have been conducted, a recent review on the development of MSI abilities concluded that the age at which optimal integration occurs is still unclear (Dionne-Dostie et al., 2015). This is likely due to differences in task complexity and the sensory inputs under investigation as well as the limited age range of participants. Some studies report that, in tasks requiring MSI, younger children tend to rely solely on one sense over another. Yet, this 'dominant' sense appears to vary within and between tasks and the age at which adult-like integration is seen varies across studies. Nardini et al., (2008), for example, found no evidence of optimal visuo-proprioceptive integration in 4- to 5- or 7- to 8-year-olds. However, in a latter study, Nardini et al., (2013) found that adults and 7- to 9-year-olds optimally integrated visuo-proprioceptive information but 4- to 6- and 10- to 12-year-olds did not, indicating that optimal MSI may be unstable in childhood.

Gori et al., (2008), reported that 5- to 7 year-olds did not integrate visual and tactile spatial information to discriminate the height of objects. Instead, one sense dominated, irrespective of its reliability. Integration, though, was statistically optimal in 8- to 10-year-olds. This suggests that the sensory systems of younger children do not reduce uncertainty in an optimal way, unlike older children and adults. However, as with the infant studies, this task does not relate to body ownership and/or localisation specifically. This was assessed more directly in Warren & Pick's (1970) study, in which visuo-proprioceptive conflict was created via prism goggles that displaced the seen location of the participant's left hand. 7- to 8-year-olds, 11- to 12-year-olds and young adults were asked to point with their unseen right hand to the seen position (using visual information) or felt position (using proprioceptive information) of their left hand. Though vision biassed proprioception in all groups, no effect of age was found. In contrast, research examining the development of postural control indicates that sensory re-weighting in response to changing sensory environments is seen in children as young as 4 years, yet the magnitude of this re-weighting increases with age over childhood (Bair, Kiemel, Jeka, & Clark, 2007; Barela, Jeka, & Clark, 2003; Polastri & Barela, 2013). King et al., (2010) found a similar development of visuo-proprioceptive integration underlying hand localisation in 7- to 13-year-olds. The experimental set-up for this study is displayed in Figure 2.1. Visual stimuli (coloured stickers) were displayed on a computer screen on the top tier of the apparatus while the proprioceptive stimulus was provided by the unseen left index finger, positioned underneath the lower tier. The participant moved his/her unseen right hand on the top of the lower tier to localise visual, proprioceptive or visuo–proprioceptive targets. In visual conditions, children pointed to a coloured circle (visual target) displayed on the top tier. In proprioceptive conditions, they pointed to the unseen finger of their other hand (proprioceptive target) without seeing either hand (see Figure 2.1). Visuo-proprioceptive conditions were identical to proprioceptive conditions except that a visual marker (a sticker) signifying target location was present. In incongruent conditions, the visual marker was moved so that it was not directly above the unseen finger. In these conditions, accuracy in the proprioceptive conditions predicted reliance on proprioception.

When congruent visual and proprioceptive information was available, children's estimates were more reliable than in conditions when information from only one modality was present. This indicates that 7- to 13-year-olds are able to flexibly re-weight sensory information according to changes in the experimental context. However, in an incongruent condition in which the visual marker and proprioceptive target (the unseen finger) were in conflicting locations, older children increased the weighting given to proprioceptive inputs while younger children utilised visual information more. This is interesting since, in adult studies, vision is a more reliable source of information for hand localisation than proprioception when the hand is stationary (Mon-Williams et al., 1997), thus, MSI in the younger participants appear to be more adult-like than in older children. However, in King et al., (2010), while proprioceptive information originated from the participant's actual (unseen) hand, visual information was merely a sticker indicating possible hand location. Therefore, in this specific task, older children may have deemed the proprioceptive inputs to be more informative for finger localisation than vision. In contrast, younger children continued to rely on vision more heavily than proprioception even though it was a less reliable information source in the given circumstances. Therefore, younger participants could have been demonstrating a reduced ability to flexibly re-weight sensory information depending on its context-dependent reliability. Thus, this task cannot be seen as a direct measure of MSI underlying normal body localisation since, unlike in every-day life, information relating to embodiment of the hand was present only for the proprioceptive inputs. Moreover, though this study and postural paradigms suggest that optimal integration underlying body representation develops over childhood, the tasks employed necessitate motor skills that also develop with age. Consequently, it is unclear whether age effects are due to changes in motor adaptation, sensory integration or both (Barkley, Salomonczyk, Cressman, & Henriques, 2014).

Other studies (e.g. Cowie, Makin, & Bremner, 2013; Cowie, Sterling, & Bremner, 2016) have used rubber hand illusion (RHI) tasks that avoid the issues outlined above. However, for this illusion to take place, children must overcome the discrepancies in physical characteristics between the fake and real hand (i.e. texture, shape). This may impact on the extent to which the rubber hand is embodied (Tsakiris & Haggard, 2005) and could be underlying age-related differences in results. Furthermore, the study design in King et al. (2010) necessitated each child completing 90 trials while RHI tasks typically require participants to maintain attention towards the fake hand for blocks of 3 minutes or longer. The reliability of the findings in these studies thus depends on children's attention and working memory skills, which improve considerably between 4 and

15 years (Gathercole et al., 2004). Furthermore, the majority of studies in this area have divided children into broad, and seemingly arbitrary, age ranges and compared average group performance (e.g. Gori et al., 2008; Nardini et al., 2008; 2013). These comparisons could be contributing to inconsistent findings since they may be masking critical periods in sensory integration development within year groups.

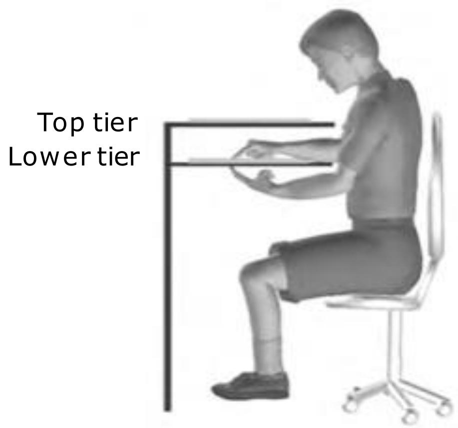


Figure 2.1. Experimental set-up from King et al., (2010).
Visual stimuli (coloured stickers) were displayed on a computer screen on the top tier of the apparatus. The proprioceptive stimulus was provided by the location of the unseen left index finger underneath the lower tier. The participant moved his/her unseen right hand on the lower tier to localise visual, proprioceptive or visuo–proprioceptive targets.
Adapted from "Improvements in proprioceptive functioning influence multisensory-motor integration in 7- to 13-year-old children," by B.R. King, M.M. Pangelinan, F.A. Kagerer and J.E. Clark, 2010, *Neuroscience Letters 483,* p. 36-40. Copyright 2010 by Elsevier Ireland Ltd.

The current experiment aimed to avoid the limitations of the research described above. The first aim of this experiment was to systematically assess the effect of age on visuo-proprioceptive integration for hand localisation in TD children. This is important to understand in order to specify when and how MSI may be atypical in autism spectrum disorders (ASD). A second aim was to investigate the relationship between visuo-proprioceptive integration and social skills in TD children, as measured by a parental questionnaire. The normal integration of visual, tactile and proprioceptive inputs underlies body representation, which is necessary for higher order social processes. These include the capacity to compare and differentiate between the self and others (Cascio et al., 2012), self-awareness, imitation and empathising (Schütz-Bosbach et al., 2006), all of which are compromised in ASD (American Psychological Association, 2013). Thus, as put forward in Chapter One, atypical MSI could alter the typical development of these social abilities in ASD, offering an explanation for some of the core traits of the disorder. ASD has been defined as the extreme end of a continuum of quantitative traits on which the general population lies (Constantino & Todd, 2003; Happé, Ronald, & Plomin, 2006). Consequently, it is possible that a relationship between under-developed MSI for body localisation and reduced social skills will be seen in typical populations also.

Unlike prior studies, a brief task was used, which did not rely on children remembering instructions and sustaining attention over a large number of trials. Additionally, the current task was designed to promote the integration of vision and proprioception. Firstly, in contrast to the task used in King et al. (2010), both the visual and proprioceptive information was directly related to embodiment of the hand, such that the participant's own hand served as the incongruent visual 'target' as well as the proprioceptive 'target'. Secondly, the current task used a MIRAGE mediated reality system (Newport et al., 2010), which does not require participants to embody a 'fake' hand, as is necessary for the classic RHI. Thirdly, instead of group analyses, a developmental trajectory analysis was used to track age-related changes in MSI over typical development.

The task comprised of two control conditions and one experimental condition in which children aged 4 to 11 years were asked to locate their right index finger. In the first control condition, congruent visual and proprioceptive information regarding limb location was available to establish whether all children understood the task. In the second control condition, only proprioceptive inputs were available, to assess age-related differences in unimodal (proprioceptive) accuracy. The experimental condition presented incongruent visual and proprioceptive inputs to assess the degree that one or the other sense dominated and the extent that visuo-proprioceptive integration is adult-like in typically developing children. A very similar task conducted by Bellan et al., (2015) found that, in this condition, adults integrate the visual and proprioceptive information but weight visual inputs more strongly than proprioceptive information, since vision is deemed as a more reliable indicator of hand location when the hand is passive (Mon-Williams et al., 1997). It was predicted that MSI abilities would develop with age such that, when vision and proprioception are incongruent, older children, like adults, will demonstrate visuo-proprioceptive integration but will weight vision more strongly than proprioception. Although findings on visuo-proprioceptive integration in children are inconsistent, based on evidence from MSI studies pertaining to other sensory inputs (e.g. visuo-tactile; Cowie et al., 2013), I also predict that, in younger children, one sense will dominate over the other in the current task. Additionally, since studies have shown evidence for atypical MSI in individuals with ASD – a disorder defined by social impairments - I predict that children with more highly developed social skills will show more adult-like MSI.

2.3. Method

2.3.1. Participants

75 children aged 4 to 11 years (mean= 8.44, SD= 1.94, 43 females, 8 left-handed) participated as part of a Summer Scientist Week event held at The University of Nottingham for which children were invited to complete short experiments. Children came from a range of socioeconomic backgrounds but on average they were of mid socioeconomic status. Parents of all children completed the Social Aptitudes Scale (SAS; Liddle, Batty, & Goodman, 2008), which measures social skills, and the Strengths and Weaknesses of ADHD symptoms and Normal behaviour rating scale (SWAN; Swanson et al., 2006), which measures positive attention and impulse

control. The British Picture Vocabulary Scale III (BPVS III; Dunn & Dunn, 2009), was used to assess verbal mental age, to check that all children had verbal language skills in the average range.

Table 2.1. Participant descriptives.

	Age (years)	BPVS raw score	BPVS Standardised score	SAS	SWAN	SWAN inattentive subscale	SWAN hyperactive subscale
Mean	8.78	120.72	105.05	25.31	-21.64	-6.22	-7.38
SD	1.79	21.21	11.40	6.19	9.68	9.09	9.68
Min	4.51	59	72	6	-74	-24	-27
Max	11.95	156	131	39	43	21	15

Data from 11 children was excluded: nine children did not keep their hands still during the task, one (aged four years) did not want to complete the task, and age data for one child was missing, leaving 64 children (40 females, 7 left-handed) who were included in the analysis (see Table 2.1). In the remaining sample, data were missing for three participants on the SAS, three on the BPVS and four on the SWAN. However, no children had a diagnosis of ASD, attention deficit hyperactivity disorder (ADHD) or a learning disability. The parents of all children gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

2.3.2. Procedure

All participants were tested in a quiet room at the University. Children completed a MIRAGE task lasting approximately 15 minutes and the BPVS, which was administered either before or after the MIRAGE task. The experimental procedure was conducted using a MIRAGE (see Section 1.6 and Figure 1.1 for more details). The basic task required children to make judgements about the location of their seen or unseen finger by verbally responding when they perceived a slow moving arrow to be in line with their index finger. Judgements were made after exposure to congruent or incongruent visuo-proprioceptive sensory input regarding the location of the hand. All participants were tested individually in a within-subjects experiment that consisted of three conditions completed in the following order: congruent with vision of the hands (congruent seen), congruent without vision (congruent unseen) and incongruent without vision (incongruent unseen). Each condition had two trials.

At the start of the task, a glove tip was placed on the child's right index finger. This was referred to as 'the finger with the hat on' so that there could be no confusion about which finger was being referred to during the experiment. Children knelt or sat on a chair to allow them to view their hands when placed on the work surface of the MIRAGE (Newport et al., 2010). The MIRAGE uses a rectangular horizontal mirror, suspended equidistant between the work surface below and a computer screen above, which reflects live camera images of the hands displayed on the computer screen. These appear in the same physical location as the real hands with a minimal delay (~16 ms), thus giving the child the impression that they are viewing their own hand, in its real location, in real time. A black bib attached across the length of the mirror was tied comfortably around the participant's shoulders to obscure a direct view of their upper arm.

Control Condition One: Congruent Seen

In the congruent seen condition, participants watched as the experimenter moved their hands to a pre-specified position. They were instructed to keep their hands still and to judge the location of their right index finger. Participants saw a red arrow (reflected from the computer screen above) travelling laterally across the MIRAGE workspace and said 'stop' when they judged the arrow to be directly in line with their index finger (see Figure 2.2). The X-axis coordinate (in pixels; 1 pixel=0.75mm) of the arrow was recorded to give a measurement of perceived finger location. Each measurement was taken twice, once with the arrow travelling from right to left and once from left to right (order counterbalanced across conditions and participants). The purpose of this condition was to ensure that participants understood the task requirements and assess whether they could use

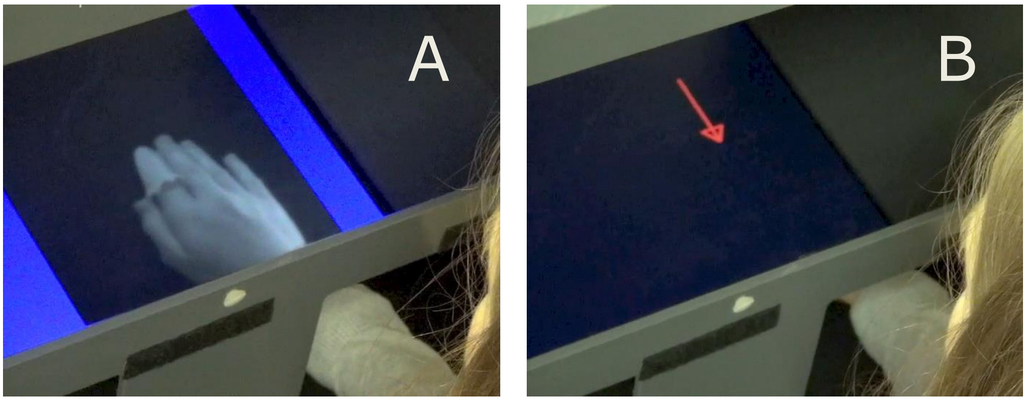


Figure 2.2. Localisation judgments.

A) Index finger with 'hat' (glove tip).
B) In each condition, participants made judgements about the location of their seen or unseen finger by verbally responding when they perceived a slow moving arrow to be in line with their index finger.

congruent visual and proprioceptive information to accurately estimate the location of their seen finger.

Control Condition Two: Congruent Unseen

In the congruent unseen condition, the participants' hands remained in the same location as in the congruent seen condition but vision of the hands was occluded and the two finger localisation judgments were repeated. This condition was included to assess finger localisation accuracy when only proprioceptive inputs were available.

Experimental Condition: Incongruent Unseen

For the incongruent condition, participants placed their hands in MIRAGE and held

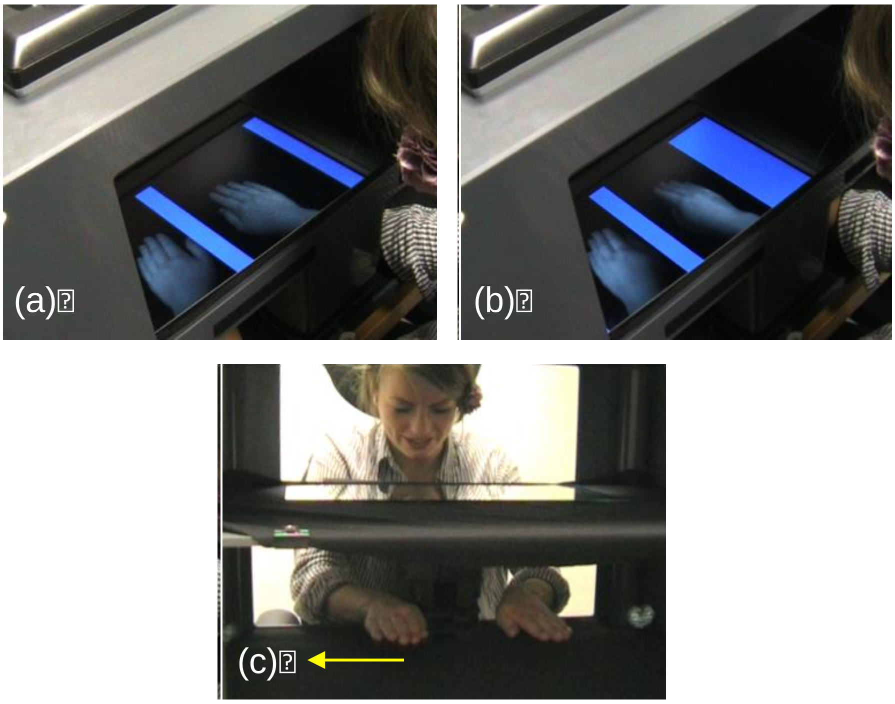


Figure 2.3. Incongruent condition adaptation procedure.
(a) At the start of the adaptation procedure, the seen location of the right hand matches its real location (note the alignment of the seen right hand and the participant's real arm).
(b) Over the course of the adaptation procedure, the superimposed blue bars slowly expand to constrict the hand space. At the same time, and without the participant's awareness, the image of the right hand is shifted slowly leftwards so that in order to keep the hand visible between the blue bars, the participant must move their hand rightwards. This results in a separation between the seen and real location of the right hand (note the misalignment of the seen right hand and the participant's real arm). In the actual experiment, a bib occluded the participant's view of his/her arm.
(c) The participant's hands resting on the MIRAGE work surface, from the experimenter's viewpoint. The arrow indicates the direction in which the right hand moves during the adaptation procedure.

them approximately 5cm above the work surface. They were instructed to not touch blue bars which could be seen to box in each hand to the left and right (see Figure 2.3). The blue bars were graphically superimposed on the visual workspace and expanded slowly over the course of 25 seconds so as to constrict the space in which the hands could be positioned. During this period, the spatial relationship between the seen location of the right hand and its real location was manipulated using an adaptation procedure modified from Newport and Gilpin (2011) and similar to that used in Bellan et al. (2015). This was achieved by moving the image of the right hand smoothly and incrementally leftwards at a rate of 4.5mm/s. Thus, in order to keep the right hand in the same visual location, the participant had to move their hand rightwards at the same rate with the result that after 25 seconds, the seen hand was viewed 11.25cm to the left of its true location. During the same period, the visual image of the left hand oscillated slowly leftwards and rightwards at an average velocity of 4.5mm/s but ended up in the same location as it had started (i.e. with the seen left hand in the same location as the real left hand). This oscillation was included so that the movement of the image relative to the hand, and the tracking of that movement by the real hand, was equivalent across both hands. It is very rare for people to notice the movement of either hand relative to its seen image and conscious awareness of this has never been observed under experimental conditions (see Newport and Gilpin, 2011; Bellan et al. 2015). Once the adaptation procedure was complete, the participants' hands were placed on the work surface of the MIRAGE (see Figure 2.4), vision of the hands was occluded and finger localisation judgments were recorded (again, once with the arrow travelling from right to left and once from left to right).

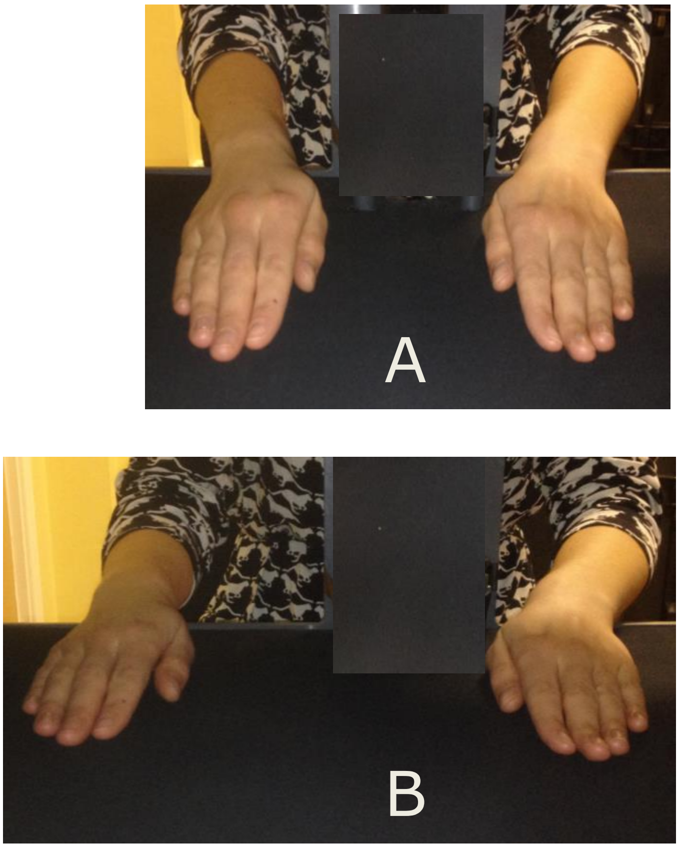


Figure 2.4. Hand position during finger localisation estimates in A) congruent seen and congruent unseen conditions and B) incongruent unseen condition. In the incongruent unseen condition, the participant saw their hands in the position shown in panel A, but the actual, final location of their hands after the adaptation procedure are shown in panel B.

2.4. Results

2.4.1. Data Analysis

There were two trials in each condition. For each trial, the x-axis coordinate of the position of the tip of the right index finger was recorded in pixels (100 units equates to 7.5cm). For each condition, the average of the two estimates of finger position was calculated and subtracted from the actual finger position to give an indication of how sensory information had been integrated. A score of zero would represent a completely accurate estimate of hand location. Positive values indicate estimates to the right of the actual finger location and negative values indicate estimates to the left (i.e. closer to the midline). Therefore, in the congruent seen and congruent unseen conditions, lower scores indicate higher accuracy. In the incongruent unseen condition, the hand was seen 11.25cm to the left of the real location; thus, a score of zero in this condition would represent total reliance on proprioception (very high accuracy), a score of -11.25 represents total reliance on vision, with scores in between indicating the level of weighting given to proprioception and vision respectively, with -5.625 indicating equal weighting.

2.4.2. Developmental Trajectories

Developmental trajectory analysis was used to determine how estimates of finger position in each of the three conditions change with age. Trajectory analysis is comparable to ANOVAs except that linear regressions represented by an intercept and a gradient are compared instead of group means. Intercepts indicate when an ability starts to develop while the gradient shows the rate of development. It was therefore not necessary to split children into age groups and compare them, which could mask a change in behaviour at a critical period within an age group. Instead, trajectories reveal a more precise identification of the age at which, for example, children's' relative weightings of visual and proprioceptive inputs may shift. If, for example, vision is relied on more than proprioception during one period of development after which the opposite occurs, a trajectory can reveal this whereas a group analysis may not. Furthermore, a trajectory allows the testing of a wider age range of children, rather than only testing children who fall within predefined age groups.

The age of the youngest child tested (54 months) was subtracted from the ages of all participants such that the youngest child's age becomes zero months. Rescaling age in this way ensures that when the trajectory is plotted the y-intercept occurs at the youngest age tested, thus the model predicts performance from children only in the age range tested. Firstly, I investigated the within-subjects main effect of condition using a one-way ANOVA. To assess the interaction between condition and age, the analysis was re-run as an ANCOVA with rescaled age entered as a covariate. It was necessary to investigate the main effect of condition separately from the condition by age interaction because the addition of a covariate changes

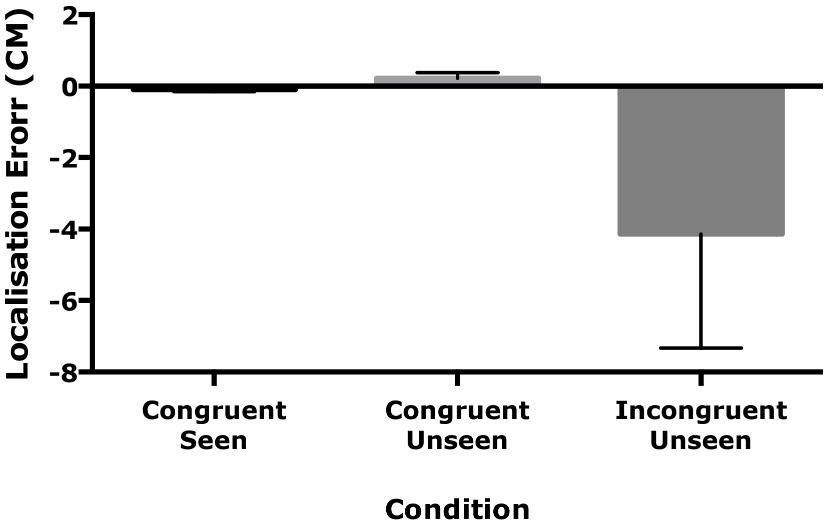


Figure 2.5. Mean localisation errors in cm for each condition across the whole sample. Positive values represent mislocalisation to the right of the real hand; negative values represent error to the left of the real hand. Error is low in all congruent conditions but significantly increases when visual and proprioceptive inputs are incongruent. Error bars represent standard error of the mean.

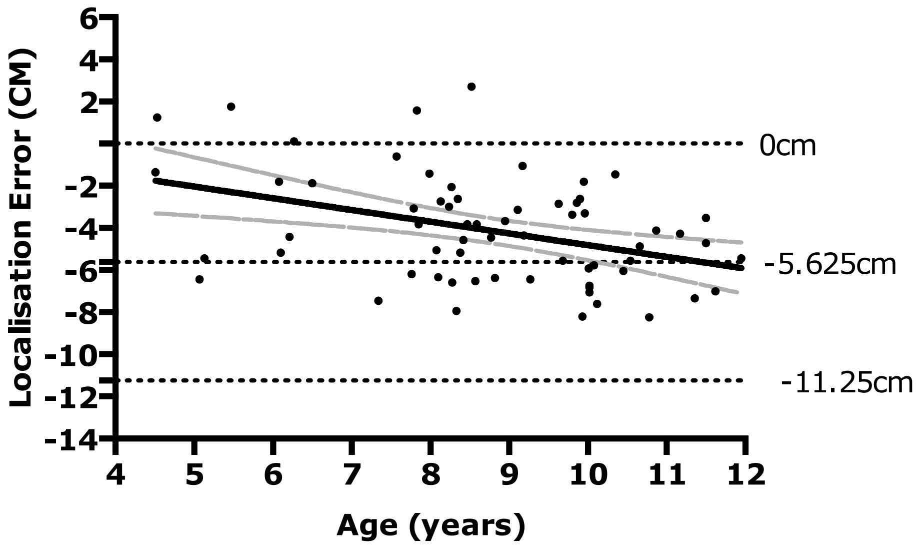


Figure 2.6. Localisation error in the incongruent unseen condition.
The hand was seen 11.25 cm to the left of the real location therefore 0cm= total reliance on proprioception (i.e. no error); -11.25cm= total reliance on vision; -5.625cm= equal weighting of proprioception and vision. Dashed grey lines show 95% confidence intervals.

the main effect of the within-subjects factor (Delaney & Maxwell, 1981) leading to an overly conservative estimate of the effect (Thomas et al., 2009).

2.4.3. Developmental Trajectories for each condition

Figure 2.5 shows performance in each condition across the whole sample. There were no significant outliers in any condition (Cook's D values all <1). Accuracy remained high in the congruent unseen condition when only proprioceptive inputs were present at judgement. However, as predicted, accuracy was significantly reduced in the incongruent condition compared to both congruent conditions. The one-way ANOVA revealed a main effect of condition, $F(1,63)=151.70$, $p<.001$, $\eta^2 =.716$. Pairwise comparisons (Bonferroni adjustment for multiple comparisons) revealed no significant difference in accuracy between the congruent seen and congruent unseen conditions ($p=.159$) but significant differences were found when the incongruent unseen condition was compared to the congruent seen and congruent unseen conditions (both $p<.001$). Children were highly accurate at locating their index finger when congruent visual and proprioceptive information was available, indicating that they all understood the task.

The ANCOVA revealed a main effect of age, $F(1,62)=7.64$, $p=.007$, $\eta^2 =.110$ and a significant condition by age interaction, $F(1,62)=12.77$, $p=.001$, $\eta^2 =.171$. Parameter estimates showed that age did not predict performance in the congruent seen condition, $B=-.004$, $t(62)=1.64$, $p=.106$ or congruent unseen conditions, $B=-.008$, $t(62)=-1.11$, $p=.272$. However, age was a significant predictor of performance in the incongruent unseen condition, $B=-.046$, $t(62)=-3.34$, $p=.001$. As age increased, localisation estimates were increasingly further from the actual hand and closer to the seen hand. Age explained 15% of the variance in accuracy scores in the incongruent unseen condition ($R^2=.153$). Figure 2.6 displays the developmental trajectory for this condition, to demonstrate how the weighting of vision and proprioception changes with age.

2.4.4. Regression analyses

King et al. (2010) found a positive relationship between proprioceptive accuracy and weighting of proprioceptive inputs, over and above the effect of age, thus, a hierarchical regression was conducted to investigate whether accuracy in the congruent unseen condition predicted the weighting given to proprioception in the incongruent unseen condition. Age (in months from youngest tested) and congruent unseen error (absolute value) were entered as predictors with incongruent unseen error (percentage) as the outcome variable. Congruent unseen error was not a significant predictor of accuracy in the incongruent unseen condition, $B=-5.63$, $t(62)=-1.54$, $p=.129$.

Children with ASD demonstrate atypical MSI (Cascio et al., 2012), with some evidence for an increased reliance on proprioception over integrating these inputs with other sensory information (Haswell et al., 2009; Marko et al., 2015). Since ASD is characterised by social impairments, SAS scores were entered into a regression to investigate whether poorer social skills predict reduced MSI and greater proprioceptive weighting. Additionally, it is possible that the younger children may not have continually attended to the visual display throughout the incongruent unseen condition, which could reduce reliance on visual inputs. This is unlikely since the experimenter was facing the child and reminded them to keep looking at the screen. If the experimenter saw the child looking away from the screen then the trial was repeated. However, to explore whether variability in attention influenced performance, scores on the inattentive subscale of the SWAN were entered into a regression.

To investigate whether these factors predicted accuracy of estimates in the incongruent unseen condition, age, and congruent unseen accuracy scores were added as predictors into the first block of a hierarchical regression model, with SAS and SWAN inattentive subscale scores entered in the second block. Seven participants (10.94%) were excluded from the regression due to list-wise missing data across measures. None of these additional variables were significant predictors of accuracy ($p>.5$ for all).

2.5. Discussion

The present study used a hand localisation task to investigate the developmental trajectory of visuo-proprioceptive integration in typically developing 4 to 11-year-olds. When given incongruent visual and proprioceptive information about the location of the hand, younger children favoured proprioceptive input more than older children who weighted vision and proprioception more equally. Variability in social skills or inattention did not predict task performance.

As expected, all children were highly accurate in locating their finger in the congruent seen condition (see Figure 2.5), indicating that they understood the task and could accurately estimate the location of their seen hand by four years of age. Children's estimates were also accurate in the congruent unseen condition when recent congruent vision of the hand was removed and only proprioceptive information was available. Again, performance did not improve with age, suggesting that, when visual information is not available, age does not affect the ability to use proprioceptive inputs to localise the hand. This is inconsistent with King et al's (2010) findings that proprioceptive accuracy increased with age in a slightly older sample (7 to 13-year-olds). In the current task the visual information about the location of the target had recently been available, thus, it is possible that this condition is not a direct test of pure proprioceptive ability. Nonetheless, although children may have relied on a memorial representation, or visual trace, of the hand's visual location in this condition, performance in the incongruent unseen condition would indicate that this is not the case. When visual and proprioceptive inputs were incongruent, localisation estimates were between the seen and real location of the hand rather than being anchored at the last seen position. Furthermore, estimates for younger children were shifted more towards the proprioceptive (true) location. Younger children appeared to rely more on proprioception to locate their unseen finger than older children, who weighted visual inputs more strongly (see Figure 2.6). Indeed, older children, aged 10-11 years (n=18), judged the real hand to be ~50% of the distance to the seen hand, which is approaching the weighting of ~60% observed in adults on an almost identical task (Bellan et al., 2015). By contrast, the youngest children, aged 4 to 6 years (n=11), judged the distance at less than 30% towards the seen hand. This indicates that, though visuo-proprioceptive integration is present even at 4 years, adult-like, optimal integration is not reached until at least 10-11 years. Unlike, Nardini et al., (2013), there was no evidence for a 'U-shaped' development of visuo-proprioceptive integration in the current experiment. Instead, the results are more in line with findings from Gori et al's (2008) visuo-tactile integration task, in which 10-year-olds displayed optimal MSI, which was reduced in 8-year-olds while 5-year-olds relied solely on information from only one sense, regardless of its reliability.

One limitation of the current study is that there were only two trials per condition, thus there may be variance in the data, which cannot be adequately controlled for. A future study could repeat this experiment with more trials and calculate each individual's average performance. This would reduce the noise in the data and increase the accuracy, reliability and replicability of the results. Furthermore, future research could include additional conditions in which the hand location is varied, to assess whether these findings generalise across peripersonal space.

In the present study, sensory integration in the incongruent condition was not related to proprioceptive accuracy in the congruent unseen condition nor did it appear to be influenced by variability in social skills or inattention. This could be because the vast majority of children showed average or high levels of social aptitude and low levels of inattention. Moreover, these factors were measured via parental questionnaires. These are designed primarily as screening tools to identify children who have a reasonable probability of meeting criteria for assessment for ASD and ADHD. Thus, these measures may lack the sensitivity necessary to discriminate between more subtle differences in social skills and attention in the general population.

It is interesting that the results appear to contradict King et al's (2010) observation of an increased reliance on vision over proprioception in younger children, with proprioceptive reliance increasing with age. However, as put forward in Chapter One, I believe that inconsistent findings in the literature are because the ability to re-weight sensory inputs depending on their *context-specific* reliability improves with age. There are several procedural (and thus contextual) differences between the tasks, which could have led older children to down-weight visual inputs in King et al. (2010) and up-weight these in the current task.

Firstly, although the separation between visual and proprioceptive information was smaller in King et al., (2010), the incongruent visual indicator suddenly appeared in a location previously used as a different target location (see Section 2.2 and Figure 2.1). Thus, it may have been in a location noticeably different to the hidden finger. Older children, therefore, may have actively discounted the visual information and instead favoured the more reliable proprioceptive information, while younger children may be less skilled at flexibly re-weighting inputs. In the current study, by contrast, the separation of visual and proprioceptive information was gradual and constant and should not have reached conscious awareness. In fact, it is highly likely that the felt position of the hand became recalibrated during the adaptation process, providing a truer indicator of multisensory integration and sensory weighting than the sudden onset of incongruent sensory input.

Secondly, the visual information in the current study was a live image of the participant's own hand whereas in King et al., (2010) it was only a symbolic representation of where the hand might be (i.e. a coloured sticker). Therefore, importantly, information relating to embodiment of the hand was present in both types of sensory estimates measured in the current task but only in the proprioceptive inputs in King et al., (2010). In everyday life, visual cues of limb localisation originate from vision (and proprioception) of the body rather than from visual targets signalling body position. Thus, older children may have up-weighted vision in the current task (since it is normally more reliable than proprioception in determining passive hand location; Mon-Williams et al., 1997) but down-weighted it in King et al., (2010), when it was a less reliable indicator of finger location. This explanation coheres with other studies showing that the ability to flexibly re-weight sensory inputs increases with age. In Cowie et al's (2013) RHI study, for example, merely the sight of a fake hand influenced 4 to 9-year-olds' judgements of unseen hand position, even when temporally asynchronous brushstrokes were applied to the real and fake hand. In contrast, older children and adults' judgements were only shifted towards the fake hand when synchronous brush strokes were applied to the real and fake hand. This indicates that visual information alone biasses young children's estimates of hand location, whereas older children are more sensitive to the reliability of these sensory inputs i.e. whether visual and tactile inputs are temporally congruent. Younger children, therefore, may not adjust the weightings given to sensory information to the same degree. This relates to the proposal that sensitivity and awareness of which inputs should, and should not, be integrated together, improves with age (Hillock-Dunn & Wallace, 2012), and will be investigated in more detail in Experiment Three. An alternative explanation is that older children were more influenced by a memorial representation of the hand's visual location in the incongruent condition than younger children. This could be due to developments in working memory capacity (Gathercole et al., 2004). This account will be tested in Experiment Two.

Chapter Three: Sensitivity to the temporal and spatial constraints of multisensory integration in typical development

Experiment Two: How does spatial incongruency affect visuo-proprioceptive integration for hand localisation in typical development?

3.1. Abstract

The likelihood that multisensory inputs are integrated together depends on their temporal and spatial proximity. A recent study by Hillock-Dunn and Wallace (2012) reported that the ability to accurately determine which visuo-auditory inputs should, and should not, be integrated together develops over childhood. It is not clear if multisensory integration underlying body representation also follows this developmental trajectory. This study tested children's ability to detect a discrepancy between visual and proprioceptive inputs for hand localisation. Results showed that, when localising the hand, younger children are significantly more likely to integrate spatially separated visuo-proprioceptive information than older children, indicating that visuo-proprioceptive binding becomes more refined with age. These findings support the conclusions from Experiment One and suggest that multisensory integration abilities underlying body representation develop over childhood.

3.2. Introduction

The results from Experiment One indicate that, when visual and proprioceptive information about hand location is incongruent, younger children weight proprioceptive input more heavily than older children, who weight vision and proprioception more equally. The current experiment firstly asks whether these results are due to an inherent proprioceptive dominance in body representation in younger children, as indicated by Bremner et al., (2013). If this is the case then, when visual and proprioceptive inputs are incongruent but vision of the hand remains, younger children should continue to rely on proprioception over vision, to a greater extent than older children. Alternatively, younger children may show a reduced ability for optimal multisensory integration (MSI), which leads to proprioceptive *or* visual dominance depending on the constraints of the task, rather than a fundamental over-reliance on proprioception per se. The current experiment was designed to test the evidence for this.

Additionally, it could be argued that the age differences seen in Experiment One were due to older children having a more robust memorial representation, or visual trace, of the hand's visual location, since visuo-spatial working memory develops over childhood (Alloway, Gathercole, & Pickering, 2006). Thus, when visuo-proprioceptive information is incongruent, younger children may have discounted the recently processed visual inputs more readily than older children. To investigate this possibility, the current experiment assesses visuo-proprioceptive integration for hand localisation when visual and proprioceptive inputs remain present throughout the task, such that differences in visuo-spatial working memory ability should not affect task performance.

In Experiment One, participants were not consciously aware of the spatial discrepancy between the seen hand and the actual hand, due to the recalibration of the felt hand position during the adaption process. Thus, this procedure enabled assessment of *how* children weight sensory inputs in a multisensory estimate of hand position. A third aim of the current experiment is to explore *when* MSI for body representation occurs (and does not occur) in children. Specifically, the spatial constraints necessary for the brain to integrate multisensory inputs were investigated. In Experiment Three, the temporal constraints of MSI are assessed in the same participants.

As discussed in Chapter One, the occurrence of MSI depends on the nature of the sensory inputs being combined (Soto-Faraco et al., 2003; Stein et al., 1988). Animal studies reveal that stimuli in the same location will stimulate cells with overlapping receptive fields in the superior colliculus. This gives rise to a greater overall neuronal response compared to stimuli that are presented far apart from each other, leading to multisensory facilitation effects such as faster response times (Meredith & Stein, 1986, 1996). These findings have been replicated in multimodal studies with human adults, provided that the task involves spatial discrimination (Spence, 2013). The likelihood that MSI and MSI enhancement effects occur decreases linearly as the distance between sensory inputs increases (Jackson, 1953; Lewald et al., 2001, Slutsky & Recanzone, 2001). This makes intuitive sense since the further apart two inputs are, the less likely it is that they arose from the same source. Thus, operating according to this 'spatial rule' helps us to optimally integrate inputs originating from the same multisensory event and distinguish these from information originating from different stimuli.

Findings from rubber hand illusion (RHI) studies by Cowie et al. (2013; 2015) indicate that sensitivity to spatial constraints of MSI may be reduced in younger children. In these studies, synchronous or asynchronous visuo-tactile brushstrokes were applied to a proprioceptively incongruent fake hand and the participant's unseen hand. Regardless of synchrony, 4 to 9-year-olds' perceived hand position was closer to the fake hand than older children and adults' estimates, suggesting that younger children are more likely to integrate spatially incongruent visual and proprioceptive inputs. This may be because they are less sensitive to the spatial constraints of MSI. The current Experiment is designed to test this. Alternatively, or as well as this, younger children may have temporally extended visuo-tactile binding, such that both synchronous and asynchronous brushing was perceived as synchronous, leading to hand localisation estimates that were shifted towards the fake hand in both conditions. Experiment Three will explore this explanation.

The current study used a hand localisation task with 5 to 11-year-olds. Participants placed their right hand into the MIRAGE and saw it in the same spatial location as their actual hand (congruent visuo-proprioceptive inputs) or displaced to the right by 0.5, 1, 1.5 or 2 times the width of their hand (incongruent visuo-proprioceptive inputs). Children were asked if the hand on the screen was in the same place as their actual hand. The study was designed to investigate whether the ability to determine which inputs underlying hand representation should, and should not, be integrated together, based on their spatial proximity, improves with age. It was predicted that, even after controlling for visual memory of the hand, sensitivity towards, and specificity of, spatial constraints governing MSI would improve with age.

3.3. Method

3.3.1. Participants

Table 3.1. Participant descriptives

	Age (years)	BPVS raw score	BPVS standardised score	SAS	SWAN
Mean	8.69	119.77	102.19	25.45	-.90
SD	1.65	20.33	11.95	6.08	1.04
Min	5.52	78	73	9	-2.89
Max	11.64	159	135	39	1.04

Sixty typically developing (TD) children aged 5 to 11 years participated as part of a Summer Scientist Week event held at The University of Nottingham in which children were invited to complete short experiments. Children came from a range of socioeconomic backgrounds but on average they were of mid socioeconomic status. They were screened for developmental difficulties (e.g. motor, attention, visual, language delay) via a parental background questionnaire. Additional screening was carried out for attention deficit hyperactivity disorder using the SWAN questionnaire (Swanson et al., 2006) and for autism spectrum disorders (ASD) using the SAS (Liddle et al., 2008). The British Picture Vocabulary Scale III (BPVS III; Dunn & Dunn, 2009) was used to assess verbal mental age.

Data from three 5-year-olds was excluded, as these children did not keep their hands still during the tasks. Date from one 11-year-old was also excluded since this child had a diagnosis of ASD. This left 56 children (mean age=8.69 years, SD=1.65, 29 females) who were included in the analysis. In the remaining sample, data was missing for five participants on the SAS and SWAN and four on the BPVS, however, no children had a diagnosis of a developmental or learning disability. The parents of all children gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

3.3.2. Procedure

All participants were tested in a quiet room at the University. Children completed the current MIRAGE task, which lasted approximately 10 minutes, followed by the MIRAGE task presented in Experiment Three. The BPVS was administered either before or after the MIRAGE tasks.

Children placed their hand into MIRAGE and saw it in a spatially congruent or incongruent position. They were asked to judge whether the hand on the screen was in the same place as their own hand. All participants were tested individually in a within-subjects experiment that consisted of five conditions, with five trials in each condition. All trials were completed in a randomised order.

At the start of the task, a black bib attached across the length of the mirror was tied around the participant's shoulders to obscure direct view of the upper arm. Depending on their height, participants sat or knelt on a chair to allow them to

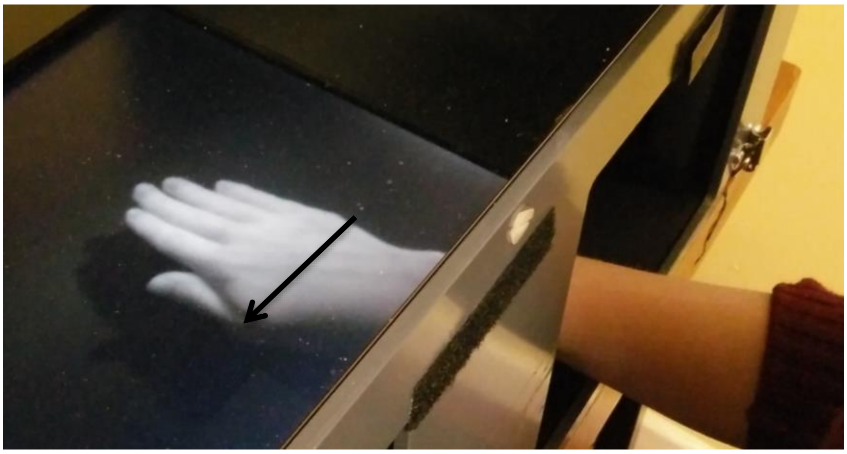


Figure 3.1. The participant's hand in the MIRAGE before the start of the task. The arrow shows the hand width measurement. This was taken from the knuckle of the little finger to the knuckle of the index finger.

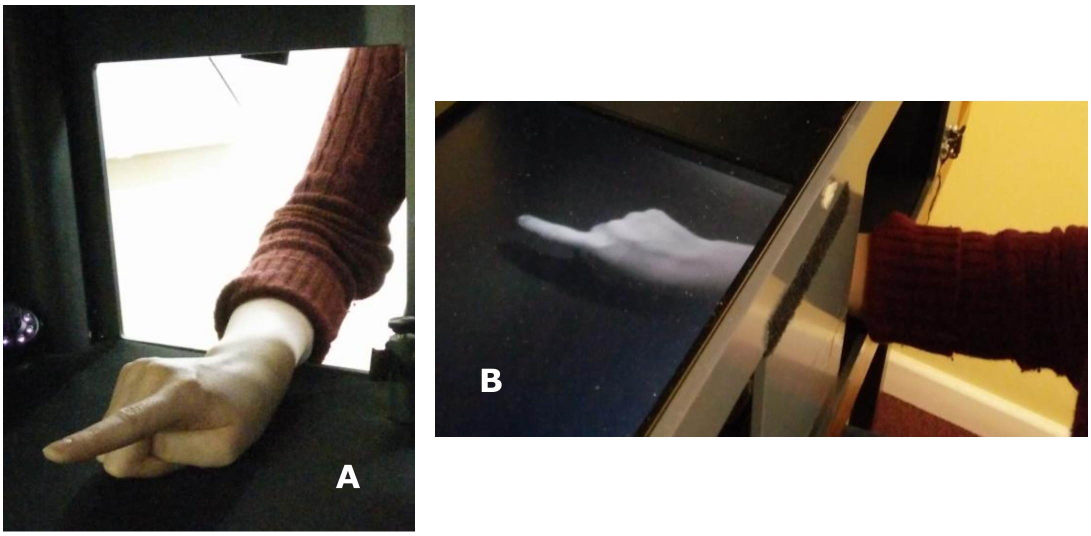


Figure 3.2. Hand position for all trials from the perspective of the experimenter (A) and the participant (B).

comfortably view their right hand when they placed it onto the work surface of the MIRAGE. Children placed their right hand palm down into MIRAGE and a blank screen occluded sight of the hand. They were instructed to keep their hand still while the experimenter recorded the width of their hand from the knuckle of the first finger to the knuckle of the fourth finger, in pixels (see Figure 3.1). Children were then asked to make a fist and point their index finger straight out in front of them while resting their fist on the MIRAGE work surface (see Figure 3.2). The participants were reminded to keep their hand as still as possible throughout the task and trials were repeated if the experimenter saw a child's hand move.

Children first completed two types of practice trials to ensure that they 1) were comfortable with the set-up, 2) were able to keep their hand still and 3) understood the task requirements. In the first practice trial, the blank screen was removed and children saw their hand in the same spatial location as if they were viewing it directly. They were asked if the hand on the screen was in the same place as their own hand, or in a different place (forced-choice response). Once an answer had been given, vision of the hand was occluded again for approximately two seconds. The hand was then presented 2.5 hand widths to the right of the actual hand location (away from the midline). Again, children were asked whether the hand on the screen was in the same place as their actual hand or a different place. These trials were repeated as necessary until it was clear that the children understood and were able to complete the task.

Experimental trials were identical to practice trials except that there was either no displacement of the visual hand (congruent visuo-proprioceptive inputs), or the visual hand was displaced by 0.5, 1, 1.5 or 2 times the width of participant's hand (incongruent visuo-proprioceptive inputs). In incongruent conditions, the visual hand was always presented to the right of the actual hand. There were five trials in each condition, and trials were presented in a randomised order. The spatial displacements in the incongruent conditions were chosen following a pilot study with nine children aged 5 to 12 years and five adults. For the pilot, the visual hand was displaced rightwards by 0.25, 0.5, 0.75, 1, 1.5 and 2 times the participant's hand width (HW). Four of the five adults could detect the visual displacement of their hand when the displacement was 0.5 HW or more. The majority of children were only able to detect a displacement of 1 HW or more, though almost all could detect a displacement of 2 HW. Thus, for the current experiment, I aimed to include conditions that would reveal potential age differences in performance, whilst avoiding ceiling and floor effects.

3.4. Results

3.4.1. Data Analysis

There were five trials in each condition. For each child, the total number of times that the participant gave a correct answer (answering 'the same place' in the zero condition and 'a different place' in the remaining conditions) was calculated as a percentage of the number of trials in each condition. Data was missing from one trial in the 0.5 HW condition for one child and from one trial in the 1.5 HW condition for one further child. For these children at these conditions, the mean percentage correct per condition was calculated as a percentage of the remaining, answered, trials.

Participants were first split at the median age (8.76 years) into a younger group and an older group. Bonferroni corrected one-sample t-tests against chance (50%) were conducted for each group in each condition to assess accuracy. For all other analyses, participants were not split into age groups. Instead, a developmental trajectory was conducted across the whole data sample to investigate, firstly, the effect of displacing the seen hand, secondly, the effect of age on performance and, lastly, to assess whether there was an interaction between age and displacement. A repeated-measures ANOVA was first run with displacement as the within-subjects variable. An ANCOVA was then conducted with displacement entered as the dependent variable and age entered as a covariate. As in the analysis for Experiment One (see Section 2.3.2), the age of the youngest child tested (66 months) was subtracted from the ages of all participants such that the youngest child's age becomes zero months. The main effect of condition was assessed separately from the condition by age interaction since the covariate alters the main effect of the within-subjects factor (Delaney & Maxwell, 1981). This leads to an overly conservative estimate of the effect (Thomas et al. 2009).

3.4.2. Accuracy

Accuracy was significantly above chance (p<.001) for the younger group (aged 5.52 to 8.67 years) in the 0, 1.5 and 2 HW conditions and for the older group (aged 8.84 to11.64 years) in the 0, 1, 1.5 and 2 HW conditions (see Figure 3.3). No other results were significant. This indicates that children understood and could complete the task and that accuracy was highest when there was no proprioceptive discrepancy, and when there was a large discrepancy. Older children show increased sensitivity to visuo-proprioceptive discrepancies for hand localisation

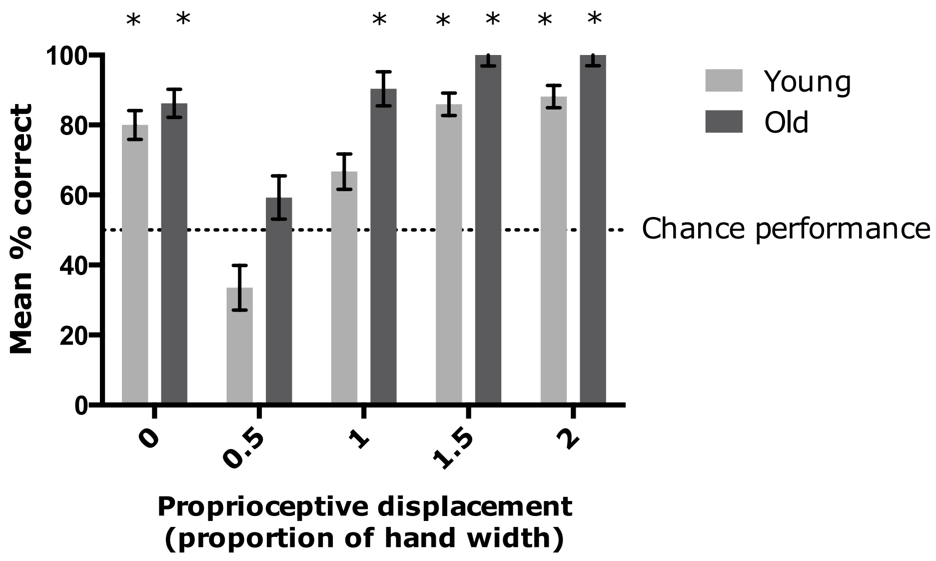


Figure 3.3. Mean percentage correct for each condition. Error bars show ± 1 standard error of the mean. Participants were split at the median age (8.76 years) into a younger and an older group to assess accuracy. Stars indicate performance that is significantly above chance (50%).

relative to younger children. A developmental trajectory was carried out to assess these findings in more detail.

Table 3.2. Mean percentage correct in each displacement condition.

Hand displacement as a proportion of hand width (HW)	Mean (SE)
0	83.21 (21.50)
0.5	49.29 (34.53)
1	78.93 (28.65)
1.5	93.21 (18.00)
2	94.29 (17.36)

3.4.3. Developmental Trajectory

Table 3.2 displays the mean percentage accuracy scores in each condition. A repeated-measures ANOVA found a main effect of displacement, $F(1,55)=66.45$, $p<.001$, $\eta^2=.547$. Pairwise comparisons (Bonferroni corrected for multiple comparisons) revealed significantly higher accuracy scores at the 0 HW condition compared to the 0.5 HW ($p<.001$), 1.5 HW ($p=.013$) and 2 HW conditions ($p=.020$). Scores were also significantly higher in the 2 HW condition compared to the 0.5 HW ($p<.001$) and 1 HW ($p<.001$) conditions and in the 1.5 HW condition compared to the 0.5 HW ($p<.001$) and 1 HW conditions ($p<.001$). Lastly, accuracy was significantly higher in the 1 HW condition compared to the 0.5 HW condition ($p<.001$). No significant differences were found between the remaining comparisons. Overall, this pattern of results indicates firstly that children understood the task and were aware of when visual and proprioceptive inputs for hand localisation were congruent (high accuracy scores in the zero displacement condition). Secondly, this suggests that accuracy increases as the space between the visual and proprioceptive inputs increases (i.e. with increased HW displacement).

The ANCOVA showed a main effect of age, $F(1,54)=25.49$, $p<.001$, $\eta^2<.353$. Figure 3.3 demonstrates that performance improves with age across all conditions. There was no significant interaction between age and task, $F(4,54)=.22$, $p=.64$, $\eta^2=.004$, suggesting no strong difference in the rate of development between the HW displacement conditions.

3.5. Discussion

The current study shows that children aged 5 to 11 years are highly accurate in correctly identifying when visual and proprioceptive inputs relating to hand localisation are spatially congruent. They are also highly accurate at detecting incongruent visuo-proprioceptive information when the visual hand is 1.5 or 2 hand widths (HW) to the right of their actual hand. This coheres with body representation studies showing that even infants under a-year-old appear to detect and differentiate incongruent from congruent visuo-proprioceptive inputs for body representation. In Rochat and Morgan's (1995) study, for example, infants watched live video feedback of their legs. 3 to 5 month-olds looked at the video for longer, and moved more, when the display was inverted, such that seen movements were in the opposite direction to felt movements, compared to when there was no left-right inversion. The current experiment extends this literature by showing that children's ability to detect a spatial incongruency between the seen position and the felt position of their hand improves as the degree of spatial incongruency increases. Moreover, performance across conditions improves with age in 4 to11-year-olds. It is necessary to note that the incongruent information was presented suddenly and no procedures or other sensory information were used to specifically encourage visuo-proprioceptive integration. This is in contrast to the RHI, in which visual and proprioceptive inputs are presented in incongruent locations but with the addition of synchronous visuo-tactile inputs, which aids MSI. This also differs from Experiment One, in which the felt position of the hand was likely recalibrated during an adaptation process that encouraged visuo-proprioceptive integration of incongruent inputs. This procedure was not used in the current study since the main aim of the experiment was to investigate the effect of age on children's ability to decide when integration should occur and, just as importantly, when it should *not*. The results indicate that the capacity to achieve this improves with age. The same task has not been conducted with adults, thus, the age at which this ability reaches adult-like maturity, cannot, as yet, be specified. However, the findings support the hypothesis that MSI is less tightly constrained in younger children, such that sensitivity towards spatial properties of multimodal stimuli develops with age in TD children.

An additional aim of the current experiment was to investigate whether the developmental findings from Experiment One are due to older children having a more robust visual representation of the last seen location of their hand. If this is the case then, when visual and proprioceptive information relating to hand localisation are incongruent but vision of the hand remains throughout, age differences in children should not be seen. The current findings found no support for this hypothesis. A significant improvement in multisensory abilities was found with age, despite vision of the hand remaining.

Another aim of this experiment was to assess whether the results of Experiment One could be due to younger children over-relying on proprioception instead of integrating this with other sensory inputs. Such a hypothesis would predict higher accuracy for younger children in the current experiment. Specifically, younger children would be better able to disregard incongruent visual inputs and instead rely more on proprioceptive information, which, in the current task, always signals the true position of the hand. Older children, in contrast, would be more likely to integrate visuo-proprioceptive information, leading to more errors. Again, no support was found for this hypothesis. Indeed, the results suggest that, under these conditions, younger children are *more* likely to inappropriately integrate incongruent visuo-proprioceptive inputs than older children. Thus, taken together, the results of Experiment One and Two cohere with the argument put forward in Chapter One that children of a very early age can demonstrate MSI but the ability to do this optimally and flexibly, in response to changes in the reliability of inputs, shows a protracted development over childhood. For older children, the adaption procedure used in Experiment One maintained the reliability of both visual and proprioceptive inputs for hand localisation. In Experiment Two, the spatial incongruency between seen and felt hand location was more prominent, thus older children down-weighted incongruent visual inputs and up-weighted accurate, proprioceptive information. Younger children showed reduced MSI in Experiment One and thus focused more on proprioceptive inputs instead of integrating these with vision. In Experiment Two, though, vision out-weighted proprioception in younger children. I propose that this occurs because vision is more prominent than proprioceptive information in the current task (as vision of the hand remains throughout the task). This explanation corresponds with Cowie et al's (2013) findings that the sight of a fake hand placed to the right of a child's unseen hand is sufficient to shift hand localisation estimates to the right, even when tactile brushes applied to the real and fake hand are temporally incongruent.

iIt could be argued that this task did not assess the occurrence of MSI for body localisation specifically, since children were not asked to judge the location of their hand but instead were asked to detect a *discrepancy* between the visual and proprioceptive location of their hand. However, the ability to do this arguably underlies appropriate body representation. Integrating visual, proprioceptive and tactile inputs that do not occur in the same spatial location could lead to erroneous integration of information from separate events. The importance of deciding which inputs should be integrated depending on their spatial properties is necessary for accurate and appropriate MSI, which underlies body representation.

Moreover, the results suggest that, instead of, or as well as, temporally extended visuo-tactile binding in young children, Cowie et al’s (2013) findings could be due to developmental improvements in sensitivity towards the spatial constraints governing MSI. The current experiment adds to this finding by demonstrating a significant improvement in this ability across development. It is not yet known whether this developmental progression is specific to spatial properties of MSI underlying body representation, or whether it is also seen for other amodal aspects, such as their temporal properties. This question will be investigated in Experiment Three.

Experiment Three: How does temporal asynchrony affect visuo-tactile integration for hand localisation in typical development?

3.6. Abstract

The results from Experiment Two indicate that in typical development, spatial rules governing the occurrence of multisensory integration underlying body representation become more refined with age. This study investigated whether this finding is also seen with regards to the temporal constraints of sensory binding. Children were asked to judge whether visual and tactile touches to the hand were temporally synchronous or asynchronous. Across participants, accuracy improved significantly as visuo-tactile delay increased. Across conditions, accuracy improved significantly with age in 5 to 11-year-olds. This indicates that visuo-tactile temporal binding is less tightly constrained in younger children, who consequently are more likely to erroneously integrate inputs from distinct events. This coheres with findings from the audio-visual domain and suggests that temporally extended binding in younger children is not modality-specific.

3.7. Introduction

Results from Experiment Two indicate an age-related increase in sensitivity to spatially incongruent visuo-proprioceptive inputs underlying body localisation. Evidence suggests that sensitivity to the temporal properties of MSI also develops with age. In a study by Lewkowicz (1996), 2 to 8 month-old infants and adults were presented with an auditory stimulus followed by a visual event. Infants required a 350 ms delay between auditory and visual inputs to detect the asynchrony, while adults were sensitive to audio-visual delays as small as 65ms. More recently, Hillock-Dunn and Wallace (2012) reported that the temporal binding window (TWB - the period of time during which MSI is very likely to occur) for audio-visual integration narrows linearly with age in 6 to 23-year-olds. The authors found that the likelihood of MSI decreases as the delay between simple auditory stimuli (tones) and visual stimuli (light flashes) increases. However, younger participants integrated inputs separated by longer delay lengths, relative to older individuals.

There is less research on age-related changes in sensitivity towards temporal properties of MSI underlying body representation specifically. The majority of studies in this area have assessed infants' ability to detect a temporal lag applied to a video of self-generated movement, as determined by looking time (e.g. Hiraki, 2006; Rochat & Striano 2000). However, this type of procedure has failed to show consistent results across studies while non-linear findings within studies make interpretation difficult, In Collins & Moore (2008), for example, 6 to 11 month-olds distinguished live videos from videos delayed by 2 seconds yet did not discriminate live videos from those with a 1 or 10 second delay. Thus, it could be that looking times are not an appropriate proxy for temporal asynchrony detection in infants since they can only *infer* that such detection has taken place. More informative is a recent study by Jaime, Longard, & Moore (2014) reporting age-related increases in sensitivity to temporally asynchronous visuo-proprioceptive inputs in 5 to 8-year-olds. When participants observed self-generated movements on a monitor, compared to older children (aged 7 to 8 years) and adults, younger children (aged 5 to 6 years) were less likely to notice a visual delay of 200 or 300ms. However, results from Experiment One indicate that optimal visuo-proprioceptive integration does not occur before 10 to 12 years. It would be informative to assess sensitivity to temporal asynchrony in relation to the body over a wider age range, to establish when adult-like temporal thresholds for MSI are achieved. Moreover, in Jaime et al's study (2014), children were divided into age groups (5-, 6-, 7- and 8-year-olds) and between-groups analyses were conducted, which, as detailed in Section 3.2.1, could mask important developmental changes within year groups.

Additionally, the development of sensitivity to *temporal* properties of *visuo-tactile* inputs underlying body representation has not been systematically investigated. This is important to establish since findings from Cowie et al's (2013; 2015) RHI studies indicate age-related changes in visuo-tactile integration underlying body representation. The authors found that, when visual and tactile brushstrokes were synchronous, children aged 4 to 13 years and adults' estimates of hand location were closer to the rubber hand than in pre-touch baseline conditions, indicating the occurrence of visuo-tactile integration. Interestingly, though, when brushstrokes were asynchronous, unlike older participants, 4 to 9-year-olds estimates were also closer to the fake hand than in baseline conditions, which could indicate a reduced sensitivity to the constraints of MSI. However, the classic RHI cannot specify whether this is due to younger children's reduced sensitivity to spatial properties of visuo-proprioceptive integration or to their reduced sensitivity to temporal properties of visuo-tactile integration, or both. Experiment Two suggests the former, yet it is not known if the latter also plays a role in the development of body localisation and ownership. Indeed, in the RHI brushstrokes are applied manually, thus, the effect of small but precisely defined changes in temporal delay between visual and tactile inputs cannot be assessed. Therefore, to investigate developmental changes in the temporal thresholds for visuo-tactile integration underlying body representation, the current study used the MIRAGE, in which visual presentation of the hand can be delayed with millisecond precision.

Assessing sensitivity to temporal properties of visuo-tactile integration is also important to establish since one prominent theory of ASD - which this thesis aims to investigate - proposes that MSI is temporally extended in individuals with the disorder. As discussed in Section 1.4.3, this would lead to erroneous integration of inputs from distinct events, which could contribute to the socio-communication problems and sensory sensitivities characterising the disorder (American Psychological Association, 2013). Thus, if young children show temporally extended binding relative to older children, this could indicate that the maturity of optimal MSI in individuals with ASD is not necessarily deviant from the normal population but is instead developmentally *delayed*.

For the current study, 5 to 11-year-olds placed their right hand into the MIRAGE and saw it in the same spatial location as their actual hand. The experimenter touched the participant's hand with a pencil and they saw the pencil touch their finger at the same time as they felt it (congruent visuo-tactile inputs) or 100, 150, 200, 300 or 400 ms after they felt it (incongruent visuo-tactile inputs). Children were asked if they felt the touch at the same time as they saw it, or a different time. It was predicted that, as children age, they will be more accurate in detecting and distinguishing synchronous from asynchronous visuo-tactile inputs underlying body representation. This proposal is based on findings of a reduced sensitivity to temporal asynchrony in visuo-proprioceptive integration in younger children (Jaime et al., 2014). Moreover, evidence suggests that the visuo-auditory TBW narrows linearly with age across childhood (Hillock-Dunn & Wallace, 2014). The existence of a TBW is believed to be necessary since sensory inputs that are derived from the same event reach the brain at different speeds, due to variations in processing and travel and times (Calvert et al., 2004). Thus, a TBW permits multisensory interactions to be flexibly specified. It is possible that the TBW is extended in children relative to adults because children's brains need more time for on-line processing of sensory inputs. In order to compensate for this, the specificity of multisensory binding would be compromised, such that the likelihood of temporally asynchronous inputs being bound together is increased.

3.8. Method

3.8.1. Participants

Sixty typically developing children aged 5 to 11 years participated. Participants were the same as those in Experiment Two; for further details see Section 3.3.1 The parents of all children gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

3.8.2. Procedure

All participants were tested in a quiet room at the University. Children completed the current MIRAGE task, which lasted approximately 10 minutes, followed by the MIRAGE task presented in Experiment Two. The BPVS was administered either before or after the MIRAGE tasks.

Children placed their right hand in MIRAGE and the experimenter touched the tip of their index finger with a pencil. In some conditions, a delay was applied to the video image of the hand such that the felt touch preceded the seen touch. Children's ability to detect and distinguish synchronous from asynchronous visuo-tactile inputs was measured. Delay rates were calculated and monitored online and required no mechanical apparatus. The precise delay was calibrated using software 'probes' which can determine the number of milliseconds that have elapsed at any given stage within the program cycle. Importantly, even if the touches do not occur at a fixed frequency, the seen delayed touch will always follow at a set time after the felt touch.

At the start of the task, a black bib attached across the length of the mirror was tied around the participant's shoulders to obscure a direct view of the upper arm. Depending on their height, participants sat or knelt on a chair to allow them to comfortably view their right hand when they placed it onto the work surface of the MIRAGE. Children placed their right hand into MIRAGE and saw it on the screen in the same spatial location as if they were viewing it directly. As in Experiment Two, children were instructed to make a fist and point out their index finger, while resting their hand on the MIRAGE work surface (see Figure 3.2). This hand position was

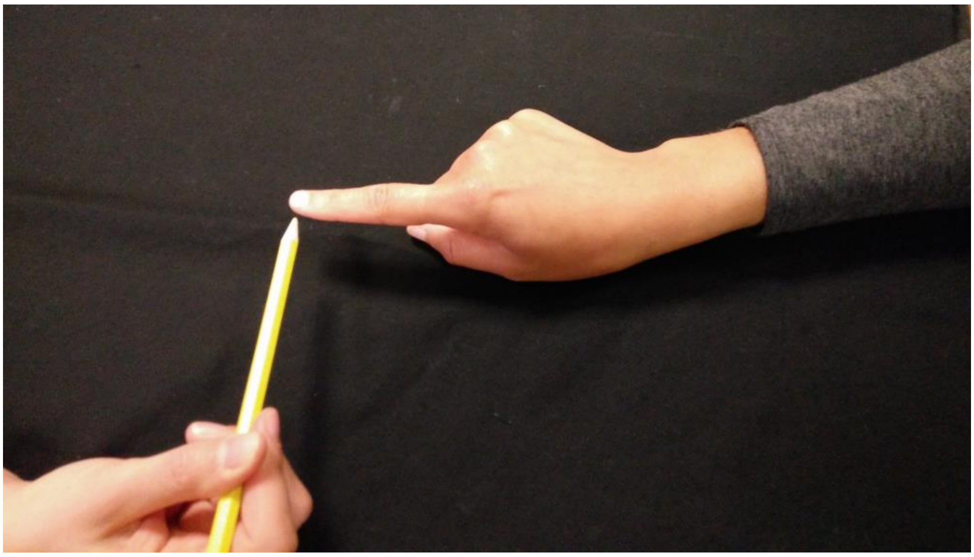


Figure 3.4. Pencil touching the participant's index finger.

chosen so that touches could be applied to the tip of the index finger since this is the area of the hand with the highest spatial acuity for touch (Mancini et al., 2014). Additionally, piloting showed that participants could more clearly observe the point of contact on the fingertip than on the side or palm of the hand. Participants were reminded to keep their hand as still as possible throughout the task and trials were repeated if the experimenter saw a child's hand move.

Children first completed two types of practice trials to ensure that they 1) were comfortable with the set-up, 2) were able to keep their hand still and 3) understood the task requirements. At the start of these trials, the experimenter held a whiteleaded pencil approximately 3cm perpendicular to the tip of the child's right index finger (see Figure 3.4). On each trial, the experimenter moved the pencil forward until the pencil lead touched the tip of the participant's finger, before returning the pencil to its original position. This movement lasted approximately one second in total. The child was then asked if he/she felt the pencil at the same time as seeing it or at a different time (forced-choice response). In the first type of practice trial the visual and tactile touch occurred at the same time (i.e. the stimulus onset asynchrony (SOA) was 0ms); in the second practice trial, the visual touch occurred 400 ms after the felt touch (400 ms SOA). These trials were repeated if necessary until it was clear that the child understood and was able to complete the task.

Experimental trials were identical to practice trials except that the visual and tactile stimuli were either synchronous (0 ms SOA) or were separated by an SOA of 100, 150, 200, 300 or 400 ms. As in practice trials, in asynchronous conditions, the visual touch always followed the tactile touch. These SOAs were chosen following a pilot study with nine children aged 5 to 12 years, in which SOAs of 0, 100, 150, 200, 250, 300, 400, 500, 600, 700 and 800 ms were used. Results showed that children aged 5 to 12 could easily detect an SOA of ≥400ms but performance decreased with decreasing delay such that only one child (aged 12) could detect a 100 ms SOA. Thus, the experimental trials were chosen with the aim of avoiding ceiling and floor effects. There were five trials in each condition and all trials were presented in a randomised order. Between each trial, a blank screen replaced the visual display.

3.9. Results

3.9.1. Data Analysis

There were five trials in each condition. For each child, the total number of times that the participant gave a correct answer (answering 'no delay' in the 0 ms SOA condition and 'delayed' in the remaining conditions) was calculated as a percentage of the number of trials in each condition. Data was missing from one trial in the 100 ms condition for four children and from one trial in the 400 ms condition for one further child. For these children at these conditions, the mean percentage correct per condition was calculated as a percentage of the remaining, answered, trials.

Participants were first split at the median age (8.76 years) into a younger group and an older group. Bonferroni corrected one-sample t-tests against chance (50%) were conducted for each group in each condition to assess accuracy. For all other analyses, participants were not split into age groups. Instead, a developmental trajectory was conducted to investigate the effect of SOA on performance; the effect of age on performance and to assess whether there was an interaction between age and SOA. A repeated measures ANOVA was first run with SOA as the within-subjects variable. An ANCOVA was then conducted with SOA entered as the dependent variable and age entered as a covariate. As in Experiments One and Two, this two-phase analysis was employed since the covariate in a repeated-

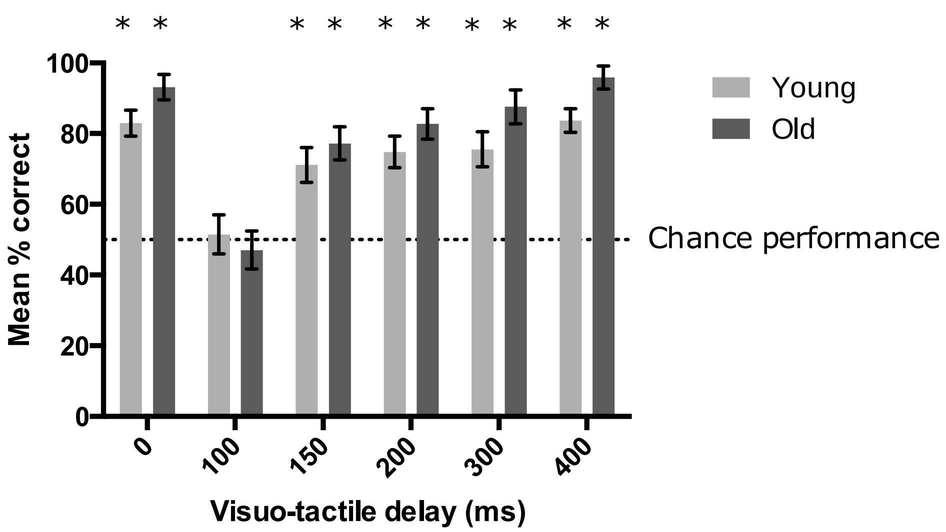


Figure 3.5. Mean percentage correct in each condition. Error bars show ± 1 standard error of the mean. Participants were split at the median age (8.76 years) into a younger and an older group to assess accuracy. Stars indicate performance that is significantly above chance (50%). All other analyses were run using age as a linear covariate.

measures ANCOVA typically weakens the main effect of the repeated measure. This results in an overly conservative test of the repeated measure, compared to assessing this main effect via an ANOVA (Delaney and Maxwell, 1981; Thomas et al, 2009). For this analysis, the age of the youngest child tested (66 months) was subtracted from the ages of all participants such that the youngest child's age becomes zero months.

3.9.2. Accuracy

Accuracy was significantly above chance ($p<.001$) for the younger group (aged 5.52 to 8.67 years) and the older group (aged 8.84 to 11.64 years) in all conditions except for the 100 ms SOA (see Figure 3.5). No other results were significant. This indicates that children understood and could complete the task. To assess changes in performance across age in more detail, a developmental trajectory was then conducted.

3.9.3. Developmental Trajectory

Table 3.3 displays the mean percentage accuracy scores in each condition. A repeated-measures ANOVA found a main effect of SOA, $F(1, 55)=39.31$, $p<.001$, $\eta^2= .405$. Pairwise comparisons (Bonferroni corrected for multiple comparisons) revealed significantly higher accuracy scores at the 0 ms SOA condition compared to the 100 ms ($p=.015$) and 200 ms ($p=.028$) SOA conditions. Accuracy was significantly greater in the 150 ms, 200 ms, 300 ms and 400 ms SOA conditions compared to the 100 ms condition (all at $p<.001$). Lastly, accuracy was significantly higher in the 500 ms SOA condition compared to the 400 ms condition ($p=.002$) and in the 400 ms SOA condition compared to the 150 ms and 200 ms SOA conditions (both at $p<.001$). No significant differences were found between the remaining comparisons. Overall, this pattern of results indicates that children understood the task (high accuracy in the 0 ms SOA and 400 ms SOA condition) and that accuracy in detecting a visuo-tactile SOA increased with increased SOA.

Table 3.3. Mean percentage correct at each visuo-tactile SOA.

Stimulus Onset Asynchrony (SOA)	Mean (SE)
0	88.21 (19.74)
100	49.20 (28.63)
150	74.29 (25.50)
200	78.93 (23.33)
300	81.79 (26.22)
400	90.00 (18.29)

The ANCOVA showed a main effect of age, $F(1, 54)=5.96$, $p=.018$, $\eta^2<.099$. As Figure 3.5 indicates, except for the 100ms condition (in which mean percentage correct was very similar between groups), older children were more accurate than younger children. Overall, this demonstrates that accuracy improved with age across the conditions. There was no significant interaction between age and task, $F(1, 54)=3.93$, $p=.053$, $\eta^2=.028$, suggesting no strong difference in the rate of development between the SOA conditions and that differences in the 100 ms conditions on the graph were not due to younger children being significantly better at this condition.

3.10. Discussion

The present study investigated the effect of age on children's ability to detect whether visuo-tactile inputs for hand representation were temporally synchronous or asynchronous. All children were highly accurate in correctly detecting when inputs were synchronous. When inputs were temporally asynchronous, performance decreased as the delay between inputs reduced. Critically, the study showed that this ability improves with age in children aged 5 to 11 years. This is an important finding since it demonstrates that visuo-tactile binding is less tightly constrained in younger children who, therefore, may be more likely to mistakenly integrate inputs from separate events together.

As detailed in Section 1.3.1, appropriate integration of visual, tactile and proprioceptive inputs is necessary for the development of accurate body representation. This finding fills a notable gap in the literature since the majority of the research in this area has employed infant studies (e.g. Collins & Moore, 2008; Hiraki, 2006; Rochat & Striano, 2000), which can only infer visuo-tactile synchrony detection based on looking times. Previous studies with children suggest that sensitivity to visuo-tactile temporal binding develops with age, however, participants were divided into age groups for between-group comparisons (Cowie et al., 2013, 2015; Jaime et al., 2014), which could obscure critical periods of development within year groups. In contrast, the current study used a developmental trajectory analysis to demonstrate that the ability to determine when visuo-tactile inputs underlying body representation should, and should not, be integrated together develops significantly with age in 5 to 11-year-olds. Thus, despite not specifying the precise degree to which the visuo-tactile TBW narrows with age, in line with findings from visuo-auditory research, this study shows clear evidence of temporally extended visuo-tactile binding in early childhood, which reduces between the ages of 5 to 11 years.

3.11. General Discussion of Experiments Two and Three

This chapter investigated developmental changes in sensitivity to spatial and temporal rules governing MSI for body representation. Results showed that sensitivity to the *spatial* properties of visuo-proprioceptive integration and sensitivity to the *temporal* properties of visuo-tactile integration improve significantly with age in 5- to 11-year-olds. This extends previous research demonstrating that the audio-visual TBW narrows with age, by indicating that MSI underlying body representation is also less tightly constrained in younger compared to older children. Together the findings can also help to explain the results from Cowie et al's (2013, 2015) RHI studies. These showed that, regardless of whether visuo-tactile brushstrokes were synchronous or asynchronous, 4 to 9-year-olds, but not older children and adults, estimated their unseen hand to be closer to the fake hand than in baseline conditions. The current findings suggest that reduced sensitivity to the constraints of both visuo-proprioceptive integration *and* visuo-tactile integration could underlie this developmental effect. A future study could conduct the tasks in Experiments Two and Three alongside the traditional RHI to assess if one of these abilities is predominantly underlying the development differences found by Cascio et al (2013, 2015).

One limitation of Experiments Two and Three is that the design could have led to a response bias for saying 'difference' since this was the correct answer in 80% of the trials. To control for this, a future study could have included an equal number of trials in which the correct answer is 'same' (i.e. 0 ms SOA) versus 'different.' A second limitation of these experiments is that there were only five trials per condition and individuals' thresholds for detecting visuo-proprioceptive and visuo-tactile discrepancies were not measured. Spatial (Experiment Two) and temporal (Experiment Three) windows could have been derived for each participant from curves fitted to the mean probability of reporting 'same' at each SOA. Sigmoid functions could then have been produced from responses across the SOAs to establish the spatial or temporal distance at which individuals perceived synchrony 75% of the time. This is commonly taken as a proxy for the width of each person's binding window (e.g. Hillock-Dunn and Wallace, 2012). A future study could conduct this analysis and compare these thresholds across ages to investigate the maturity of multisensory function more precisely.

It would also be interesting to investigate whether visuo- proprioceptive and visuo-tactile integration abilities mature at an equivalent rate within participants.

Although the current experiments were not designed to test this, a significant, positive correlation was found between performance on the 0.5 hand width condition in Experiment Two and the 100 ms condition in Experiment Three, after controlling for age $r(53)=.373$, $p=.005$. These conditions were chosen since they were the most variable, as assessed by standard deviation. This finding suggests that the same underlying processes may underpin performance across experiments. Alternatively, sensitivity to the spatial properties of visuo-proprioceptive integration may contribute to the development of sensitivity to the temporal properties of visuo-tactile integration, or vice versa. Although these different explanations cannot be tested in the present experiments, this could be examined more directly in a future study.

The results of Experiments Two and Three further suggest that the developmental effect reported in Experiment One cannot be due to either an increased reliance on visual memory in older children or a fundamental over-reliance on proprioception in younger children. This latter finding is particularly important since it suggests that, if individuals with ASD show a proprioceptive over-reliance (Marko et al., 2015), this is due to a deviance in MSI processing, not a developmental delay. This theory for atypical MSI in ASD will be explored in more detail in the following chapter.

Chapter Four: Visuo-proprioceptive integration across the non-clinical autism spectrum

Experiment Four: Visuo-proprioceptive integration across the non-clinical autism spectrum

4.1. Abstract

Evidence suggests that atypical multisensory integration in autism spectrum disorders (ASD) could be due to a bias towards unimodal processing and, specifically, an over-reliance on proprioception. A recent study found that, in the general population, adults with a higher degree of autistic traits showed reduced susceptibility to the rubber hand illusion (RHI; Palmer, Paton, Hohwy, & Enticott, 2013), as measured by proprioceptive drift towards the fake hand. This could be due to proprioceptive over-reliance, yet, the same findings were not replicated in a more recent study (Palmer et al., 2015). The current experiment assessed whether the weighting of visual and proprioceptive inputs for hand localisation differed in adults along the non-clinical autism spectrum. Participants were asked to estimate the position of their index finger after viewing congruent or incongruent visuo-proprioceptive information regarding hand position. Replicating previous findings in typically developing adults (Bellan et al., 2015), vision initially out-weighed proprioception in incongruent conditions. However, following continued visual occlusion, proprioception was up-weighted over time. There was no relationship between performance and autistic traits. This could be because proprioceptive over-reliance may only be seen in those with a clinical diagnosis of ASD. Alternatively,

the self-report measure of autism symptoms employed (The Autism Quotient) may not have placed participants accurately along the non-clinical autism spectrum.

4.2. Introduction

As discussed in the General Introduction, research demonstrates that adults integrate sensory inputs in an optimal way, in order to understand, and interact with, their environment (e.g. Alais & Burr, 2004; Trommershauser et al., 2011). When integrating sensory inputs to determine the size of an object, for example, a general principle is followed that aims to reduce variance in the final estimate (Ernst & Banks, 2002). Estimates of size derived from different sensory inputs are averaged and combined to construct a coherent percept and a greater weighting is given to estimates with less variance since these are deemed as more reliable. Consequently, this weighted average reduces the variance in the overall percept (Langy et al., 1995).

Chapters Two and Three examined the development of optimal visuo-proprioceptive and visuo-tactile integration in typically developing (TD) children. Experiment One showed that the degree to which children integrate visual and proprioceptive inputs underlying hand localisation increases with age in 4 to 11-year-olds. Younger children relied more on proprioception while older children integrated this with vision to a greater extent. Experiments Two and Three found that sensitivity towards the temporal and spatial constraints of multisensory integration (MSI) underlying body representation also matures across this age range. Together, these findings indicate that optimal MSI develops in TD children over a protracted time course.

As described in Chapter One, a growing body of research indicates that MSI is atypical in individuals with ASD (Bahrick & Todd, 2012; Cascio et al., 2012; Kwakye et al., 2011). Interestingly, research suggests that autistic characteristics are seen in the general population and it is only the number and severity of these that distinguishes those with and without a clinical diagnosis of ASD (Happé et al; 2006). In support of this, studies show that relatives of individuals with ASD show behaviours, preferences and cognitive styles that are in line with a broader autism phenotype (Murphy et al., 2000; Piven, Palmer, Jacobi, Childress, & Arndt, 1997). Consequently, ASD is currently viewed as the extreme end of a continuum of quantitative traits on which the general population lies (Constantino & Todd, 2003; Happé et al; 2006). In addition, correlations between ASD characteristics and atypical audio-visual temporal processing have been reported in a study of over 100 TD adults (Donohue, Darling, & Mitroff, 2012). This indicates that atypical MSI in ASD, and the processes underlying this, may be seen, albeit to a lesser extent, in healthy individuals who have a high number of ASD features.

This theory was tested by Palmer et al., (2013) in an RHI study conducted with two groups of TD adults categorised as having either high or low ASD traits, as assessed via the Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001). The AQ is a brief self-report questionnaire purported to measure autistic features in adults with normal IQ levels. Respondents rate their level of agreement to 50 statements on a four-point Likert scale ("definitely agree", "slightly agree", "definitely disagree" and "slightly disagree"). After synchronous visual and tactile brushstrokes were applied to a seen, fake hand and the participant's unseen hand, respectively, Palmer et al., (2013) found that hand localisation estimates were significantly closer to the fake hand for the low AQ group compared to the high AQ group. Furthermore, estimates were also significantly closer to the fake hand when the distance between the hands was 30cm compared to 20cm, for the low AQ group only. The authors propose that this group was more influenced by the synchronous visuo-tactile inputs than the high AQ group, who, by contrast, was more accurate in hand localisation, due to a bias for processing proprioceptive estimates over integrating these with visuo-tactile inputs (Marko et al., 2015).

However, Lloyd (2007) reports that, if the distance between the real and the fake hand increases, localisation errors in the direction of the fake hand reduce significantly in TD adults. Lloyd (2007) proposes that the illusion only occurs when the fake hand is positioned up to approximately 27.5cm from the actual hand since this distance represents the boundaries of visuo-tactile peripersonal space surrounding the participant's hand. The seen fake hand may be beyond the limits of the visual receptive fields around the observer's hand if it is placed beyond this boundary. It is unclear why Palmer et al., (2013) found an *increase* in drift in the low AQ group when the fake hand was placed further away from the actual hand. Indeed, these findings do not actually cohere with the notion that the low AQ group flexibly up-weight more reliable cues.

In a more recent study, Palmer et al., (2015) investigated susceptibility to the RHI in a high AQ group and a low AQ group of TD participants and a group of adults with ASD. Interestingly, Palmer et al's (2013) findings were not replicated. Hand localisation estimates were closer to the fake hand following synchronous, but not asynchronous, brushstrokes, across all three groups. However, the study did find group differences in the extent that synchronous visuo-tactile inputs influenced subsequent reach-to-grasp movements, in which participants grasped a cylinder located 13cm forward and 5cm to the right of their hidden hand. Compared to those with less autistic traits, the high AQ and ASD groups appeared to show a reduced influence of context such that movements were similar across synchronous and asynchronous conditions. In contrast, the low AQ group had a higher peak velocity in the second sub-component of reaching and an increased integrated jerk, following synchronous compared to asynchronous brushing. The authors propose that for this group only, a conflict between proprioceptive input and illusory expectations for arm position occurs when movement starts. Evidence for the true hand location is accumulated during reaching leading to on-line corrections to the movement. In contrast, proprioceptive weighting in the high AQ group and ASD group is less influenced by changes in the illusory context. Thus, there is less conflict between prior knowledge and incoming sensory inputs regarding hand location, even during reaching. Nevertheless, this interpretation does not fit with the lack of group differences in hand localisation seen in this study.

The mixed results regarding proprioceptive drift make interpretation of Palmer et al's (2013, 2015) studies difficult. These inconsistencies could be due to inherent problems with the RHI design, as discussed in Section 1.4.4. The illusion requires participants to keep their hands still, attend to the fake hand for several minutes and overcome discrepancies in physical characteristics between the fake and real hand. These are all requirements that could be more challenging for people with ASD and those with a high number of ASD characteristics, due to the attention problems and imagination deficits seen in the disorder (American Psychological Association, 2013). The current task was designed to avoid these issues. A MIRAGE hand localisation task, similar to that used in Experiment One and Bellan et al., (2015), was used to assess whether individuals with a high number of ASD traits show an over-reliance on proprioception relative to those with fewer ASD characteristics. In Bellan et al., (2015), participants placed their hands into the MIRAGE and saw them through the MIRAGE screen before vision of the hands was occluded and participants estimated the location of their unseen finger. In congruent conditions, the hands were seen in the proprioceptively correct location (congruent visuo-proprioceptive information). In as incongruent condition, an adaptation procedure was used (as in Experiment One) resulting in an incongruency between the location of the seen hand and the actual hand (incongruent visuo-proprioceptive information). Adults were highly accurate at localising their finger in congruent conditions while in incongruent conditions, vision initially out-weight proprioception, which is line with findings that it is normally a more reliable sensory source (Ernst and Banks, 2002). However, when localisation estimates in incongruent conditions were repeated over successive trials (with vision of the hands remaining occluded), vision was down-weighted relative to proprioception. The authors propose that this is due to the memory of the visually encoded hand position decaying over trials (Chapman, Heath, Westwood, & Roy, 2001) and, thus, becoming less reliable. If individuals with ASD have a fundamental proprioceptive over-reliance, then we might expect them to consistently up-weight proprioception across trials and conditions in this task, instead of integrating this with visual inputs. The current experiment investigated whether individuals from the general population with a high number of autistic traits showed this pattern of performance.

It was predicted that all participants would be more accurate at localising their hand when presented with congruent compared to incongruent visuo-proprioceptive inputs. Due to findings of proprioceptive over-reliance in individuals with ASD (e.g. Marko et al., 2015), it was also predicted that an interaction between AQ score and condition would be seen. Specifically, participants with low AQ scores should be more accurate in congruent versus incongruent conditions while high scorers should show a reduced effect of congruency. As in Bellan et al., (2015), several trials were conducted following the adaptation procedure in the incongruent condition. I, thus, further predicted that there would be a time by AQ score interaction such that the weighting given to proprioception should increase over time in low AQ scorers, while proprioceptive weighting should remain consistently high across trials in those with high AQ scores.

4.3. Methods

4.3.1. Participants

Participants were 34 adults aged 19 to 65 years (mean=29.5, SD=13.01, 17 female). They were recruited via posters placed around the university campus and via an email sent to members of the local community who had previously shown an interest in taking part in studies. No participants had a diagnosis of ASD. Written informed consent was gained from all participants prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

4.3.2. Procedure

All participants were tested in a quiet room at the University. Participants were administered The Autism Quotient Questionnaire (AQ; Baron-Cohen et al., 2001) before completing the MIRAGE task. Respondents rated their level of agreement to 50 statements on a four-point Likert scale (“definitely agree”, “slightly agree”, “definitely disagree” and “slightly disagree”). In the current study scores on the AQ

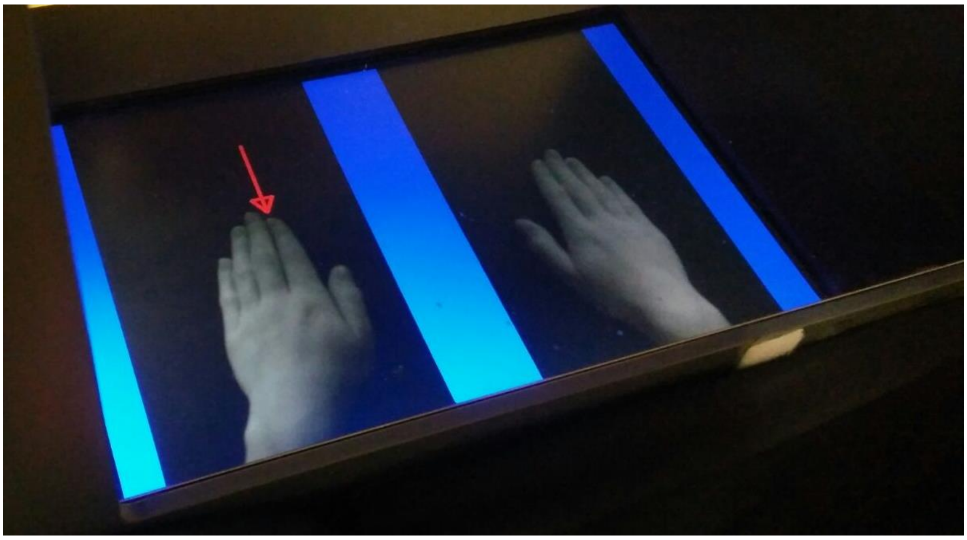


Figure 4.1. Localisation judgments.
Participants judged the location of their seen or unseen finger by verbally responding when they perceived a slow moving arrow to be in line with their index finger. Vision of the hands remained in the Congruent Seen condition. For all other conditions, vision of the hands was occluded during judgments.

ranged from 9-37 (mean=19.15; SD=6.74) with higher scores reflecting more autistic traits. Total testing time was approximately 45 minutes.

The basic procedure for the MIRAGE task was similar to the hand localisation task used in Experiment One. Participants judged the location of their seen or unseen finger by verbally responding when they perceived a slow moving arrow to be in line with their right index finger (see Figure 4.1). Judgements were made after exposure to congruent or incongruent visuo-proprioceptive sensory input regarding the location of the hand. All participants were tested individually in a within-subjects experiment that consisted of three control conditions and one experimental condition, completed in the following order: congruent seen; congruent unseen

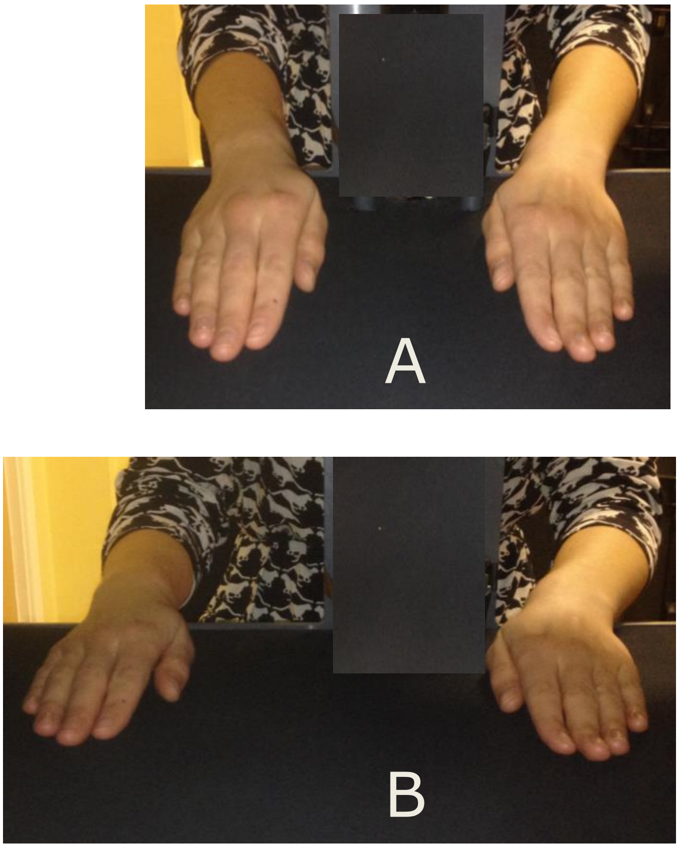


Figure 4.2. Hand positions during finger localisation estimates in A) congruent seen and congruent unseen (hands in) conditions and B) congruent unseen (hands out) and incongruent unseen conditions. Note that in the incongruent condition the hands had previously been seen in the position shown in panel A but they were actually in the position shown in panel B.

(hands in); congruent unseen (hands out) and incongruent unseen. For all conditions, participants placed their hands on the work surface of the MIRAGE and saw them in the same spatial location and visual plane as if viewing their hands directly. A black bib attached across the length of the mirror was tied comfortably around the participant's shoulders to obscure a direct view of their upper arm.

Control Condition One: Congruent Seen

In the congruent seen condition, the participant watched as the experimenter moved their hands to a pre-specified position. Participants were instructed to keep their hands still and to judge the location of their right index finger using the procedure employed in Experiment One. Participants saw a red arrow (reflected from the computer screen above) travelling laterally across the MIRAGE workspace and said 'Stop' when they judged the arrow to be directly in line with their index finger (see Figure 4.1). The X-axis coordinate (in pixels; 1 pixel=0.75mm) of the arrow was recorded to give a measurement of perceived finger location. Each measurement was taken twice, once with the arrow travelling from right to left and once from left to right (order counterbalanced across conditions and participants). The purpose of this condition was to ensure that participants understood the task requirements and could use congruent visual and proprioceptive information to accurately estimate the location of their seen finger.

Control Condition Two: Congruent Unseen (hands in)

In the congruent unseen (hands in) condition, the participant's hands remained in the same location as in the congruent seen condition but vision of the hands was occluded and the two finger localisation judgments were repeated. This condition was included to assess finger localisation accuracy when only proprioceptive inputs were available.

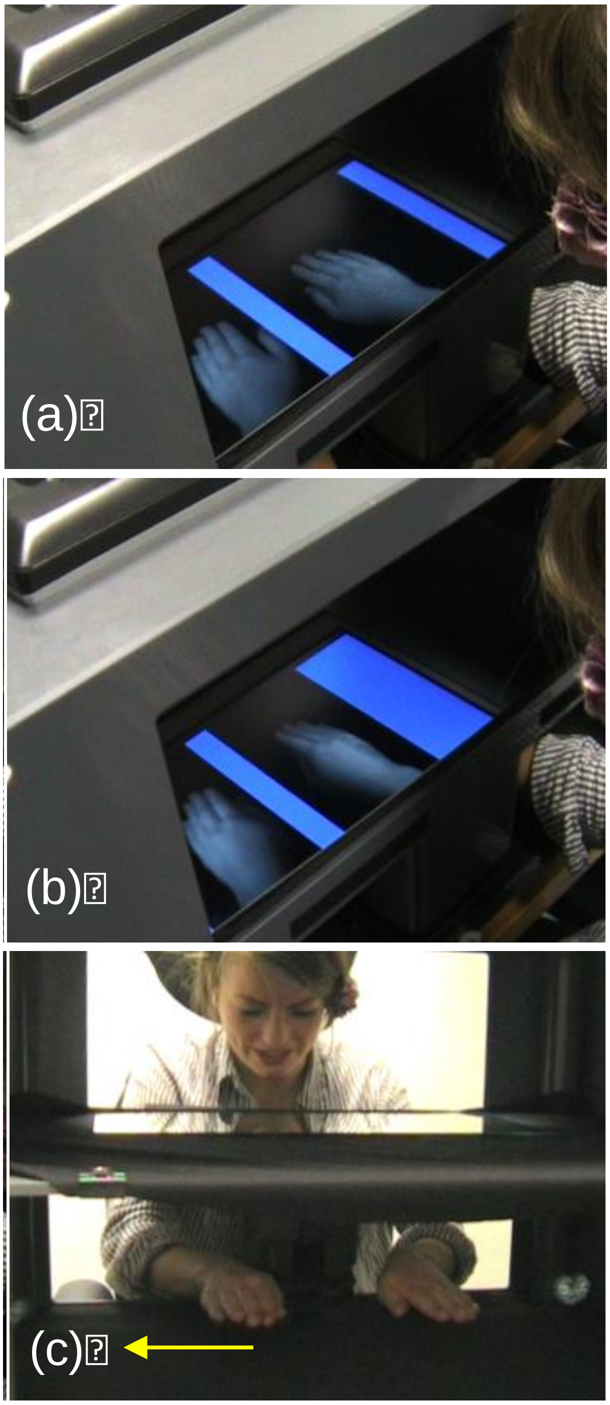


Figure 4.3. Incongruent condition adaptation procedure.
(a) At the start of the adaptation procedure, the seen location of the right hand matches its real location. (b) The superimposed blue bars slowly expand to constrict the hand space while the image of the right hand is shifted slowly leftwards, without the participant's awareness. To keep the hand visible between the blue bars, the participant moves their hand rightwards resulting in a separation between the seen and real location of the right hand. In the actual experiment, a bib occluded the participant's view of his/her arm. (c) The participant's hands resting on the MIRAGE work surface, from the experimenter's viewpoint. The yellow arrow indicates the direction in which the right hand moves during the adaptation procedure.

Control Condition Three: Congruent unseen (hands out)

In the congruent unseen (hands out) condition, the experimenter moved both hands away from the midline to a specified location and the participant viewed their hands briefly before vision was occluded and the two finger localisation judgments were repeated. Hand positions were the same in the congruent seen and congruent unseen (hands in) conditions and approximately the same in the congruent unseen (hands out) and incongruent unseen conditions (see Figure 4.2). The two different congruent unseen conditions were included to control for differences in hand localisation ability depending on hand position since hand localisation accuracy is reduced when the hand is positioned further away from the shoulder (van Beers, Sittig & Gon, 1998).

Experimental Condition: Incongruent Unseen

For the incongruent condition, the participant placed his or her hands in MIRAGE and held them approximately 5cm above the workspace and was instructed to not touch blue bars which could be seen to box in each hand to the left and right (see Figure 4.3). The blue bars were graphically superimposed on the visual workspace and expanded slowly over the course of 25 seconds so as to constrict the space in which the hands could be positioned. During this period, the spatial relationship between the seen location of the right hand and its real location was manipulated using an adaptation procedure modified from Newport and Gilpin (2011) and similar to that used in Bellan et al. (2015). During this, the image of the right hand moved smoothly and incrementally leftwards at a rate of 4.5mm/s. Thus, in order to keep the right hand in the same visual location, the participant had to (unknowingly) move his or her hand rightwards at the same rate, with the result that, after 25 seconds, the seen hand was viewed 11.25cm to the left of its true location. During the same period, the visual image of the left hand oscillated slowly leftwards and rightwards at an average velocity of 4.5mm/s but ended up in the same location as it had started (i.e. the seen left hand remained in the same location as the real left hand). This oscillation was included so that the movement of the image relative to the hand, and the tracking of that movement by the real hand, was equivalent across both hands. It is very rare for people to notice the movement of either hand relative to its seen image, and conscious awareness of this has never been observed under experimental conditions (see Newport and Gilpin, 2011; Bellan et al. 2015). Once the adaptation procedure was complete, the participant's hands were placed on the work surface of MIRAGE, vision of the hands was occluded and finger localisation judgments were recorded (again, once with the arrow travelling from right to left and once from left to right). In the incongruent condition only, seven sets of two judgments were made following the adaption procedure. There was a 15-second interval between each set and the participant's hands remained stationary, with vision occluded, throughout the trials. The purpose of this condition was to assess whether reliance on proprioception, in the presence of incongruent visual inputs, changed over time and whether this differed in participants depending on their AQ score.

4.4. Results

4.4.1. Data Analysis

For each trial, the x-axis co-ordinate of the position of the tip of the right index finger was recorded in pixels (100 units equates to 7.5cm). For each condition (and for each pair of estimates in the incongruent condition), the average of the two estimates of finger position was calculated and subtracted from the actual finger position to give a localisation error score. A score of zero would represent a completely accurate estimate of hand location. Positive values indicated estimates to the right of the actual finger location and negative values indicated estimates to the left (i.e. closer to the midline). As in Experiment One, in the incongruent unseen condition, the hand was seen 11.25cm to the left of the real location. Thus, a score of zero in this condition would represent total reliance on proprioception, a score of -11.25 total reliance on vision, with scores in between indicating the level of weighting given to proprioception and vision respectively, with -5.625 equivalent to equal weighting of both.

A general linear models approach was used to assess the data. Firstly, I investigated the within-subjects main effect of condition using a one-way ANOVA. To explore whether there was an interaction between condition and AQ score, the analysis was re-run as an ANCOVA with mean-centred AQ scores entered as a covariate. I then ran a second one- way ANOVA on the within-subjects main effect of time in the incongruent condition. There were only two trials per condition in the congruent condition (compared to seven in the incongruent condition) thus time was only assessed in the incongruent condition. To investigate whether there was an interaction between time in the incongruent condition and AQ score, this analysis was re-run with mean centred AQ scores entered as the covariate. The main effects and interactions were assessed separately to ensure that the test of the main effects was not overly conservative.

4.4.2 Results

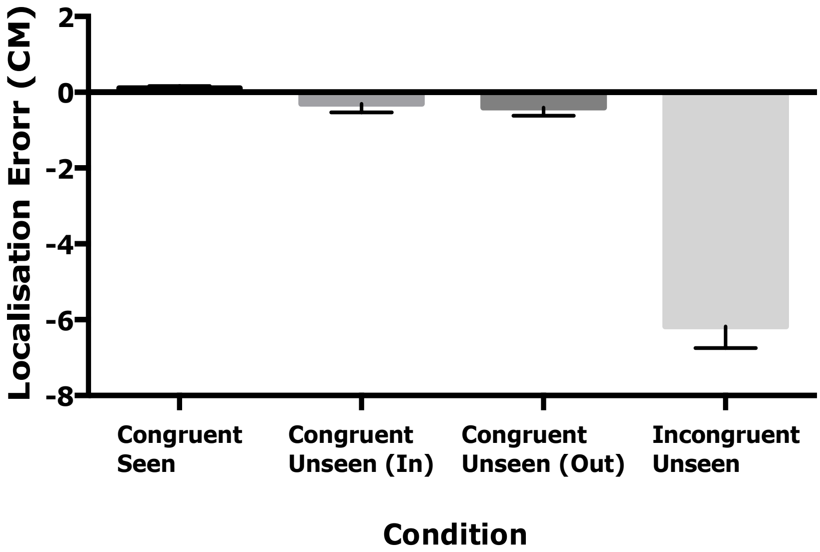


Figure 4.4. Mean localisation errors in cm for each condition across the whole sample. For this analysis only, the mean of the first set of judgments only in the incongruent condition was included. Positive values represent mislocalisation to the right of the real hand; negative values represent mislocalisation to the left of the real hand. Error is low in all congruent conditions but significantly increases when visual and proprioceptive inputs are incongruent. Error bars represent standard error of the mean.

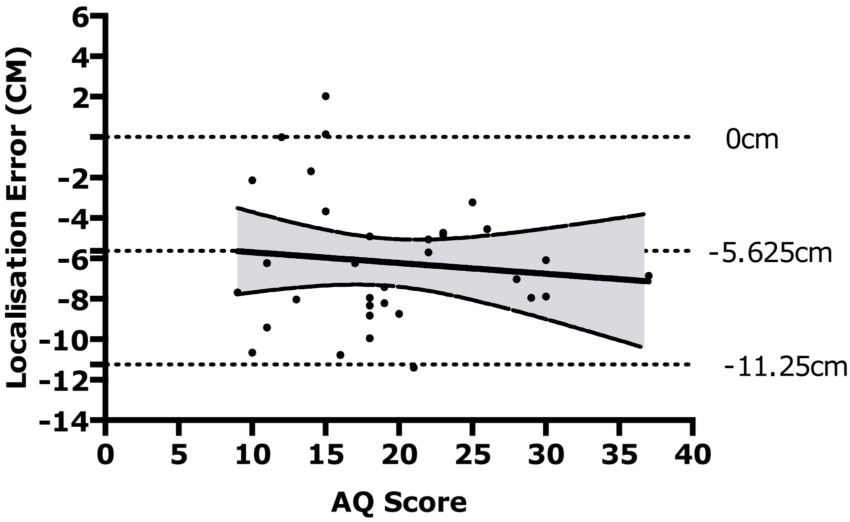


Figure 4.5. Localisation error in the first set of judgment trials in the incongruent unseen condition. The hand was seen 11.25cm to the left of the real location therefore 0 cm= total reliance on proprioception (i.e. no error); -11.25cm= total reliance on vision; -5.625cm= equal weighting of proprioception and vision. Shaded region shows 95% confidence intervals.

Figure 4.4 shows performance in each condition across the whole sample; for this analysis only, the mean of the first set of judgments in the incongruent condition was included. Positive values represent mislocalisation to the right of the real hand; negative values represent mislocalisation to the left of the real hand. There were no significant outliers in any condition (Cook's D values all <1). A one-way ANOVA found a main effect of condition across participants, $F(1,33)=153.53$, $p<001$, $\eta_p^2=.823$. Pairwise comparisons (Bonferroni corrected for multiple comparisons) revealed significant differences in accuracy between the incongruent condition and the congruent seen ($p<.001$), congruent unseen (hands in) ($p<.001$) and congruent unseen (hands out) ($p<.001$) conditions. No other significant differences between the conditions were found. A one-way ANCOVA found no interaction between condition and AQ scores, $F(1,33)=.831$, $p=.369$, $\eta^2=.026$. Accuracy was high in all congruent conditions and reduced significantly in the incongruent condition, but was not affected by AQ score in any condition (see Figure 4.5).

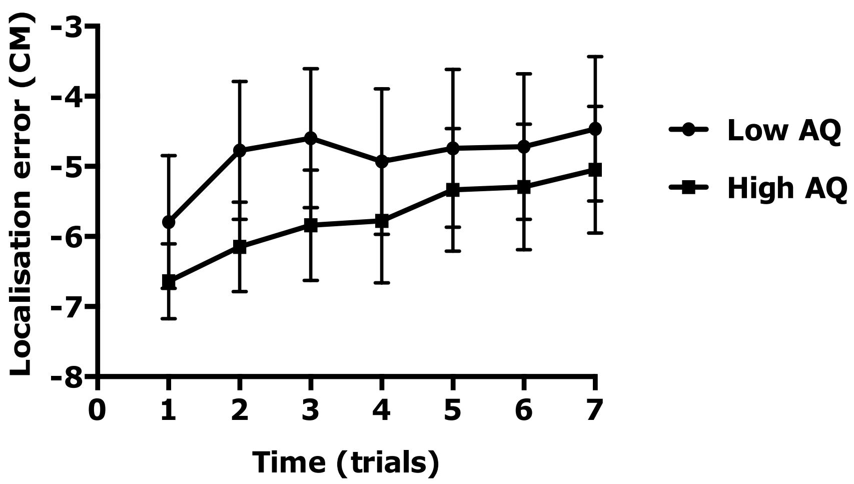


Figure 4.6. Localisation error in the incongruent unseen condition across trials. Error bars show ± 1 standard error of the mean. For visualisation purposes only, participants were separated into a high AQ and a low AQ group based on a median-split of AQ scores. All analyses were run using AQ score as a linear covariate.

A second one-way ANCOVA found a main effect of time in the incongruent unseen condition, $F(1,33)=10.01$, $p=.003$, $\eta^2=.233$. Pairwise comparisons (Bonferroni corrected for multiple comparisons) revealed significant differences in accuracy between the first pair of judgments and the third (p=.01), fifth (p=.012), sixth (p=.029) and seventh (p=.003) pairs. No other comparisons were significantly different. There was no interaction between time and AQ scores in the incongruent condition, $F(1,31)=.161$, $p=.691$, $\eta^2=.005$. As shown in Figure 4.6, accuracy increased over time (i.e. localisation error was closer to zero) as estimates shifted towards the true hand location, and AQ score did not affect this.

Table 4.1. Cross-study comparison of mean (M) and standard deviation (SD) AQ scores for participants divided into two groups based on a median-split of AQ scores.

	Palmer et al., (2013)	Palmer et al., (2015)	Current Study
High AQ group	M=26.67, SD=4.56	M=22.13, SD=5.74	M=24.93, SD=5.06
Low AQ group	M=16.0, SD=3.84	M=8.07, SD=3.96	M=14.33, SD=3.20

4.5. Discussion

The present study investigated whether visuo-proprioceptive integration during a hand localisation task differs across the non-clinical autism spectrum. All participants were highly accurate in locating their finger when congruent visual and proprioceptive information were both available (congruent seen condition). As in Experiment One, accuracy remained high when visual inputs were removed (congruent unseen conditions). Replicating previous findings (Bellan et al., 2015), accuracy was significantly reduced when proprioceptive and visual inputs regarding finger location were incongruent, but accuracy increased over time as the memory of the incongruent visual inputs decayed. However, levels of autistic traits did not affect performance in any condition. I now discuss possible reasons for this.

Firstly, the procedure may not be sensitive enough to reveal significant differences in visuo-proprioceptive integration across the sample. However, this is unlikely since significant developmental differences were found using a very similar task in

Experiment Two. Indeed, the only differences between the procedures were that the current task included an additional condition to control for differences in hand location between congruent and incongruent unseen conditions, and additional measures of finger localisation in the incongruent unseen condition.

It is also possible that an effect of AQ score could have been found if a non-linear function was fitted to the data. Thus, a future study could be conducted exploring the possibility of fitting other functions to the data, to assess whether there could be a specific range of scores that are significantly associated with decreased localisation error in the incongruent condition.

Alternatively, atypical MSI may be specific to clinical autism, such that it is not seen in those on the non-clinical spectrum. Findings from Palmer et al (2013; 2015) could argue against this, however, since significant differences in reach-to-grasp movements following synchronous visuo-tactile inputs were seen in a high AQ group compared to a low AQ group. The authors interpret this as a reduced influence of environmental context in individuals with higher levels of autistic traits and, consequently, an over-reliance on proprioception. However, significant group differences in hand localisation accuracy (proprioceptive drift) following the RHI were seen in the authors' first study but not their second. This inconsistency is surprising if higher number of autistic characteristics is indeed related to increased reliance on proprioception. Perhaps the group differences found in Palmer et al's (2013; 2015) studies were in fact due to differences in the ease at which participants were able to imagine that the rubber hand was their own. The illusion requires participants to embody a static rubber hand, which may be more challenging for participants with high AQ scores since imagination impairments are characteristic of ASD. In contrast, the visual information in the current study came from a video image of the participant's actual hand, thus embodiment does not require participants to overcome discrepancies in physical characteristics between a fake hand and their own hand.

Alternatively, it could be argued that the sample size was insufficient to reveal performance differences. However, the sample was larger than in previous studies at N=33, compared to N=22 in Palmer et al., (2013) and N=30 in Palmer et al., (2015). Instead, the range of AQ scores in the current experiment (9-37; mean= 24.93, SD=5.06) may have been too narrow to show group differences. Palmer et al., (2013, 2015) divided participants into two groups based on a median-split of AQ scores. Yet, separating participants in the current study in this way again leads to comparable AQ scores across studies (see Table 4.1 - note the range and median of the AQ scores were not reported in the studies by Palmer et al., (2013; 2015)).

Instead, it is possible that the AQ predominantly measures socio-communicative impairments and repetitive behaviours characterising ASD, but does not tap into the sensory sensitivities associated with the condition. However, sensory atypicalities are seen in over 90% of individuals with ASD (Tomchek & Dunn, 2007) and these are also highly prevalent in mothers of children with ASD (Uljarević, Prior, & Leekam, 2014). Thus, if ASD is the extreme end of a continuum of traits on which the general population lies (Constantino & Todd, 2003), then high scores on the AQ should be associated with an increased likelihood of sensory sensitivities. I, therefore, suggest that individuals with a high number of autistic characteristics may demonstrate atypical MSI, yet the AQ may not be an appropriate measure of such traits. Indeed, few empirical tests have assessed whether the AQ is a valid measure of these and, as yet, it is unclear whether the questionnaire is measuring one or several latent variables and exactly what these are.

Baron-Cohen et al., (2001) proposed that the AQ taps into five autistic traits, each measured by 10 items: reduced abilities in social skills, communication, imagination and attention switching and exceptional attention to detail. However, these domains were theoretically derived and for each AQ-measured trait, Baron-Cohen et al., (2001) reported Chronbach's alphas of 0.77 (social skills), 0.67 (attention switching), 0.63 (attention to detail), 0.65 (communication) and 0.65 (imagination). A scale is generally considered as reasonably reliable only if Chronbach's alpha exceeds 0.7 (Kline, 2011), suggesting that only items in the social skills subset adequately and consistently measure the same underlying construct. Moreover, published studies applying factor analysis (FA) to the AQ report mixed findings. A confirmatory FA on AQ data from over 1000 respondents found that a model comprising of just two factors - reduced social interaction and heightened attention to detail - provided the best fit for the data (Hoekstra, Bartels, Cath, & Boomsma, 2008). In contrast, Austin's (2005) exploratory FA found evidence for three factors (poor social skills, heightened attention to detail and impaired communication/ theory of mind). However, FA of ordinal data can lead to overdimensionalisation, whereby more factors are produced than are actually warranted. Thus, to avoid this shortcoming, I investigated the extent that the AQ measures autistic traits using Mokken scaling analysis of AQ data on a dataset of 618 respondents.

I found, firstly, that the AQ was unscalable, indicating that together the questionnaire items do not measure one latent trait (i.e. 'autisticness'). Secondly, excluding six items that did not load onto any subscale, results suggested that the original subscales of communication, social skills, and attention switching are better seen as one domain while the remaining scales seem to measure attention to detail, poor imagination, and good memory skills. The latter three scales, however, did not have adequate reliability thus their use and meaningfulness is limited. Moreover, the first subscale did not conform to the Mokken scaling model, indicating overdimensionalisation. Therefore, these findings suggest that the AQ cannot capture a clear and consistent pattern of autistic traits in individuals without the condition. In line with this, a recent study by Murray, Booth, Kuenssberg, & O'Donnell (2014) reported scalar invariance in the AQ when it is used to compare individuals with ASD with participants from the general population. Thus, equal scores on the questionnaire do not necessarily denote equal levels of autistic traits if participants are from different populations. This, accordingly, reduces the AQ's discriminatory power and use as a gauge of autistic traits in TD individuals.

Thus, in conclusion, I believe that, while atypical MSI may be present in individuals with a high number of autistic traits in the general population, the AQ may not be a suitable measure of 'autisticness'. Consequently, the remainder of the experiments in this thesis are conducted with people with ASD and matched control groups, to more directly assess the processes underlying atypical MSI in ASD. Moreover, I will use a different MIRAGE task aimed at comparing the evidence not only for an over-reliance on proprioception but also extended sensory temporal binding – another main theory purported to explain atypical MSI in this disorder.

Chapter Five: Multisensory integration underlying body representation in children with autism

Experiment Five: Multisensory Integration underlying perceptual embodiment in children with autism

Experiment Five is a modified version of the paper by Greenfield, Ropar, Smith, Carey and Newport (2015), 'Visuo-tactile integration in autism: atypical temporal binding may underlie greater reliance on proprioceptive information', published in Molecular Autism, 6, 51. DOI 10.1186/s13229-015-0045-9.

5.1. Abstract

Evidence indicates that social functioning deficits and sensory sensitivities in autism spectrum disorders (ASD) are related to atypical sensory integration underlying body representation. The exact mechanisms underlying these integration difficulties are unknown; however, two leading accounts are 1) an over-reliance on proprioception and 2) temporally extended sensory binding. These theories were directly tested by selectively manipulating proprioceptive alignment and visuo-tactile synchrony to assess the extent that these impact upon body ownership. Participants placed their right hand into a MIRAGE and saw two, identical live video images of their own hand. One virtual hand was aligned proprioceptively with the actual hand (the veridical hand), and the other was displaced to the left or right. While a brushstroke was applied to the participants' actual (hidden) hand, they observed the two virtual images of their hand also being stroked and were asked to identify their real hand. During brushing, one of three different temporal delays was applied to either the displaced hand or the veridical hand. Thus, only one virtual

hand had synchronous visuo-tactile inputs. No clear evidence was found for a fundamental proprioceptive dominance. Instead, results showed that visuo-tactile synchrony overrides incongruent proprioceptive inputs in typically developing children, but not in children with ASD, indicating temporally extended visuo-tactile binding. This could lead to failures in appropriately binding information from related events, which would impact upon important social processes such as empathy and imitation.

5.2. Introduction

As described in Chapter One, ASD is characterised by both socio-communicative impairments and sensory sensitivities (American Psychological Association, 2013). Recent theories suggest that both aspects of the disorder could be due, at least in part, to atypical multisensory integration (MSI; Bahrick & Todd, 2012; Cascio et al., 2012; Kwakye et al; 2011). It could be, for example, that difficulties integrating multisensory inputs could lead to an increased focus on one sensory channel at the expense of others resulting in hypersensitivies to stimuli from this channel and hyposensitivities to the remaining, neglected sensory stimuli. Since social stimuli are inherently multisensory - for example, face-to-face communication involves seamlessly integrating speech, tone, facial expressions, and body language (Kwakye et al., 2011) - atypical sensory integration could also contribute to problems with social functioning and social interaction.

Visuo-tactile-proprioceptive integration underlies our sense of bodily self - which includes body localisation and body ownership (Nava et al., 2014). Both of which are needed for the development of important behavioural, cognitive and social skills such as navigation, inferring others' mental states and imitation (Chaminade et al., 2005; Gallese et al., 2003, 2005; Meltzoff & Moore, 1997). Only three published studies have directly investigated visuo-tactile-proprioceptive processing in individuals with ASD and all have used the rubber hand illusion (RHI; Cascio et al., 2012; Palmer et al., 2015, Paton et al., 2012), in which synchronous visual and tactile brushstrokes are applied to a seen fake hand and the participant's unseen hand, respectively. The degree to which the fake hand is embodied can inform us on the degree to which MSI takes place. Paton et al's (2012) study found that adults with ASD displayed not only reduced embodiment of the rubber hand, but also more accurate localisation estimates of their hidden hand than a control group. This could indicate a bias towards proprioceptive processing in ASD, such that proprioceptive inputs are weighted more strongly than other sensory information, irrespective of prior knowledge and contextual information. Although Experiment Four found no evidence of this in adults with higher levels of autistic traits relative to those with fewer characteristics, this does not rule out the possibility that a fundamental proprioceptive dominance is present in individuals with a *clinical* diagnosis of ASD. As described in Section 1.4.2, it is important to note that an over-reliance on proprioception does not necessarily equate to more accurate estimates of hand location when using proprioceptive inputs alone. Indeed, it could be that, for an individual with ASD, the variance (or noise) in proprioceptive estimates is as high, or higher than in those without the disorder, yet they may continue to rely on this information regardless of whether the circumstances deem it to be reliable. This is in contrast to typically developing (TD) adults, who optimally integrating proprioception with other sensory inputs to reduce variance in the overall estimate. This interpretation could explain why anecdotal reports suggest that those with ASD often have problems using proprioceptive information when localising the body, pointing or balancing (Biklen & Attfield, 2005). Thus, the apparent increased proprioceptive accuracy in ASD compared to TD groups in Paton et al., (2012) may actually indicate sub-optimal MSI, rather than a superior ability to use proprioceptive information per se.

In addition to Paton et al's (2012) findings in adults, Cascio et al., (2012), found a delayed onset of the RHI in children with ASD compared to TD controls. Specifically, hand localisation accuracy was high after one 3-minute block of synchronous brushing, but reduced significantly following a second block for the ASD group, while localisation accuracy remained reduced across blocks for the control group. The authors suggest that the 500 ms offset between the visual and tactile inputs in the asynchronous condition was not large enough to be outside the temporal binding window (TBW) for the children with ASD. Thus, asynchronous brushing was perceived as synchronous such that synchronous and asynchronous conditions were initially indistinguishable. Since drift was no longer exhibited after the second block of asynchronous stroking, the authors suggest that the TBW may have narrowed with continued visual-tactile stimulation, such that the asynchronous events are no longer perceived as temporally synchronous. As described in Section 1.4.3, this coheres with findings from visuo-auditory processing studies indicating that children with ASD may have an enlarged TBW for integrating multisensory inputs. In Kwakye et al., (2011), for example, a visual-auditory temporal order judgment task was conducted in which participants observed a light flash and a tone presented simultaneously. After a variable delay, they were presented with a second light flash followed by a second tone and reported which light flash occurred first. For TD children, the auditory stimuli enhanced performance when the delay between the second flash and the second tone was between 50 and 150ms. At smaller or larger delays there was minimal or no enhancement effect. In contrast, this auditory enhancement effect was seen in children with ASD when the multisensory delay ranged from 0-300ms, indicating temporally extended visuo-auditory binding. However, this theory has not been systematically tested in relation to the sensory inputs underlying body representation.

Overall, the findings from Cascio et al., (2012), Palmer et al., (2015) and Paton et al., (2013) point to atypical visual-tactile-proprioceptive integration in ASD. However, the classic RHI paradigm cannot distinguish the evidence for an over-reliance on proprioceptive processing and temporally extended visuo-tactile binding, as both explanations would predict reduced susceptibility to the illusion. Moreover, in these studies, brushing was conducted in sets of three-minute blocks during which participants were required to keep their hand still and attend to the fake hand throughout. Since atypical attention is common in ASD (Ames & Fletcher-Watson, 2010) reduced sustained attention to the fake hand could have contributed to group differences.

Additionally, the imagination deficits characterising ASD (American Psychological Association, 2013) may play a role in reduced illusion susceptibility. The classic RHI requires an individual to overcome the discrepancies in physical characteristics between the fake and real hand (i.e. texture, shape), which impact on the extent to which the rubber hand is embodied (Tsakiris & Haggard, 2005). Such differences may be more salient for individuals with ASD since detail-focused processing is characteristic of this population (Baron-Cohen et al., 2009; Happé & Frith, 2006). Thus, these perceptual differences could also underlie reduced embodiment of the rubber hand.

Furthermore, in the classic RHI, precise measures of sensitivity to the temporal constraints of sensory inputs cannot be attained since brushstrokes are either approximately synchronous or approximately asynchronous by 1-2 seconds. As established in Experiment Three, visuo-tactile asynchronies of 100 ms reveal significant age differences in TD children's temporal binding, whereas asynchronies of 400 ms do not. Thus, it is likely that asynchronies of less than 1 second are needed to establish if visuo-tactile binding is temporally extended in children with ASD.

The current study used the MIRAGE, which avoided these inherent limitations of the classic RHI design. Children with ASD, chronological age-matched (CA) and verbal mental age-matched (MA) typically developing children placed their right hand into the MIRAGE and saw two, identical live video images of their own right hand in the same plane as their actual right hand. One virtual hand was aligned proprioceptively with the actual hand (the veridical hand) and the other was displaced to the left or right. While a brushstroke was applied to the participants' actual (hidden) hand, they observed the two virtual images of their hand also being stroked and were asked to identify their real hand. During brushing, one of three different temporal delays (60ms, 180 ms or 300 ms) was applied to either the displaced hand image or the veridical hand image. Therefore, importantly, only one virtual hand had synchronous visuo-tactile inputs. This novel task was designed to distinguish evidence for an over-reliance on proprioceptive processing and temporally extended visuo-tactile binding in children with ASD. Specifically, I assessed whether children with ASD weight proprioception more heavily than TD children, regardless of whether visuo-tactile inputs are congruent or incongruent with this information. I also assessed whether, compared to their typical peers, children with ASD need a longer delay between visual and tactile inputs before they can detect and distinguish synchronous from asynchronous inputs for body ownership.

Predicted performance for the control and ASD groups is shown in Figure 5.2. As reported in Section 1.3.2, a recent RHI study by Cowie et al., (2013) showed that, like adults, TD children integrate synchronous visual and tactile inputs to embody a fake hand even when this necessitates overcoming proprioceptive incongruity. There is no 'real hand' and 'fake hand' distinction in the current paradigm. However, in similar MIRAGE experiments in which a temporal delay was applied to the asynchronous hand, adults consistently embodied the synchronous hand, even when it was not presented in the location of their actual, unseen hand (Newport et al., 2010; Newport & Preston, 2011). The synchronous visuo-tactile inputs are therefore given greater weighting than incongruent proprioceptive information. This is line with previous findings showing that, for typical adults, vision is normally more accurate than proprioception when localising a hand in passive conditions (Plooy et al., 1998). Furthermore, as described in the General Introduction, multisensory information is more informative than unimodal inputs alone; thus, it makes intuitive sense that congruent visuo-tactile inputs are relied on more than incongruent proprioceptive information. Thus, based on the findings from previous MIRAGE studies, it was predicted that the TD children would integrate the felt brushstrokes with the visually synchronous brushstrokes and hence choose the synchronous hand in both the congruent and incongruent conditions.

To embody the synchronous hand, children must detect the visual delay applied to the asynchronous hand, and discriminate this from the synchronous hand. Experiment Three found that 4 to 11-year-olds could correctly detect a 300 ms visuo-tactile delay in 80% of trials but only correctly detected a 100 ms delay in 49% of trials. However, the present study employed a different task in which synchronous and asynchronous visuo-tactile inputs were presented simultaneously. Thus, piloting was conducted to ascertain the delay lengths applied to the asynchronous hand that were necessary for participants to discriminate it from the synchronous hand. Data from 15 adults showed that, in congruent conditions, most participants chose the synchronous hand and the number doing so increased with delay length (n=9 at 60 ms, n=14 at 180 ms, n=15 at 300 ms). These delay lengths were thus chosen for the current study to compare group performance on conditions requiring differing degrees of sensitivity to visuo-tactile synchrony. Following on from Experiment Three, it was predicted that TD children would choose the synchronous hand more systematically than the asynchronous hand as the visual delay applied to the asynchronous hand increased and synchrony, therefore, became easier to detect.

Additionally, in Experiment Three, children were asked to judge whether visual and tactile touches to the hand were temporally synchronous or asynchronous.

Accuracy improved significantly with age in 4 to 11-year-olds. This suggests that visuo-tactile temporal binding is less tightly constrained in younger children, who consequently are more likely to erroneously integrate inputs from distinct events. In the current study, the MA group is younger on average than the CA group (MA group mean age=7.88 years; CA group mean age= 12.17 years). Thus, it was predicted that, compared to the CA group, the MA group would require a longer delay before they reliably detect the synchronous hand (see Figure 5.2).

The current study makes different predictions for ASD performance depending on whether there is an over-reliance on proprioceptive processing, or temporally extended visuo-tactile binding in ASD (see Figure 5.2):

1. Over-reliance on proprioceptive inputs: If the ASD group rely more heavily upon proprioception, and weight this input more than other sensory information regardless of prior knowledge or contextual information (Paton et al., 2012; Palmer et al., 2015), then they should reliably select the synchronous hand when it is also the veridical hand (i.e. in congruent conditions). In incongruent conditions, even at larger delay lengths (when the synchronous hand is more easily detectable), synchrony should not completely override conflicting proprioceptive inputs. Consequently, participants with ASD should not consistently embody the synchronous hand but instead should choose the veridical hand across all conditions.

2. Temporally extended visuo-tactile temporal binding: According to this theory, compared to TD children, those with ASD will integrate sensory inputs separated by a longer delay (reflecting an enlarged TBW; Cascio et al., 2012; Kwakye et al., 2011). The TD controls should detect and chose the synchronous hand more consistently as the visuo-tactile delay applied to the asynchronous hand increases while one of two potential patterns of behaviour could be seen in the ASD group.

The first is that there will be no effect of delay length (i.e. the synchronous hand will not be chosen more frequently at longer versus shorter delay lengths) if a delay length of more than 300 ms is needed before synchronous and asynchronous visuo-tactile inputs for body ownership can be reliably distinguished. The second is that the delay length at which the ASD group are able to consistently discriminate and embody the synchronous hand should be longer than that seen in TD controls.

5.3. Methods

5.3.1. Participants

Table 5.1. Participant descriptives.

Group (sample size)	Statistic	Age in months	Verbal mental age in months	SAS	SWAN	SCQ	DQ
ASD (29)	Mean	151.65	103.17	10	0.77	24.64	69
	SD	23.07	37.37	5.90	0.66	5.2	24.43
	Min	99.72	59.0	0	-0.39	15	38.10
	Max	191.04	189.0	23	2.67	34	134.04
CA matched (29)	Mean	146.13	150.5	24.71	0.35	Not collected	N/A
	SD	21.35	35.19	6.17	0.75		
	Min	101.0	81.0	13	-1.89		
	Max	184	189.0	40	0.85		
MA matched (29)	Mean	94.56	100.35	25.71	-0.76	Not collected	N/A
	SD	16.68	27.33	5.71	0.96		
	Min	63.48	64	19	-2.78		
	Max	123.6	172	39	0.78		

Participants (see Table 5.1 for participant characteristics) were 31 children with ASD aged 8 to 15 years (two female, 1 left-handed), 29 chronological age-matched (CA) controls (8 female, 5 left-handed) and 29 verbal mental age-matched (MA) controls aged 5 to 10 years (10 female, 2 left-handed). Individuals with ASD were recruited from autism support groups and a local school in Nottingham. Comparison participants were (n=40) recruited from Summer Scientist Week, a community event held at The University of Nottingham, or from the university's database of local families (n=18). The British Picture Vocabulary Scale III (BPVS; Dunn & Dunn, 2009) was used to assess verbal mental age (MA) in all groups. This data was missing for one participant in the CA group. There were no significant differences in verbal mental age between the ASD and MA group or in chronological age between the ASD and CA group. The individuals with ASD varied in their cognitive abilities, thus, developmental quotient (DQ) scores were calculated (Chaoying, Junwu, & Chituwo, 1999) to give an indication of the range of delay in the group (see Table 5.1). The parents of all children gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

All children in the ASD group had received a previous diagnosis of autism, autism spectrum disorder or Asperger Syndrome by an independent clinician using the autism diagnostic observation scale (ADOS; Rutter, Dilavore, Risi, Gotham, & Bishop, 2012) or the autism diagnostic interview (ADI-R; Rutter, Le Couteur, Lord, & Faggioli, 2005). Confirmation of diagnosis was obtained via a parent/caregiver in a background questionnaire and additionally through parents' ratings on the Social Communication Questionnaire (SCQ; Rutter & Lord, 2003) and the Social Aptitude Scale (SAS; Liddle et al., 2008). Parents of two individuals did not return the completed questionnaires, however, as participants in the ASD group were recruited from a specialist Autism unit requiring a formal diagnosis and statement of special educational needs, it is very unlikely they did not have ASD.

Children in all groups were screened for other developmental difficulties (e.g. motor, attention, visual, language delay) via a parental background questionnaire. Additional screening was carried out for attention deficit hyperactivity disorder using the Strengths and Weaknesses of ADHD symptoms and Normal behaviour rating scale (SWAN; Swanson et al., 2006) and for social deficits using the SAS. None of the TD children had a diagnosis of ASD or any other learning difficulty, confirmed by parent questionnaire and additional screening measures, therefore, all were included. In the ASD group one individual had dyspraxia, one had dyslexia, one had ADHD and one was reported to have hypermobile joints.

There were several criteria participants were required to meet to be included in the study. Firstly, all needed to have normal or corrected-to-normal vision. Secondly, all participants took part in practice trials in which they needed to demonstrate: 1) an ability to keep their hand still and 2) comprehension of the task. Two children from the ASD group were excluded, as they could not keep their hand still to complete the task, leaving 29 children with ASD whose results were included in the analyses.

5.3.2. Procedure

All participants were tested in a quiet room at the University or their school. All children completed a MIRAGE task lasting approximately 15 minutes, followed by a second MIRAGE task described in section 6.3.2, and the BPVS, the order of which varied between participants. Breaks were given between the two tasks, or whenever they were needed and total testing time was approximately 50 minutes, including breaks.

As detailed in Section 1.6, the MIRAGE presents live video images of the hand in real time as if viewing the hand directly; that is, in the same spatial location and from the same visual perspective. Depending on their height, participants sat or knelt on a chair to allow them to comfortably view their right hand when they placed it onto the work surface of the MIRAGE. A rectangular black bib was attached across the length of the MIRAGE, on the side that the participant was seated, to obscure the work surface from view. Participants wore a black adjustable sleeve, which covered their right wrist and forearm, ensuring that only the hand was visible when their arm was in the MIRAGE. Children first completed practice trials in which they placed their right hand into MIRAGE and saw two virtual representations of their hand. These trials were identical to experimental trials described below except that

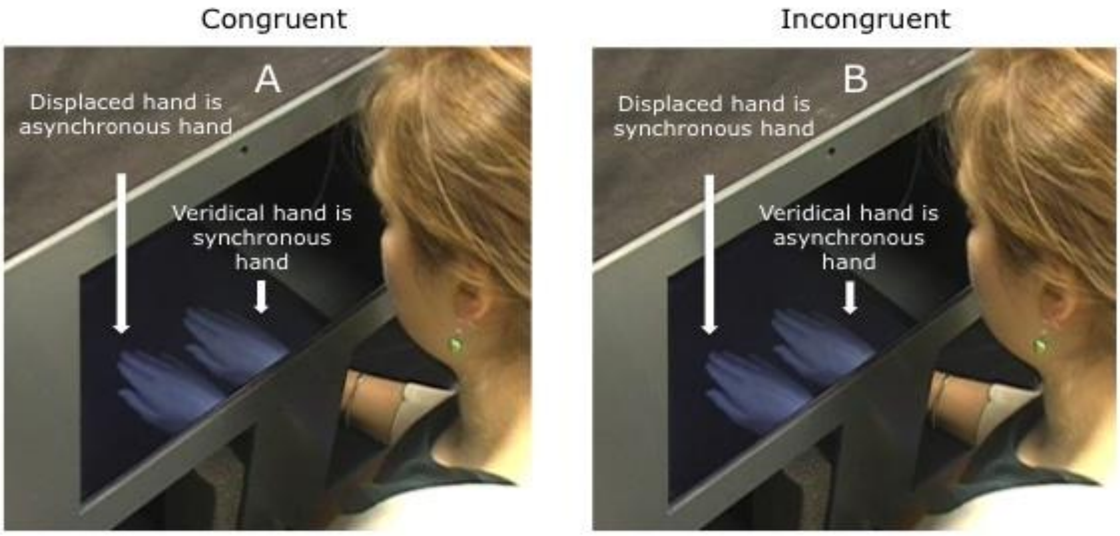


Figure 5.1. MIRAGE task.
The participant placed his/her right hand into the MIRAGE and saw two live video images of the hand. The veridical hand was in the same location as the actual hand; the displaced hand was immediately to the left or right of the veridical hand (position of the displaced hand was counterbalanced).
(A) In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300ms applied to it (asynchronous hand); the veridical hand did not (synchronous hand).
(B) In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300ms applied to it (asynchronous hand); the displaced hand did not (synchronous hand).
The arm is here uncovered for illustrative purposes, but it was covered in the experiment so that participants were unable to see the exact relationship between the limb and image.

neither hand image showed a visual-tactile delay. These were included to ensure that participants were comfortable with the set-up and understood the task requirements.

In the experimental trials, proprioceptive alignment and visuo-tactile synchrony were selectively manipulated to explore the extent to which these impact on body ownership. Proprioceptive alignment was manipulated by presenting one hand (the veridical hand) in the same location as the child's actual hand while a duplicate hand was displaced immediately to the left or right of this (displaced hand; see Figure 5.1). Since hand sizes varied between children, the displaced hand was located such that the two hands did not overlap and also that there was a visible <5mm gap between the hands. That is, the hands were immediately adjacent to each other.

The experimenter brushed the participant's right index finger with a paintbrush at 1Hz for 10 seconds while he/she saw the brushstrokes on both right hands. After brushing, a yellow shape appeared above one hand image and a different, red shape appeared above the other. The images were a circle or a square and their location, colour, and shape were counterbalanced for each trial. Participants were reminded to keep their hand still and asked to verbally name the shape they thought was above their real hand. After responses were given, vision of the hand was occluded whilst the experimenter placed the participant's hand at the starting point for the next trial. Previous MIRAGE studies employing this supernumerary illusion demonstrate that a brushing time of 20 seconds is sufficient for participants to embody the synchronous hand (Newport et al., 2010; Newport & Preston, 2011; Preston & Newport, 2011). However, piloting for the current study revealed that children and adults distinguished and embodied the synchronous hand after only 10 seconds of brushing. Additionally, the effect is consistently seen in children at public engagement events when brushing is less than 10 seconds. Thus, to keep testing time to a minimum, brushing lasted 10 seconds in all conditions of the current study.

On each trial, visuo-tactile synchrony was manipulated by applying a temporal delay of either 60, 180 or 300 ms to either the veridical or the displaced hand. Thus, the felt brushstrokes were synchronous with the visual brushstrokes on that hand (the synchronous hand) and asynchronous with the brushstrokes on the other hand. For each condition, therefore, either the veridical hand or the displaced hand was the synchronous hand, while the other hand had a temporal delay applied to it. As in Experiment Three, delay rates were calculated and monitored online and required no mechanical apparatus. The precise delay was calibrated using software 'probes,' which can determine the number of milliseconds that have elapsed at any

	Congruent 60ms	Congruent 180ms	Congruent 300ms	Incongruent 60ms	Incongruent 180ms	Incongruent 300ms
CA group	?	✓	✓	?	✓	✓
MA group	?	?	✓	?	?	✓
ASD Proprioceptive over-reliance	✓	✓	✓	✖	✖	✖
ASD Temporally extended sensory binding	✖	?	?	✖	?	?

Figure 5.2. Predictions.
Key
✓ = choose synchronous hand significantly above chance
? = may choose synchronous hand significantly above chance
✕☐= will not choose the synchronous hand significantly above chance
Children in the control groups were predicted to consistently choose the synchronous hand across all conditions provided they could detect and distinguish it from the asynchronous hand.
If children in the ASD group have an over-reliance on proprioception they should choose the synchronous hand in all the congruent conditions but in none of the incongruent conditions.
If children in the ASD group have temporally extended visuo-tactile binding, they should choose the synchronous hand in both congruent and incongruent conditions, but only at longer delay lengths, relative to the control group.

given stage within the program cycle. The delay is only applied to one of the visual presentations of the hand on each trial. Therefore, even if the real brushstroke is not at a fixed frequency, the seen delayed brush stroke will always follow at the set time after.

In congruent conditions, visuo-tactile inputs were synchronous for the veridical hand (congruent proprioceptive and visuo-tactile input) while the visual touch on the displaced hand was delayed. In incongruent conditions, the visual touch on the veridical hand was delayed; therefore, proprioception and information from visuo-tactile synchrony were incongruent. There were six conditions in total (see Figure 5.2; congruent 60ms, 180 ms and 300 ms delay and incongruent 60 ms, 180 ms and 300 ms delay) and two trials in each condition. For each condition the displaced hand was presented once to the left of the veridical hand and once to the right of it (counterbalanced across conditions). Trials and conditions were presented in a randomised order.

5.4. Results and Discussion

5.4.1. Data Analysis

In order to test the evidence for the above accounts of atypical sensory integration in ASD, I was interested in the extent to which the ASD group chose the synchronous hand across different conditions, and in comparison to TD controls. There were two trials in each condition; therefore, each participant could choose the synchronous hand once, twice or not at all in each condition. Chi-square analyses were conducted for each group at each condition to assess whether the number of participants choosing the synchronous hand was more than expected if the group was performing at chance level; i.e. not performing systematically (Table 5.2). Bonferroni corrections were used such that all analyses comparing results against chance are reported at a .003 level of significance.

Chi-square analyses were also conducted to assess whether there were significant group differences in the frequency that participants chose the synchronous hand (Table 5.3). Although some of these chi-square group comparisons had more than 20% of cases with expected frequencies less than five, it has been demonstrated that, when this occurs, it is extremely unlikely that an increase in type one errors will occur (Bradley, McGrath & Cutcomb, 1979). Nonetheless, significance levels were set at .025 to protect against this.

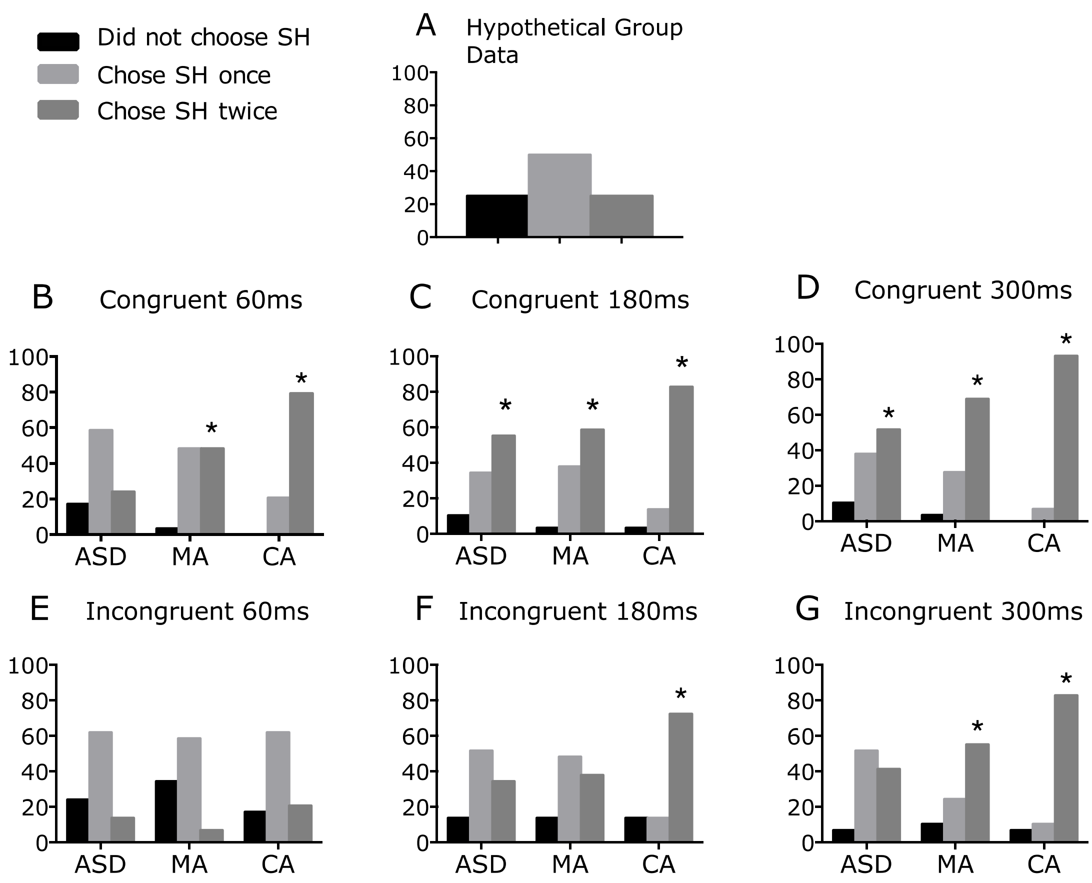


Figure 5.3. Chi-square results.
SH = synchronous hand.
Y-axis = number of participants.
CA- chronological age-matched group, MA- verbal mental age-matched group, ASD- autism spectrum disorder group.
Panel A = Hypothetical data showing a group choosing the synchronous hand at chance level. Panels B-F = Chi-square analyses comparing the frequency of individuals choosing the SH against chance level. Asterisks indicate performance that is significantly different to chance at .003 level of significance.

5.4.2. Results and Discussion

Chance level per condition equates to 25% of the group not choosing the synchronous hand, 50% choosing the synchronous hand in one trial and 25% choosing it in both trials. For comparison purposes, Figure 5.3 panel A shows what the frequency data would look like if a group's performance was at chance level. Figure 5.3 panels B to G display the frequency that participants chose the synchronous hand in each group, in each condition. These show that, across conditions, both TD groups chose the synchronous hand more than the ASD group. Across groups, the synchronous hand was chosen more in congruent, compared to incongruent, conditions and at longer, compared to shorter, delay lengths.

Table 5.2. Chi-square analyses comparing the frequency of individuals choosing the synchronous hand against chance level in each group. * indicates performance that is significantly different to chance at .003 level of significance.

	Congruent 60ms	Congruent 180ms	Congruent 300ms	Incongruent 60ms	Incongruent 180ms	Incongruent 300ms
CA	$\chi2(2)=46.45$ $p<.001$*	$\chi2(2)=51.69$, $p<.001$*	$\chi2(2)=71.83$, $p<.001$*	$\chi2(2)=1.75$, $p=.42$	$\chi2(2)=35.14$, $p<.001$*	$\chi2(2)=29.15$, $p<.001$*
MA	$\chi2(2)=11.69$ $p=.003$*	$\chi2(2)= 19.35$ $p<.001$*	$\chi2(2)= 30.72$ $p<.001$*	$\chi2(2)=5.28$, $p=.07$	$\chi2(2)=3.41$, $p=.18$	$\chi2(2)=14.45$, $p<.001$*
ASD	$\chi2(2)=1.14$ $p=.57$	$\chi2(2)=14.45$ $p<.001$*	$\chi2(2)=11.62$ $p=.003$*	$\chi2(2)=2.31$ $p=.32$	$\chi2(2)=2.52$ $p=.28$	$\chi2(2)=6.93$ $p=.03$

Both TD groups chose the synchronous hand above chance level in all congruent conditions. Children with ASD, though, did not consistently choose the synchronous hand in the congruent 60 ms condition but did so in the congruent 180 ms and 300 ms delay conditions, signifying that a 60 ms delay length was difficult for the children with ASD to detect. Between groups chi-square analyses comparing the frequency for choosing the synchronous hand are shown in Table 5.3. These found no significant differences between the ASD group and the MA group while the CA group chose the synchronous hand significantly more often than the ASD group in the congruent 60ms, $\chi^2(2)=18.79$ $p<.001$ and 300 ms conditions, $\chi^2(2)=12.66$ $p=.002$. If the ASD group had a fundamental over-reliance on proprioception then the synchronous hand should not have been chosen in any incongruent conditions but should have been selected in all congruent conditions, even when the delay was short, yet this pattern of data was clearly not observed (see Figures 5.3 and 5.4). It could be argued that the ASD group do over-rely on proprioception, regardless of changes in the illusory context, yet proprioceptive accuracy is poor thus, they cannot use this sense alone to confidently embody the veridical hand. However, if this was the case, then performance should not be above chance in any condition yet this was not found. The group systematically chose the synchronous hand in congruent 180 ms and 300 ms conditions only, suggesting that they are, therefore, influenced by changes in the illusory context, such that the weighting given to different sensory inputs varies across conditions. However, it appears that the circumstances in which this occurs differ between children with ASD and their TD peers, in a way that reflects temporally extended visuo-tactile binding. Consequently, for the ASD group, visuo-tactile and proprioceptive information seem to be weighted such that neither the synchronous hand nor the veridical hand is consistently chosen in any incongruent conditions. Hence, it is not that there is an over-reliance on proprioception across all contexts in ASD. Instead, unlike the TD controls, synchrony does not override proprioception when the two are incongruent, suggesting the inputs may be more equally weighted.

Table 5.3. Between-groups chi-square analyses comparing the number of participants choosing the synchronous hand. * indicates significant group difference at .025 level of significance.

	Congruent 60ms	Congruent 180ms	Congruent 300ms	Incongruent 60ms	Incongruent 180ms	Incongruent 300ms
CA vs. ASD	$\chi2(2)=18.79$ $p<.001$*	$\chi2(2)=5.17$ $p=.075$	$\chi2(2)=12.66$ $p=.002$*	$\chi2(2)=.73$ $p=.69$	$\chi2(2)=10.27$ $p=.006$*	$\chi2(2)=12$ $p=.002$*
MA vs. ASD	$\chi2(2)=5.29$ $p=.07$	$\chi2(2)=1.08$ $p=.58$	$\chi2(2)= 2.19$ $p=.34$	$\chi2(2)=1.23$ $p=.54$	$\chi2(2)=.08$ $p= .96$	$\chi2(2)=1.72$ $p=.41$

Without detecting and distinguishing synchronous from asynchronous inputs in the 60 ms condition, proprioceptive information alone was not sufficient for the ASD group to embody the (veridical) synchronous hand. With an increased delay length, however, the combined weighting of visual, tactile and proprioceptive inputs led to embodiment of the synchronous hand in congruent 180 and 300 ms conditions. Therefore, compared to age-matched controls, the ASD group appear to need a longer delay between synchronous and asynchronous inputs before they can clearly discern the synchronous hand -indicating extended and less precise sensory binding. Though previous research has demonstrated this for auditory-visual processing in children with ASD (e.g. Kwakye et al., 2011) this is the first study to provide strong evidence for temporally extended visuo-tactile binding in this population.

The CA group chose the synchronous hand above chance level in the incongruent 180 ms and 300 ms conditions while the MA group only did so in the 300 ms condition (see Figure 5.4). These results indicate that the TD children were guided by visuo-tactile temporal synchrony, even when this information was incongruent with proprioceptive information. This tendency is seen in RHI studies with both children (Cowie et al., 2013) and adults (Botvinick & Cohen, 1998), and in supernumerary limb illusions (Ehrsson, 2008; Newport et al., 2010; Newport & Preston, 2011; Preston & Newport, 2011), indicating that in these circumstances visuo-tactile information is considered to be more reliable than unimodal proprioception in typical populations. Although the synchronous hand was chosen less in incongruent versus congruent conditions for TD controls, the findings are consistent with the broader embodiment literature in that we are more likely to embody a fake hand when there is less proprioceptive discrepancy between it and our real unseen hand (Lloyd, 2007; Preston, 2013; Preston & Newport, 2014). This is also in keeping with data from Paton et al's (2012) RHI study in which the illusion was stronger for TD individuals in conditions when video goggles were worn such that there was no proprioceptive discrepancy between the fake hand and the real hand. Again, this is in line with the idea that MSI involves up-weighting sensory inputs with less variance (Landy et al., 1995). Thus, when visuo-tactile information coheres with proprioceptive estimates of hand location, it is likely to be given a greater weighting compared to when incongruent proprioceptive information is present. The non-significant difference in performance between the ASD and CA group in the congruent 180 ms condition is likely an artefact related to different rates of improvement between the groups since the trend for more children in the CA group to choose the synchronous hand is still present in this condition. In the congruent 60 ms condition, detecting the delay is very difficult for the ASD group while in the congruent 300 ms condition it is very easy for the CA group. Thus, group differences are exaggerated at these two extremes. In the congruent 180 ms condition, the ASD group are able to perform above chance in selecting the synchronous hand with congruent proprioceptive information, therefore, the difference in performance between the CA and ASD groups is not as strong at this point.

Chance level performance by the control groups in the incongruent 60 ms condition suggests that the synchronous hand was difficult to detect and not sufficient to completely override conflicting proprioceptive inputs. The MA group required a longer delay (300 ms versus 180 ms) than the CA group before they reliably chose the synchronous hand in incongruent conditions, which is likely due to age-related differences in temporal sensory binding, as indicated by the results of Experiment Three and previous research (e.g. Hillock-Dunn & Wallace, 2012; Jaime et al., 2014). The older CA group would have been more sensitive to the discrepancy between synchronous and asynchronous visuo-tactile information in the 180 ms delay conditions than the (younger) MA-matched children, who, consequently, did not systematically embody the synchronous hand in that condition. These observations are further strengthened by between groups analyses, which revealed that the CA group chose the synchronous hand significantly more often than the ASD group in the incongruent 180 ms ($\chi^2(2)=10.27$ $p=.006$) and 300 ms conditions

($\chi^2(2)=12$, $p=.002$), but there were no significant differences between the ASD and MA group. Thus, the ASD group were performing differently to CA matched TD children but were in line with younger TD children, demonstrating a developmental delay in sensitivity to visuo-tactile temporal synchrony.

In summary, the results of the current experiment indicate temporally extended visuo-tactile binding in children with ASD compared to chronological age-matched TD children. Participants with ASD performed in line with younger TD children, suggesting that this atypical MSI could reflect a developmental delay. However, it could be argued that the current study does not specifically test MSI abilities underlying body representation since children may have been choosing the synchronous hand without embodying it. Experiment Six was thus conducted to assess whether the current findings were also seen when a more objective measure of hand ownership was employed.

Experiment Six: Multisensory Integration underlying motor embodiment in children with autism

5.5. Abstract

The results of Experiment Five indicate temporally extended visuo-tactile binding in children with ASD. The current experiment tested whether this finding could be replicated when a more objective measure of body representation is used. Participants placed their right hand into the MIRAGE and brushstrokes were applied to their hand while they saw two, identical live video images of the right hand. One virtual hand was aligned proprioceptively with the actual hand (the veridical hand), and the other was displaced to the left or right. During brushing, a 60, 180 or 300 ms delay was applied to the displaced hand in incongruent conditions and the veridical hand in incongruent conditions. Thus, only one virtual hand had synchronous visuo-tactile inputs. After brushing, both hand images disappeared from view and children pointed at a target presented equidistant between the previously seen hand images. Results showed that accuracy was lower in incongruent compared to congruent conditions for both ASD and TD children, indicating the influence of visual-tactile inputs on perceived hand position. Mirroring results from Experiment Five, unlike an age-matched control group, a 60 ms delay seemed to be too small for the ASD group to reliably detect and distinguish the synchronous hand from the asynchronous hand. This suggests that temporally extended visuo-tactile binding could underlie atypical body representation, which may impact upon sensory processing and socio-communicative functioning in ASD.

5.6. Introduction

Results from Experiment Five indicate that children with ASD show temporally extended visuo-tactile binding in comparison to age-matched peers. In the experiment, children's hands were brushed with a paintbrush while they saw two identical live video images of their hand being brushed. Felt brushstrokes were temporally synchronous with seen brushstrokes on one hand image while a 60ms, 180 ms or 300 ms temporal delay was applied to the seen brushstrokes on the other hand image. In congruent conditions, the displayed hand was delayed while in incongruent conditions the veridical hand was delayed. Both TD groups chose the synchronous hand above chance level in all congruent conditions. The ASD group, however, did not consistently choose the synchronous hand in the congruent 60ms condition but did so in the congruent 180 ms and 300 ms delay conditions, indicating that detecting a 60 ms delay length was difficult for the children with ASD. However, it could be argued that children's decisions were based on detecting and distinguishing synchronous from asynchronous inputs, which may not necessarily equate to embodiment of the synchronous hand. For instance, participants could determine which visual touch is out of sync with the felt touch and, from this, make a logical decision to choose the synchronous hand, without actually having a subjective sense of ownership over it. As discussed in Section 1.3.1, body representation underpins social, cognitive and behavioural processes that are compromised in ASD, including inferring others' mental states, empathising and imitation. It has been proposed that these social impairments may be due to problems with body representation. It is thus important to establish how MSI underlying body ownership *specifically* may be different, as this can increase our understanding of the links between atypical low-level processing and higher-level functioning. The current experiment was therefore designed to assess the extent that body ownership is effected by temporally synchronous and asynchronous visuo-tactile inputs in children with ASD and TD control groups.

The conditions and initial procedure were identical to Experiment Five. Children placed their right hand into the MIRAGE and saw two virtual representations of their right hand. One hand image (the veridical hand) was in the same location as the child's actual hand while the other (the displaced hand) was seen immediately to the left or right of this. The experimenter brushed the child's hand and they saw the brushstrokes on both visual hands. A 60, 180 or 300 ms delay was applied to the displaced hand in congruent conditions and the veridical hand in incongruent conditions. Unlike Experiment Five, after 10 seconds of brushing, vision of the hands was occluded and children pointed to a target presented equidistant between the two previously presented hand images. The distance between the starting position and the end position of the participant's finger following target presentation gives an indicator of perceived hand location and ownership (Jones, Cressman, & Henriques, 2010).

Based on previous findings from Experiment Five and Cowie et al., (2013), the following predictions were made. In congruent conditions (when the synchronous hand is the veridical hand) TD children should integrate the felt brushstrokes with the visually synchronous brushstrokes and congruent proprioceptive information. They should, therefore, embody the synchronous, veridical hand and thus point accurately towards the target. In incongruent conditions, synchronous visuo-tactile cues should over-ride incongruent proprioceptive inputs, thus, TD children should embody the displaced hand. Consequently, accuracy should be reduced compared to the congruent conditions, reflecting a shift in perceived hand location towards the displaced hand. Results from Experiment Five suggest that this reduction in accuracy should increase as the visual delay applied to the veridical hand increases and the synchronous hand becomes easier to detect.

The findings from Experiment Three and Five further suggest that sensory temporal binding is extended and less precise in younger compared to older TD children. Therefore, in incongruent conditions when the delay applied to the asynchronous hand is small, younger TD children may not reliably perceive and distinguish synchronous from asynchronous inputs. Thus, it was also predicted that the reduction in accuracy seen in incongruent versus congruent conditions (the congruency effect) would be greater in older children compared to younger children.

It was predicted that the ASD group would embody the synchronous, veridical hand in the congruent conditions and thus point accurately towards the target, due to the combined information from congruent proprioceptive, visual and tactile inputs. Experiment Five indicates that visuo-tactile binding is temporally extended in children with ASD, suggesting that this group cannot reliably distinguish synchronous from asynchronous inputs in the 60 ms delay conditions. Thus, accuracy may be reduced in the congruent 60 ms condition, compared to the congruent 180 ms and 300 ms conditions, if visuo-tactile synchrony cannot be used to determine hand location at shorter delay lengths. In incongruent conditions, like the TD controls, accuracy should be reduced due to the influence of synchronous visuo-tactile inputs applied to the displaced hand and the consequent embodiment of this hand image. However, relative to the CA group (and mirroring predictions for the MA group), children with ASD may only show this accuracy reduction at long delays in incongruent conditions since synchrony detection may not be possible at short delay lengths.

5.7. Method

5.7.1. Participants

Participants were 31 children with ASD aged 8 to 15 years (two female, 1 left-handed), 29 chronological age-matched (CA) controls (8 female, 5 left-handed) and 29 verbal mental age-matched (MA) controls aged 5 to 10 years (10 female, 2 left-handed). These participants also took part in Experiment Five (see Section 5.3.1 for details on participant recruitment and inclusion/exclusion criteria). In addition to the two participants with ASD who were excluded because they were unable to keep their hand still, one child in the CA group and two in the MA group did not complete the current task due to time constraints. Details of the remaining participants are shown in Table 5.4.

Table 5.4. Participant descriptives.

Group (sample size)	Statistic	Age in months	Verbal mental age in months	SAS	SWAN	SCQ	DQ
ASD (29)	Mean	151.65	103.17	10	0.77	24.64	69
	SD	23.07	37.37	5.90	0.66	5.2	24.43
	Min	99.72	59.00	0	-0.39	15	38.10
	Max	191.04	189.00	23	2.67	34	134.04
MA matched (27)	Mean	95.29	101.56	26.13	-0.77	Not collected	N/A
	SD	16.99	27.86	7.73	0.95		
	Min	64.00	64.00	19	-2.78		
	Max	123.6	172.00	39	0.78		
CA matched (28)	Mean	152.18	147.69	24.71	0.35	Not collected	N/A
	SD	19.85	32.8	6.17	0.75		
	Min	116.76	101.00	13	-1.89		
	Max	184	189.00	40	0.85		

5.7.2. Procedure

All participants were tested in a quiet room at the University or their school. All children completed the MIRAGE task described in section 5.3.2, before completing the current MIRAGE task, which took approximately 15 minutes. Children also completed the BPVS, either before or after the tasks. Breaks were given between the two tasks, or whenever they were needed and total testing time was approximately 50 minutes, including breaks.

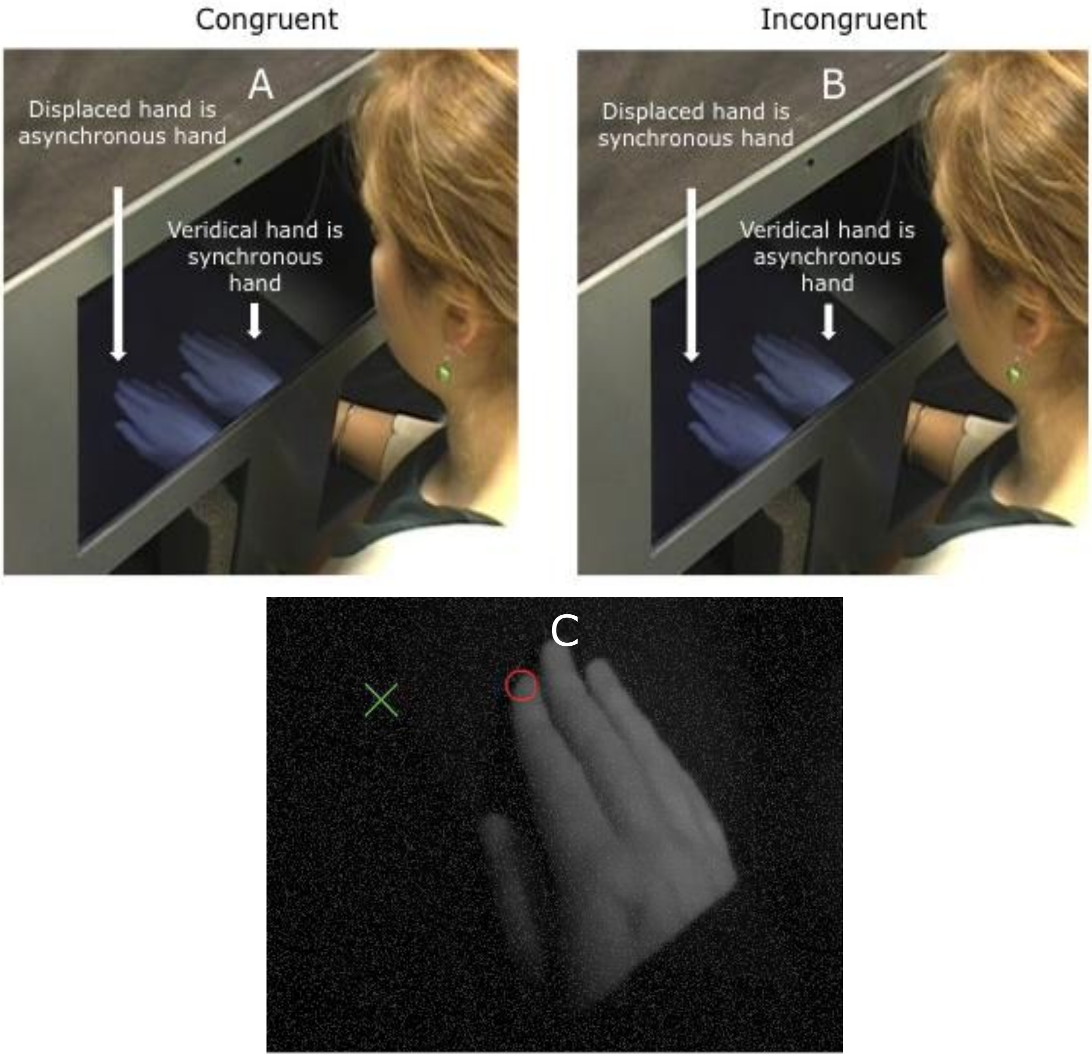


Figure 5.4. MIRAGE Task.
Participants placed their right hand into the MIRAGE and saw two live video images of the hand. The veridical hand was in the same location as the actual hand; the displaced hand was to the left or right of the veridical hand.
In (A) and (B) the arm is uncovered for illustrative purposes, but it was covered in the experiment so that participants were unable to see the exact relationship between the limb and the images.
(A) In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300ms applied to it; the veridical hand did not (synchronous hand).
(B) In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300ms applied to it; the displaced hand did not (synchronous hand).
(C) After 10 seconds of brushing, the screen went blank and participants pointed at a target (a green cross) located between the previously presented hand images. Both the hand and target are shown here for illustrative purposes but in the experiment vision of the hand was occluded when the target was presented. In this example, the displaced hand would have been seen to the right of the target from the participant's perspective.

The initial procedure was similar to that used in Experiment Five (see Section 5.3.2). Children placed their right hand into the MIRAGE and saw two virtual representations of their hand: the veridical hand was in the same location as the child's actual hand while the displaced hand was immediately to the left or right of this (see Figure 5.1). Children first completed practice trials, which were identical to experimental trials described below except that neither hand image showed a visual-tactile delay. These were included to ensure that participants were comfortable with the set-up and understood the task requirements.

The participants' right index finger was brushed at 1Hz for 10 seconds while they saw the brushstrokes on both right hands. In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300 ms applied to it; the veridical hand did not. In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300 ms applied to it; the displaced hand did not. However, unlike Experiment Five, after brushing, both hand images disappeared from view and a target (a green cross) was presented on the screen for five seconds. This appeared half way between the two previously presented hand images, aligned horizontally with the tip of the index fingers (see Figure 5.4). For each condition, the displaced hand was presented once to the left of the veridical hand and once to the right of it (counterbalanced across conditions). The target was thus presented to the left of the participants' actual index finger in half the conditions and to the right in the remaining conditions. Participants were asked to point at the green cross, quickly and accurately, with their right index finger and to hold this position until the target disappeared (5-second duration). Vision of the hand remained occluded whilst the experimenter placed the participant's hand at the starting point for the next trial. The participant's hand movements were recorded and, as in Experiment Five, there were two trials for each of the six conditions; congruent 60ms, 180 ms and 300 ms delay and incongruent 60 ms, 180 ms and 300 ms delay. These were presented in a randomised order.

5.8. Results

5.8.1. Data Analysis

There were two trials in each condition. For each trial, children's hand movements were recorded during the five-second duration that the target appeared on the screen. For each video clip, the x-axis coordinates of three locations were recorded in pixels (1 pixel=0.75mm): 1) the tip of the index finger at the start of the video (baseline measurement), 2) the tip of the index finger at the end of the video (pointing measurement) and 3) the centre of the target. These values were entered into a Labview programme to calculate the distance and direction of reaches for each trial. For each condition, the target appeared once to the left of the veridical hand and once to the right of it. However, to facilitate analysis, errors were calculated as negative if participants pointed away from the target, regardless of whether the target was to the left or right of the veridical hand. A score of 100 equates to pointing exactly on the target, positive scores represent pointing in the direction of the target and negative scores represent pointing away from the target. A score of zero equates to pointing that is in line with the baseline position along the x-axis (see Figure 5.5).

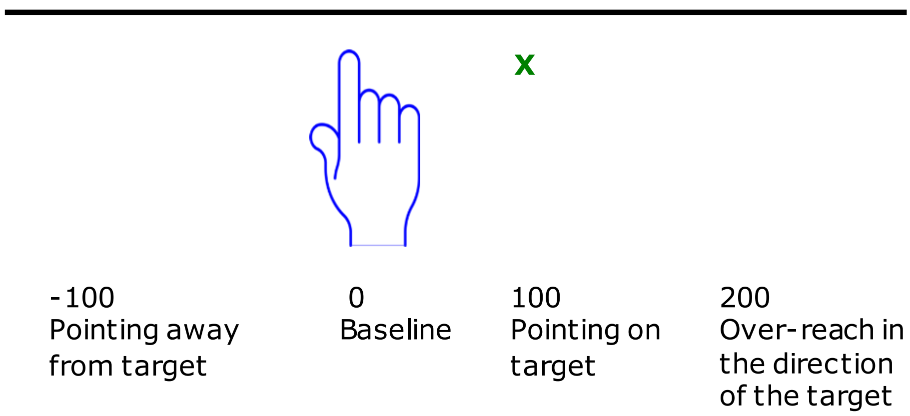


Figure 5.5. Reach values.
A score of 100 equates to pointing exactly on the target. Scores above 100 indicate over-reaches i.e. pointing in the direction of the target but beyond it. Scores below zero indicate pointing away from the target.

2.6% of the total dataset was missing due to a technical error when recording the videos. Missing data was dealt with using casewise deletion leaving 25 ASD, 26 CA-matched and 22 MA-matched participants whose data was included in the analysis. For the remaining participants, the CA and ASD groups were not significantly different on CA ($p=.619$) and the MA and ASD groups were not significantly different on MA ($p=.944$).

To assess accuracy, Bonferroni corrected ($p<.003$) one-sampled t-tests against 100 (equating to pointing directly on the target) were conducted for each group, at each condition. To assess the extent that incongruent visuo-tactile inputs affected embodiment - the congruency effect - scores in congruent conditions were subtracted from scores in incongruent conditions, for each group at each delay length. These congruency scores were entered into a repeated measured ANOVA with group (CA versus MA versus ASD) as the between-subjects factor and delay (60 ms versus 180 ms versus 300 ms) as the within-subjects factor. Assumptions for normality, homogeneity and sphericity were met unless otherwise stated. All analyses were re-run without outliers as determined by the outlier labelling rule using 2.2 as a multiplier (Hoaglin & Iglewicz, 1987). The pattern of results remained the same thus the results reported below include outliers.

5.8.2. Results

Mean reach scores for each group in each condition are displayed in Figure 5.6. One-sampled t-tests (Bonferroni-corrected) showed that scores were significantly lower than 100 (signifying reduced accuracy) for the CA group in the congruent 60ms, $t(27)=3.90$, $p=.001$); incongruent 60ms, $t(26)=5.36$, $p<.001$; incongruent 180ms, $t(27)=7.92$, $p<.001$ and incongruent 300 ms conditions, $t(26)=7.65$, $p<.001$. For the MA group, scores were significantly lower than 100 in the incongruent 180 ms condition, $t(26)=4.08$, $p<.001$ and incongruent 300 ms condition, $t(26)=7.31$, $p<.001$. For the ASD group, scores were again only

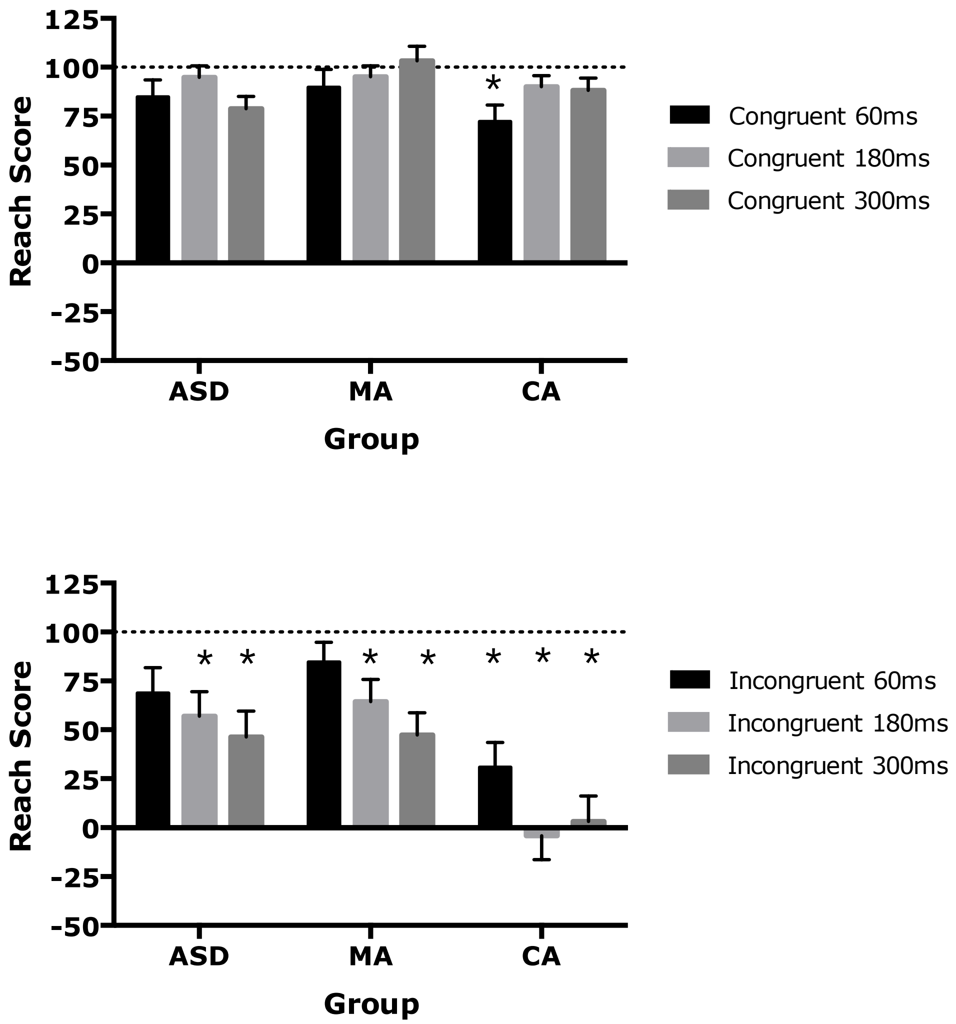


Figure 5.6. Mean reach scores for autism spectrum disorder (ASD), verbal mental age (MA) matched and chronological age (CA) matched control groups. Error bars show standard error of the mean.
A score of 100 equates to pointing directly on the target (dotted line).
* Indicates scores that are significantly different from 100 at p<.003.

significantly lower than 100 in the incongruent 180 ms condition, $t(25)=3.57$, $p=.001$ and the incongruent 300 ms condition, $t(27)=4.18$, $p<.001$. No other results were significant.

The effect of congruency is shown in Figure 5.7. The repeated-measures ANOVA found a main effect of delay, $F(1.83, 140)=13.71$, $p<.001$. The assumption of sphericity was violated for this effect, as specified by Mauchly's test, $X^2(2)=.91$, $p=.034$, thus, degrees of freedom are reported using Greenhouse-Geisser estimates of sphericity. Pairwise comparisons (Bonferroni corrected) revealed no significant difference between the 180 ms and 300 ms delays ($p=1$) but scores were significantly lower at 60 ms compared to 180 ms ($p=.001$) and 300 ms delays ($p<.001$). A main effect of group was also found, $F(1,70)=5.47$, $p=.006$. Levene's test showed that the variance in congruency scores at the 180 ms delay was smaller in the ASD and MA groups compared to the CA group ($p=.016$; see Figure 5.6). However, with large sample sizes, Levene's test can be significant when group variances are not exceptionally different, so corrections were not made for this. Pairwise comparisons (Bonferroni corrected) revealed no significant difference

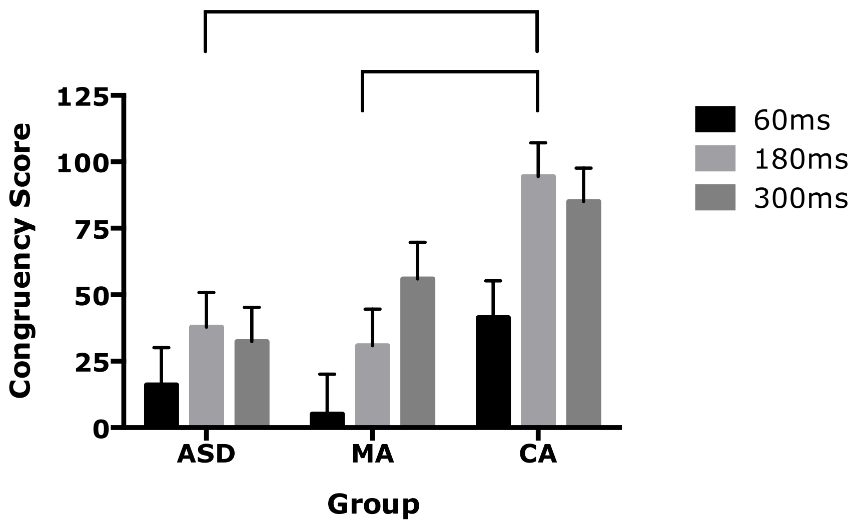


Figure 5.7. Congruency scores for the autism spectrum disorder (ASD), verbal mental age (MA) matched and chronological age (CA) matched control groups. Error bars represent standard error. Braces indicate Bonferroni-corrected significant group differences.

between the ASD and MA groups (p=1) but congruency scores were significantly lower for the CA group compared to the MA group (p=.024) and the ASD group (p=.013). No other main effects or interactions were significant.

5.9. Discussion

The current experiment assessed whether visuo-tactile integration underlying body representation is temporally extended in children with ASD. Participants pointed to a target following exposure to congruent or incongruent proprioceptive and visuo-tactile inputs for hand ownership. The influence of visuo-tactile cues on hand ownership was reduced in participants with ASD, with the specific pattern of results indicating temporally extended visuo-tactile binding. This corresponds with findings from Experiment Five and research in the audio-visual domain suggesting an enlarged temporal binding window (TBW) for sensory integration in children with ASD.

In congruent conditions, children in all groups consistently pointed in the direction of the target indicating that, after synchronous visuo-tactile information, perceived hand location was in accordance with the synchronous, veridical hand. Performance in these conditions is in line with TD adults (Newport & Preston, 2011, see also Section 6.8.2) and indicates that the participants understood and were able to do the task. It is interesting to note, however, that accuracy was lower in the congruent 60 ms condition for the CA group compared to the MA and ASD groups (see Figure 5.6). One explanation for this finding is that in this task vision of the hand is absent when reaching thus participants must rely on proprioceptive (and kinematic) feedback alone. In contrast, during judgments of perceptual embodiment in Experiment Five, the hand images remain visible. Evidence suggests that young TD children may show a preference for using unimodal over multimodal information (Gori et al., 2008). Yet, throughout childhood, the ability to integrate multiple sensory inputs develops through experience, leading gradually to optimal

MSI by late childhood (Cowie et al., 2013, 2015; Gori et al., 2008; Experiments One, Two and Three). Therefore, it could be that the MA group has more recent experience in relying only on one sensory modality than older TD children, leading to increased pointing accuracy relative to the CA group when only proprioceptive feedback is available.

In incongruent conditions, accuracy was reduced across all delay lengths, in all groups. However, in contrast to the CA group, reach scores were only significantly different to 100 (equating to pointing exactly on the target) for the medium (180ms) and long (300ms) conditions for the ASD and MA group but not the short (60ms) condition. This could suggest that sensitivity to the temporal constraints of visuo-tactile binding is reduced in younger TD children and children with ASD relative to age-matched controls. Specifically, unlike the CA group, the MA and ASD groups do not seem to reliably detect and embody the synchronous hand when the delay applied to the asynchronous hand is only 60ms.

To assess group differences, a repeated-measures ANOVA was run on congruency scores (i.e. the score in the congruent condition minus the score in the incongruent condition, at each delay length). Across groups, scores were significantly lower in 60 ms compared to 180 ms and 300 ms conditions. This indicates that embodiment of the synchronous hand is reduced when the delay applied to the asynchronous hand is small and the synchronous hand is thus more difficult to detect. Across conditions, scores in the CA group were significantly higher than in the MA and the ASD group. This indicates that, compared to the other groups, the CA group embodied the synchronous hand more consistently in both congruent conditions (when it is in the proprioceptively correct location) and incongruent conditions (when it is not in the proprioceptively correct location).

As in the previous experiment, no evidence was found for a fundamental over-reliance on proprioception in children with ASD. If this was the case then pointing should remain accurate across conditions yet this was not found; accuracy was significantly reduced in incongruent but not congruent 180 ms and 300 ms conditions for the ASD group. Thus, taken together, these findings suggest that while the temporal synchrony of sensory inputs influences body representation in all children, the ASD and MA group may have an enlarged visuo-tactile TBW relative to older TD children, which could increase the likelihood that inputs from separate events are mistakenly integrated together. Mirroring the results from Experiment Five, it seems that these groups need a longer delay between asynchronous visual and tactile brushstrokes before they can reliably detect and distinguish the synchronous from the asynchronous hand. Since the MA group were on average younger than the CA group, this coheres with findings from Experiment Three, which indicates reduced sensitivity to the temporal properties of visuo-tactile integration in younger versus older TD children. Importantly, it adds to the findings from Experiment Five by indicating that atypical MSI, and specifically temporally extended visuo-tactile binding, is seen in children with ASD in tasks that clearly necessitate body ownership.

5.10. General Discussion of Experiments Five and Six

One limitation of Experiments Five and Six is that there were only two trials per condition, thus there may be variance in the data, which cannot be adequately controlled for. A future study could repeat this experiment with more trials to increase the reliability of the results. Nonetheless, two trials per condition were used to keep the tasks brief and thereby ensure that participants could maintain concentration and keep their hand still throughout the experiments. Additionally, to keep the tasks short, the hand was in the same location across all trials in both experiments. A future study could vary the hand location to assess if the findings generalise across peripersonal space.

Although there is a growing body of research on visual-auditory processing in ASD (e.g. Kwakye et al., 2011; Stevenson et al., 2014; Woynaroski et al., 2013) the findings from Experiments Five and Six further our understanding of the processes underlying atypical visuo-tactile-proprioceptive integration in this disorder. This is important to investigate since these inputs underlie body representation. This is a necessary pre-cursor to the development of behavioural, cognitive and social skills such as spatial navigation, inferring others' mental states, empathy and imitation, all of which are impaired in ASD. Thus, it follows that atypical MSI in ASD could result in problems with accurate body representation, which in turn would have cascading effects on multiple aspects of daily functioning.

TD children seem sensitive to synchrony between the seen and felt touch, and automatically bind sensory events together on that basis. They may use this to guide their attention towards, and embody, the synchronous hand, even when this information is incongruent with proprioceptive inputs (Bahrick & Todd, 2012). Additionally, appropriate temporal binding may allow them to distinguish between relevant and unrelated sensory information. Thus, TD children may have used the discrepancy between synchronous and asynchronous information to determine not only their actual hand but also which hand was not theirs. In contrast to the TD controls, children with ASD require longer delays between the visual and tactile inputs on the asynchronous hand before body representation is guided by temporal synchrony, indicating temporally extended visuo-tactile temporal binding. This would likely lead to problems distinguishing between synchronous sensory inputs relating to the same event and asynchronous inputs originating from different events, which could inhibit the development of important social and cognitive processes. For example, infants learn that when they touch an object they can feel it (tactile information) at the same time as they see their hand touching it (visual information). Through this experience, they learn about the relationship between perception and action, which allows them to interpret and interact with their environment (Piaget & Inhelder, 2008). If children with ASD have reduced sensitivity to the temporal constraints of sensory binding then this may inhibit or delay this experience-dependent learning. It could also make 'noisy' environments, i.e. those with a high degree of sensory information, such as a classroom, overwhelming and may lead to the avoidance of social situations. To reduce feelings of sensory overload, children with ASD may then chose to focus on information from one sensory modality at the expense of other modalities, leading to hypersensitivities to that sense and hyposensitivities to the remaining, neglected sensory inputs (Bahrick and Todd, 2012).

Nevertheless, it is not clear whether extended visuo-tactile temporal binding is only seen in children with ASD, or whether it is also present in adults with the disorder. This will be examined in Experiments Seven and Eight, in which the tasks used in Experiments Five and Six will be conducted with adults with ASD and a TD control group.

Chapter Six: Multisensory integration underlying body representation in adults with autism

Experiment Seven: Perceptual embodiment in adults with autism

6.1. Abstract

The results of Experiment Five indicate temporally extended visuo-tactile binding in children with autism spectrum disorders (ASD) relative to chronological age-matched controls. The current experiment tested whether these findings were also seen in adults with ASD when compared to an age- and IQ- matched typically developing (TD) control group. Participants placed their right hand into a MIRAGE and saw two, identical live video images of their right hand. One virtual hand was aligned proprioceptively with the actual hand (the veridical hand), and the other was displaced to the left or right. While a brushstroke was applied to the participants' actual (hidden) hand, they observed the two virtual images of their hand also being stroked and were asked to identify their real hand. During brushing, one of three different temporal delays was applied to either the displaced hand or the veridical hand. Thus, only one virtual hand had synchronous visuo-tactile inputs. No significant group differences were found in any conditions, instead, results showed that visuo-tactile temporal synchrony overrides proprioceptive inputs in both groups. This could indicate that visuo-tactile temporal binding is not temporally extended in adults with ASD. Alternative explanations for the results are also discussed.

6.2. Introduction

The findings from Experiments Five and Six point to temporally extended visuo-tactile binding in children with ASD. In Experiment Five, children placed their right hand into the MIRAGE and saw two live video images of the own hand. One image was proprioceptively aligned with the actual hand, and the other was displaced to the left or right. Brushstrokes were applied to the participant's unseen hand while he/she observed the two visual hands being stroked. During brushing, a 60 ms, 180 ms or 300 ms temporal delay was applied to one hand image. In congruent conditions the displaced hand was delayed; in incongruent conditions the veridical hand was delayed - thus, only one virtual hand had synchronous visuo-tactile inputs. Children were asked to identify their real hand and results showed that, while TD children embodied the synchronous hand in all congruent conditions and in incongruent conditions with longer delay lengths, the ASD group only did so in the congruent 180 ms and 300 ms conditions. In 60 ms conditions performance was at chance level. This indicates temporally extended visuo-tactile binding in children with ASD, relative to chronological age-matched TD controls. However, it is not clear whether this pattern of behaviour is also seen in older participants with the disorder. The current study was designed to test this.

Research on visuo-tactile-proprioceptive integration in adults with ASD has been investigated by Paton et al., (2012) and Palmer et al., (2015), using the rubber hand illusion (RHI). In Paton et al., (2012), the classic RHI was conducted with and without the participant wearing goggles that display the fake hand in the same spatial location as the real hand. The goggles speeded illusion onset in TD adults by reducing proprioceptive incongruity between the real and fake hand (Hohwy & Paton, 2010). Interestingly, this effect was not seen in adults with ASD. The authors propose that TD individuals attempt to integrate visuo-tactile and incongruent proprioceptive information together and thus experience a discrepancy between the conflicting sensory inputs during the classic RHI, which is attenuated when goggles are worn. In contrast, it is argued that multisensory integration (MSI) does not occur as readily in adults with ASD, such that they are less affected by whether or not proprioceptive inputs concur with visuo-tactile information. This indicates that altered sensory processing underlying body representation is seen in adults as well as children with ASD. Nonetheless, this study did not assess whether this is due to less tightly constrained temporal binding.

As detailed in Chapter Four (Section 4.2), in the RHI study conducted by Palmer et al., (2015), reach-to-grasp movements were analysed following temporally congruent or incongruent visuo-tactile brushstrokes applied to the fake and real hand. When reaching to a cylinder located in front of their unseen, hidden hand, movements by TD adults with few autistic traits were jerkier when the previously administered brushing had been asynchronous, compared to synchronous. The authors suggest that these individuals experience a conflict between proprioceptive input and illusory expectations for arm position. In contrast, adults with ASD and TD adults with more autistic traits appeared to show a reduced influence of context, such that movements were similar across synchronous and asynchronous conditions. This study again suggests that altered visuo-tactile-proprioceptive processing may persist into adulthood in individuals with ASD. Nevertheless, (as described in Chapters Four and Five), the imagination deficits and attention problems commonly seen in ASD could be affecting illusion susceptibility and thus may underlie an apparent reduced influence of the experimental context.

Since Experiments Five and Six found evidence of temporally extended visuo-tactile binding in children with ASD, it is important to investigate this aspect of sensory processing in adults with the disorder. To my knowledge, there is only one published study assessing visuo-tactile temporal binding in adults (as opposed to children) with ASD. This study, conducted by Poole, Gowen, Warren, & Poliakoff (2015), used a cross-modal congruency task (CCT; Spence, Pavani, & Driver, 2004) with adults with ASD and an age- and IQ-matched control group. In a typical visuo-tactile CCT (e.g. Spence et al., 2004; see Figure 7.1), participants judge the height of a tactile stimulus (e.g. a vibration felt on the finger or thumb) when visual distractors (e.g. light flashes) are presented either at the same elevation level as the tactile stimulus (congruent visuo-tactile inputs) or at a different level (incongruent visuo-tactile inputs). Participants show increased accuracy and speeded response times (indicative of MSI) when the locations of the tactile and visual stimuli are congruent versus incongruent. The strength of this congruency effect increases when the visual and tactile events occur close together in time. This coheres with findings that the likelihood of MSI increases as the temporal delay between the sensory inputs decreases (Frassinetti et al., 2002; Wallace et al., 2004). As discussed in Chapter One, stimuli are processed more quickly when inputs from multiple sensory modalities are available compared to when only unimodal information is present (Laurienti et al., 2004; Foster et al., 2002). Additionally, MSI is more likely when sensory inputs are temporally synchronous versus asynchronous, as simultaneously presented sensory information is more likely to have originated from the same event (Wallace et al., 2004).

If adults with ASD show temporally extended visuo-tactile binding then, compared to TD adults, the congruency effect should continue to be seen in congruent conditions with longer stimulus onset asynchronies (SOAs) between the visual and tactile stimulus. However, Poole et al., (2015) did not find evidence of this. In their task, participants discriminated between single and double tactile pulses applied to the hand. During each trial a task-irrelevant light flash also occurred, which was either congruent (a single tactile pulse with a single light flash or a double tactile pulse with a double light flash) or incongruent (a single tactile pulse paired with double light flashes or double tactile pulses paired with a single light flash). In baseline conditions, no visual distractor was present. In congruent conditions, when the visual stimuli occurred 200 ms or 400 ms after the tactile stimuli, performance was not significantly different to baseline conditions for TD participants. However, significantly faster and more accurate responses were seen when the visual stimuli occurred 30 ms before (-30 ms) or 100 ms after the tactile stimuli. This congruency (or multisensory enhancement) effect indicates that visuo-tactile temporal binding had only occurred in conditions with visuo-tactile stimulus onset asynchronies (SOAs) of 30 ms or 100 ms. With longer SOAs, the temporal distance between the visual and tactile inputs was wide enough for them to be treated as two separate events.

Interestingly, the congruency effect was only significantly greater than baseline at

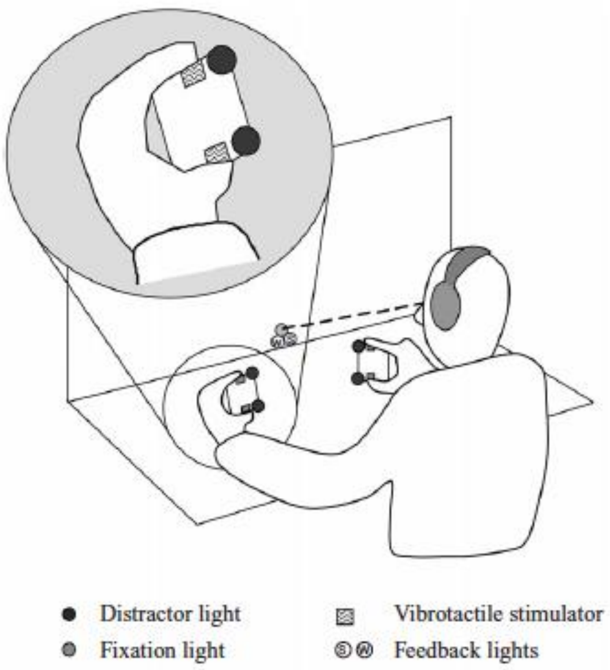


Figure 6.1. Visuo-tactile cross-modal congruency task. The participant holds a foam cube in each hand. Each cube has two vibrotactile stimulators and two visual distractor lights positioned next to the index finger or thumb. The participant makes speeded elevation discrimination responses, using foot pedals, in response to tactile stimuli presented from the 'top' (the index finger) or the 'bottom' (the thumb).
Image cited from "Spatial constraints on visual–tactile cross-modal distractor congruency effects," by C. Spence, F. Pavani and J. Driver, 2004, *Cognitive, Affective, & Behavioral Neuroscience*, 4 (2), 148-169. Copyright 2004 by Psychonomic Society, Inc.

SOAs of -30 ms (but not 100 ms) for the ASD group, indicating that they may, in fact, be *more* sensitive to the temporal constraints of visuo-tactile integration than the TD group. Nevertheless, there were no significant differences in the strength of the congruency effect between groups. Instead, the groups displayed a similar temporal profile of visuo–tactile integration. The lack of group differences cannot be explained by unisensory performance differences since the delay between the two tactile pulses was set at each individual's threshold level (the delay length at which judgments were correct 75% of the time). This is important since, if participants reach ceiling or floor level in tactile discrimination, the addition of the visual distractor will have little effect. Additionally, Autism Quotient (AQ) scores in the TD group were not significantly correlated with the strength of the congruency effect for any SOAs. However, the range of AQ scores may not have been sufficient for a potential correlation to be revealed, particularly as no participants met the cut-off score of 32, which is proposed to indicate levels of autistic traits that meet potential clinical diagnosis.

Poole et al's (2015) findings warrant further investigation since they appear to show the opposite pattern of performance to that found in children in Experiment Five. Moreover, clinical reports find that sensory sensitivities and sensory processing remain atypical in adults with ASD and, as detailed in Chapter One, it is proposed that these are due to atypical MSI, and possibly temporally extended sensory binding in particular. Leekam et al., (2006) administered the Diagnostic Interview for Social and Communication Disorders (DISCO) to 200 children and adults with ASD aged 32 months to 35 years, to elicit in-depth information about sensory abnormalities. Over 90% of participants reported sensory sensitivities and these were prevalent across age and IQ. Similarly, Minshew & Hobson (2008) found that high-functioning adults with ASD not only reported significantly more sensory sensitivities than TD adults, but they also made more errors on sensory-perceptual tests such as touch sensitivity and tactile form recognition. This corresponds with a wealth of anecdotal evidence documenting sensory abnormalities in adults with ASD, particularly in the tactile domain (Bemporad, 1979; Bogdashina, 2003;

Cesaroni & Garber, 1991). The current study thus employed the task used in Experiment Five with adults with ASD and an age- and IQ- matched TD control group to assess group differences in visuo-tactile temporal binding.

The results of Experiment Three (Section 3.9), demonstrate that, in typical development, sensitivity to the temporal constraints of visuo-tactile binding increases with age. Specifically, older children are more likely to notice a temporal delay between visual and tactile inputs than younger children. Interestingly, Hillock-Dunn and Wallace (2012) reported that developmental changes in the visuo-auditory temporal binding window (TBW) persist even into adolescence. Together theses findings indicate that TD adults may perform differently to TD children in the task employed in Experiment Five. Specifically, if TD adults are more sensitive to visuo-tactile temporal binding, then they may choose the synchronous hand not only in all the congruent conditions and the incongruent 180 ms and 300 ms conditions (as the chronological age-matched TD children do) but also in the incongruent 60 ms condition.

Due to the large number of reports documenting atypical sensory processing in adults with ASD, and the findings of atypical visuo-tactile-proprioceptive integration in this population reported by Paton et al., (2012) and Palmer et al., (2015), it was predicted that there would be significant group differences in task performance. Specifically, it was proposed that as in children with ASD, adults with the disorder should show reduced sensitivity to temporal properties of MSI. Thus, across congruent and incongruent conditions, the synchronous hand should not be consistently embodied at short delays (60ms). Again, as in children with ASD, at longer delays (180 ms and 300 ms), the synchronous hand may only be embodied in congruent conditions - when proprioception is consistent with visuo-tactile information - but not in incongruent conditions.

Table 6.1. Participant descriptives; p indicates the p-value of the independent samples t-test comparing the TD and ASD groups.

	TD	ASD	P
n	23	23	
Age	22.62 ± 5.89 (16.33-37.37)	23.23 ±5.55 (16.92-37.80)	.442
VIQ raw	92.91 ± 10.90 (77-113)	86.39 ± 21.77 (40-119)	.206
VIQ standardised	104.08 ± 13.71 (87-130)	98.39 ± 20.27 (64-131)	.270
PIQ raw	85.39 ± 11.95 (64-99)	83.83 ±15.11 (48-106)	.699
PIQ standardised	112.26 ±11.95 (90-127)	106.74 ±17.12 (61-132)	.211
FSIQ raw	178.30 ±13.65 (150-202)	170.22 ±30.60 (110-207)	.253
FSIQ standardised	108.78 ±7.89 (92-123)	103.74 ±16.73 (79-125)	.198
AQ	20.41 ±6.65 (11-33)	31.13 ±6.00 (22-45)	>. 001
ADOS	N/A	10.5 (5-19)	

6.3. Methods

6.3.1. Participants

Participants were 26 adults with ASD aged 16 to 36 years (four female) and 26 TD adults aged 16 to 40 years (17 female). Participants were recruited from local schools, colleges and autism support groups as well as via recruitment posters displayed in various locations around Nottingham and advertisements posted on reddit.com and callforparticipants.com.

All participants in the ASD group had received a previous diagnosis of autism, autism spectrum disorder or Asperger Syndrome by an independent clinician using the autism diagnostic observation scale (ADOS; Rutter et al., 2002) or the autism diagnostic interview (ADI-R; Rutter et al., 2005). To confirm ASD diagnosis, all adults in the ASD group completed Module Four of the ADOS-2, carried out with a trained examiner. None of the TD participants had a diagnosis of ASD and all participants had normal or corrected-to-normal vision. Participants completed practice trials to demonstrate: 1) an ability to keep their hand still and 2) comprehension of the task. One adult from the ASD group was excluded, as it was not clear that he understood the task requirements, as indicated by his performance in these practice trials.

I attempted to match groups on age and IQ, as measured by the short form of the Weschler Adult Intelligence Scale-Third Edition (WAIS-III; Wechsler, 1999). The vocabulary and similarities tests were used to measure verbal IQ and the block design and matrix reasoning tests were used to measure performance IQ, as recommended by Ringe, Saine, Lacritz, Hynan, & Cullum (2002). Verbal IQ (VIQ), performance IQ (PIQ) and full-scale IQ (FSIQ) scores (both raw and standardised) were significantly higher in the TD group compared to the ASD group at $p<.05$. A subset of participants matched on all IQ measures and age were thus used in the analysis ($n=23$ in each group). Participants in the ASD group had significantly higher AQ scores than the TD group ($p<.001$). All but one of the participants with ASD met the diagnosis of autism or autism spectrum disorder, as assessed by the ADOS-2. The remaining participant had received a previous diagnosis of ASD by a clinician and had a high autism quotient (AQ) score of 37, thus, he was included in the final analysis. Participant details for the final sample are shown in Table 6.1. All participants gave written informed consent prior to testing and ethical approval for the experiment was granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

6.3.2. Procedure

Participants were invited to take part in a number of experiments at the University, over a half-day session. All participants were tested in a quiet room and breaks were given every 30 minutes, or whenever they were needed. Participants completed the current MIRAGE task, which lasted approximately 15 minutes, followed by the MIRAGE task described in Section 6.3.2. Additionally, all participants completed the Autism Quotient (AQ; Baron-Cohen et al., 2001) and the short form of the WAIS-III (Wechsler, 1999). Participants in the ASD group also completed Module Four of the ADOS-2 (Rutter et al., 2012).

The MIRAGE task was identical to that used in Experiment Five. Participants placed their right hand onto the work surface of the MIRAGE and saw two virtual representations of their hand. A rectangular black bib was attached across the length of the MIRAGE, on the side that the participant was seated, to obscure the work surface from view. Participants wore a black adjustable sleeve, which covered their right wrist and forearm, ensuring that only the hand was visible when their arm was in the MIRAGE. Both groups first completed two practice trials, which were identical to experimental trials described below except that neither hand image showed a visual-tactile delay. These were included to ensure that participants were

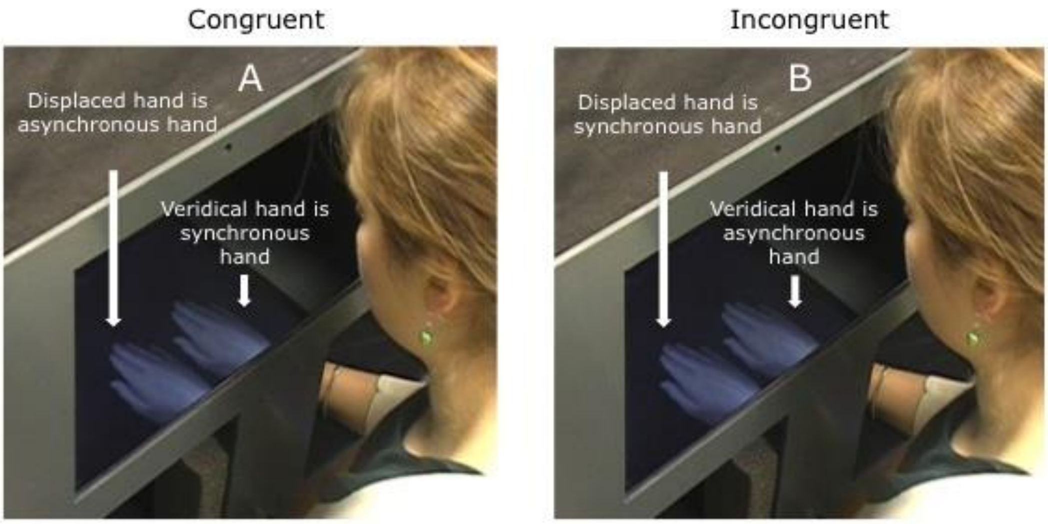


Figure 6.2. MIRAGE task.
The participants placed their right hand into the MIRAGE and saw two live video images of the hand. The veridical hand was in the same location as their actual hand; the displaced hand was immediately to the left or right of the veridical hand (position of the displaced hand was counterbalanced).
(A) In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300ms applied to it (asynchronous hand); the veridical hand did not (synchronous hand).
(B) In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300ms applied to it (asynchronous hand); the displaced hand did not (synchronous hand).
The arm is here uncovered for illustrative purposes, but it was covered in the experiment so that participants were unable to see the exact relationship between the limb and image.

comfortable with the set-up and understood the task requirements.

In the experimental trials, proprioceptive alignment and visuo-tactile synchrony were selectively manipulated to explore the extent to which these impact on body ownership. Proprioceptive alignment was manipulated by presenting one hand image (the veridical hand) in the same location as the participant’s actual hand while a duplicate hand image was displaced immediately to the left or right of this (displaced hand; see Figure 6.2). Since hand sizes varied between individuals, the displaced hand was located such that the two hands did not overlap and also that there was a visible <5mm gap between the hands. That is, the hands were immediately adjacent to each other.

The experimenter brushed the participant's right index finger with a paintbrush at 1Hz for 10 seconds while he/she saw the brushstrokes on both right hands. After brushing, a yellow shape appeared above one hand image and a different, red shape appeared above the other. The images were a circle or a square and their location, colour, and shape were counterbalanced for each trial. Participants were reminded to keep their hand still and asked to verbally name the shape they thought was above their real hand. After responses were given, vision of the hand was occluded whilst the experimenter placed the participant's hand at the starting point for the next trial.

On each trial, visuo-tactile synchrony was manipulated by applying a temporal delay of either 60, 180 or 300 ms to either the veridical or the displaced hand. Thus, the felt brushstrokes were synchronous with the visual brushstrokes on that hand (the synchronous hand) but asynchronous on the other hand. For each condition, therefore, either the veridical hand or the displaced hand was the synchronous hand, while the other hand had a temporal delay applied to it. As in Experiment Three, delay rates were calculated and monitored online and required no mechanical apparatus. The delay is only applied to one of the visual presentations of the hand on each trial. Therefore, even if the real brushstroke is not at a fixed frequency, the (seen) delayed brushstroke will always follow at the set time after.

In congruent conditions, visuo-tactile inputs were synchronous for the veridical hand (congruent proprioceptive and visuo-tactile input) while the visual touch on the displaced hand was delayed. In incongruent conditions, the visual touch on the veridical hand was delayed; therefore, proprioception and information from visuo-tactile synchrony were incongruent. There were six conditions in total (congruent 60 ms, 180 ms and 300 ms delay and incongruent 60 ms, 180 ms and 300 ms delay) and two trials per condition. For each condition, the displaced hand was presented once to the left of the veridical hand and once to the right of it. Trials and conditions were presented in a randomised order.

6.4. Results

6.4.1. Data Analysis

Data analysis was identical to the analysis carried out for Experiment Five (see Section 5.4.1). Chi-square analyses were conducted for each group for each condition to assess whether the number of participants choosing the synchronous hand was more than expected if the group was performing at chance level; i.e. not performing systematically (Table 6.2). Bonferroni corrections were used such that all analyses comparing results against chance are reported at a .0004 level of significance. Chi-square analyses were also conducted to assess whether there were significant group differences in the frequency that participants chose the synchronous hand (Table 6.3). For comparison purposes, Figure 6.2 panel A shows what the frequency data would look like if a group's performance was at chance level. Figure 6.2 panels B to G display the frequency that participants chose the synchronous hand in each group in each condition. These show that across groups the synchronous hand was chosen more in congruent, compared to incongruent, conditions and at longer, compared to the shorter delay lengths.

Table 6.2. Chi-square analyses comparing the frequency of individuals choosing the synchronous hand against chance level in each group. * Indicates performance that is significantly different to chance at .004 level of significance.

	Congruent 60ms	Congruent 180ms	Congruent 300ms	Incongruent 60ms	Incongruent 180ms	Incongruent 300ms
ASD	$\chi^2(2)=8.73$ p=.013	$\chi^2(2)=29.61$, p<.001*	$\chi^2(2)=35.52$, p<.001*	$\chi^2(2)=1.43$, p=0.49	$\chi^2(2)=13.61$ p=.001*	$\chi^2(2)=24.83$, p<.001*
TD	$\chi^2(2)=30.39$ p<.001*	$\chi^2(2)=54.04$ p<.001*	$\chi^2(2)=54.04$ p<.001*	$\chi^2(2)=4.91$ p=.086	$\chi^2(2)=24.39$ p<.001*	$\chi^2(2)=47.09$ p<.001*

6.4.2. Results

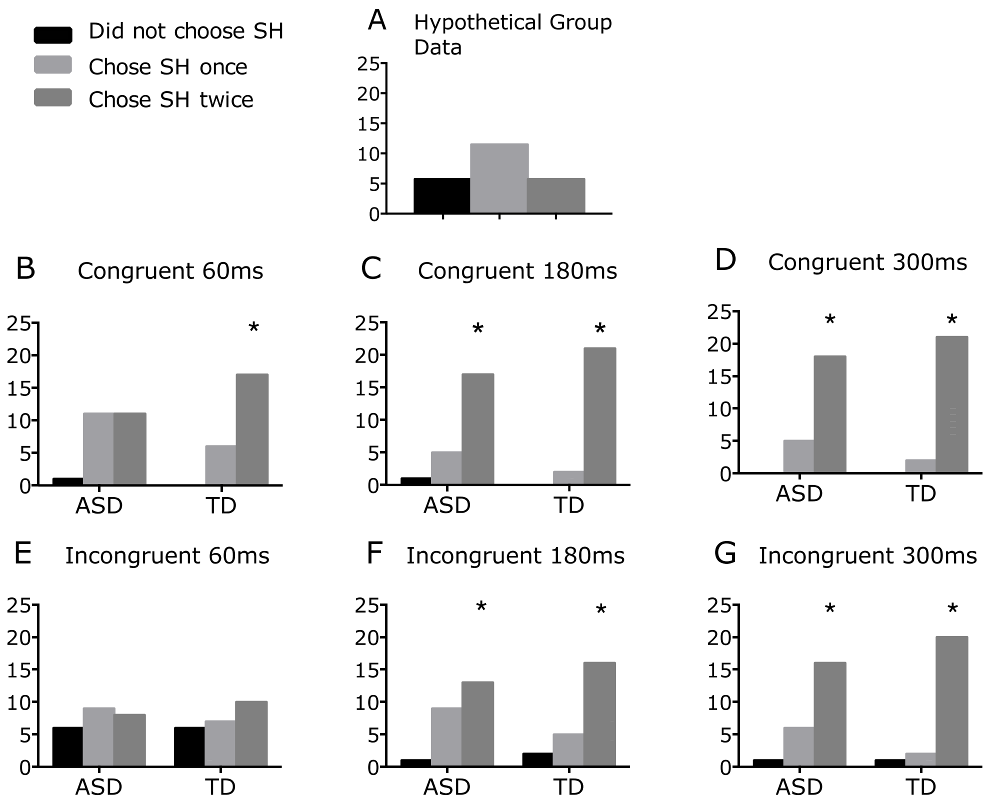


Figure 6.3. Chi-square results.
Y-axis = number of participants.
Panel A: Hypothetical data showing a group choosing the synchronous hand (SH) at chance level.
Panel B: Chi-square analyses comparing the frequency of individuals in the autism spectrum disorder (ASD) and typically developing (TD) control groups choosing the synchronous hand (SH) against chance level. Asterisks indicate performance that is significantly different to chance at .004 level of significance.

Chi-square analyses against chance (Table 6.2 and Figure 6.3) revealed that the TD group chose the synchronous hand significantly above chance in all except the incongruent 60 ms condition while the ASD group did so in all accept the congruent 60 ms and incongruent 60 ms conditions. Between groups chi-square analyses that compared the frequency for choosing the synchronous hand found no significant group differences in any conditions (see Table 6.3).

6.5. Discussion

The current experiment investigated whether visuo-tactile binding is temporally extended in adults with ASD relative to TD controls. Participants observed synchronous visuo-tactile brushstrokes on one virtual hand image and asynchronous brushstrokes on a second, identical hand image and were asked which hand was theirs. Though the findings suggest that there may be subtle differences in visuo-tactile temporal binding between TD adults and those with ASD,

Table 6.3. Between-groups chi-square analyses comparing the number of participants choosing the synchronous hand. * Indicates significant group difference at .025 level of significance.

	Congruent 60ms	Congruent 180ms	Congruent 300ms	Incongruent 60ms	Incongruent 180ms	Incongruent 300ms
TD vs. ASD	$\chi^2(2)$=3.93 p=.14	$\chi^2(2)$=4.85 p=.088	$\chi^2(2)$=.16 p=.25	χ^2 2)=.046 p=.98	$\chi^2(2)$=2.65 p=.27	$\chi^2(2)$=1.62 p=.44

no between-group differences were found in any condition, which could indicate that temporally extended visuo-tactile integration seen in children with ASD represents a developmental delay rather than a (permanent) deficit.

Both ASD and TD groups were guided by visuo-tactile temporal synchrony, even when this was incongruent with proprioceptive information. This supports previous findings from hand ownership tasks in which visuo-tactile synchrony overrides proprioception in TD adults (e.g. Botvink & Cohen, 1998; Newport et al., 2010; Newport & Preston, 2011). However, when the delay applied to the asynchronous hand was short (60ms) and proprioceptive inputs were incongruent with visuo-tactile information, neither information source dominated, i.e. participants did not strongly embody the synchronous hand or the veridical hand. This is consistent with the findings from Experiment Five (see section 5.4.2) and the broader embodiment literature, which shows that the likelihood of embodying a fake hand decreases as proprioceptive discrepancy between the real and fake hand increases (Lloyd, 2007; Preston, 2013; Preston & Newport, 2014). The results also cohere with Paton et al's (2012) RHI study, in which the illusion was reported to be stronger when goggles were worn to reduce proprioceptive conflict between the real and fake hand.

When comparing the current findings (Figure 6.2) with those in Experiment Five (see Figure 5.3 in Section 5.4.2), it is clear that, across all conditions, the adults with ASD chose the synchronous hand more consistently than the children with ASD. Moreover, the synchronous hand is chosen significantly more than chance level in four of the six conditions for the adult ASD group but in only two of the six conditions for the child ASD group. Although the effect of age was not directly tested in either study, this comparison does suggest that, as in typical development, sensitivity towards visuo-tactile synchrony is stronger in adults with ASD compared to children.

In congruent conditions, when the veridical hand is also the synchronous hand, the TD control group consistently embody this hand image across all delay lengths. However, the ASD group only do this at medium (180ms) and long (300ms) delays; at short delays (60ms) they are at chance level. Thus, even with the additional aid of congruent proprioceptive information, the ASD group require a longer delay between the visual and tactile inputs applied to the asynchronous hand before they can clearly distinguish the delay and consequently embody the synchronous hand. This provides further evidence against the idea that there is a fundamental over-reliance on proprioception in ASD. If this was the case, then the veridical hand should be consistently chosen across all conditions but, as in Experiment Five, this was not seen. Moreover, this suggests that there may still be subtle differences in sensitivity to visuo-tactile temporal binding in adults with ASD. Nonetheless, the lack of between-group differences indicates that temporally extended binding in children with ASD may represent a developmental delay that normalises by adulthood. This interpretation is discussed in more detail in the General Discussion.

It is possible, however, that participants in the current study were detecting visuo-tactile synchrony without actually embodying the synchronous hand. Specifically, they may have been able to identify which hand image had visual brushstrokes that occurred at the same time as the felt brushstrokes, without the subjective experience of ownership over the synchronous hand. This is important to assess in order to draw conclusions regarding the potential cascading effects of temporally extended sensory integration, since it has been argued that social impairments in ASD, such as problems with empathy, imitation and inferring others mental states, could be due to atypical MSI underlying body representation (Bahrick & Todd, 2012). Thus, Experiment Eight used the procedure employed in Experiment Six to assess whether temporally extended visuo-tactile integration is seen in adults with ASD in a task assessing ownership over a virtual hand.

Experiment Eight: Motor embodiment in adults with autism

6.6. Abstract

The results of Experiments Five and Six indicate temporally extended visuo-tactile binding in children with ASD yet Experiment Seven found no evidence of this in adults with the disorder. However, it is important to assess whether temporal binding underlying body ownership specifically is atypical in adults with ASD. The task in Experiment Six was conducted with adults with ASD and a TD control group. Participants placed their right hand into the MIRAGE and saw two, identical live video images of the hand – one in the proprioceptively correct location (the veridical hand) and one displaced to the left or right (displaced hand). Brushstrokes were applied to the hand and a 60, 180 or 300 ms temporal delay was applied to the displaced hand image (congruent conditions) or the veridical hand image (incongruent conditions). Thus only one hand image had temporally synchronous visuo-tactile inputs. After brushing, both hand images disappeared from view and children pointed at a target presented equidistant between the previously seen hand images, with pointing accuracy indicative of hand ownership. No between-group performance differences were found; both groups took ownership over the synchronous, veridical hand in congruent conditions, as indicated by subsequent reaching errors. In incongruent conditions, pointing accuracy was significantly reduced, indicating the influence of incongruent visuo-tactile temporal synchrony on proprioceptive information. This pattern or results was seen at all delay lengths; suggesting that, by adulthood, sensitivity to visuo-tactile temporal synchrony underlying body representation is similar across TD and ASD populations. Alternative explanations for the results are discussed.

6.7. Introduction

Results from Experiments Five and Six point to temporally extended visuo-tactile binding in children with ASD relative to chronological age-matched TD children. Specifically, children with ASD required a longer temporal delay between visual and tactile inputs before they could distinguish synchronous from asynchronous sensory information. However, Experiment Seven did not find a significant group difference in this ability when adults with ASD were compared to TD adults. This may suggest that, as in typical development, sensitivity to visuo-tactile temporal delays increases with age in ASD, yet the rate of this development may be delayed in those with the disorder, compared to TD individuals.

Nonetheless, as detailed in Chapter Five (Section 5.6), in the tasks used in Experiments Five and Seven, participants were asked which of two virtual images of their right hand was their own. Therefore, it is possible that they may have detected the hand with synchronous visual and tactile brushstrokes (the synchronous hand) without necessarily taking ownership over it. As discussed in Section 1.3.1, body ownership underpins social, cognitive and behavioural processes that are impaired in ASD. Thus, it is important to establish if and how MSI underlying body ownership specifically may be impaired, as this can increase our understanding of the links between atypical low-level processing and higher-level functioning. Therefore, the current study was conducted to assess whether atypical temporal binding is seen in adults with ASD in a task requiring ownership over a virtual hand, by measuring the effect of visuo-tactile synchrony on subsequent hand movements.

The task in the current experiment was identical to that used in Experiment Six. In brief, participants placed their right hand into the MIRAGE and saw two hand images, one in the proprioceptively correct location (the veridical hand) and one displaced to the left or right (displaced hand). The hand was brushed for 10 seconds and the participants saw the brushstrokes on both hand images (see Figure 6.3). A temporal delay of 60, 180 or 300 ms was applied to the displaced hand in congruent conditions (the veridical hand was the synchronous hand) and to the veridical hand in incongruent conditions (the displaced hand was the synchronous hand). After brushing, vision of the virtual hands was occluded and participants pointed to a target presented equidistant between the two previously presented hand images. The distance between the starting position and the end position of the participant's finger following target presentation gives an indicator of perceived hand location and ownership (Jones et al., 2010).

Based on the findings from Experiment Six and studies employing similar MIRAGE tasks (e.g. Newport et al., 2010; Newport & Preston, 2011; Preston & Newport, 2011) it was firstly predicted that there would be an effect of congruency such that accuracy in pointing at the target would be higher in congruent versus incongruent conditions across groups and delays. As in Experiment Five, in congruent conditions, the TD group should integrate the felt brushstrokes with the visually synchronous brushstrokes and congruent proprioceptive information. They should, therefore, take ownership over the synchronous, veridical hand and thus point accurately towards the target. In incongruent conditions (when the displaced hand is the synchronous hand), TD participants' reaches should be influenced by incongruent visuo-tactile information, leading to reduced accuracy relative to congruent conditions. This is based on the findings that multisensory information, in this case, synchronous visuo-tactile inputs, are weighted more strongly than incongruent unimodal information i.e. proprioception (Botvinick & Cohen, 1998; Newport et al., 2010; Ehrsson, 1998) since multimodal inputs are usually a more reliable information source (Landy et al., 1995).

Despite a lack of between-group differences in Experiment Seven, it is not known if performance across groups will be similar in a task requiring body ownership since studies suggest that visuo-tactile-temporal binding underlying body ownership is atypical in adults with ASD (Palmer et al., 2015; Paton et al, 2012). Additionally, sensory sensitivities and sensory processing differences prevail in adults with ASD, as described in Section 6.2 (Bogdashina, 2003; Leekam et al., 2007; Minshew & Hobson, 2008). Since these are proposed to be due to atypical MSI (Bahrick & Todd, 2012), the ASD group may not perform in the same way as the TD group on this task. Moreover, Experiment Six found evidence for temporally extended visuo-tactile binding in children with ASD using the same task. Thus, it was predicted that significant group differences in performance would be found. Specifically, in incongruent conditions at shorter delay lengths (e.g. 60ms) the adults with ASD may not be able to clearly detect and distinguish the synchronous hand from the asynchronous hand. Thus, accuracy should be reduced in incongruent versus congruent conditions for both groups in conditions with longer delay lengths but this should only be seen in the TD group in short delay conditions.

6.8. Method

6.8.1. Participants

Participants were 29 adults with ASD aged 16 to 36 years (four female) and 26 TD adults aged 16 to 40 years (17 female). These participants also took part in Experiment Seven (see Section 6.3.1 for details on participant recruitment and inclusion/exclusion criteria).

Due to a technical error, data was missing for one participant in the TD control group and nine in the ASD group. Additionally, one participant in the ASD group was excluded, as I was not confident that he understood the task requirements, as indicated by his performance in practice trials. For the remaining participants, I attempted to match groups on age and IQ as measured by the short form of the Wechsler Adult Intelligence Scale Third-Edition (WAIS-III; Wechsler, 1999) - vocabulary and similarities for verbal IQ; block design and matrix reasoning for

performance IQ (Ringe et al., 2002). Groups were matched on performance IQ (PIQ) raw score, however, verbal IQ (VIQ) and full-scale IQ (FSIQ) scores (both raw and standardised) and standardised performance scores were significantly higher in the TD group compared to the ASD group, at p<.05. A subset of participants matched on all IQ measures and age were thus used in the analysis (n=17 in the ASD group; 3 females and n=16 in the TD group; 12 females). Participants in the ASD group had significantly higher AQ scores than the TD group (p=.024) and all participants with ASD met the diagnosis of autism or autism spectrum disorder, as assessed with Module Four of the ADOS. Participant details of the final sample are shown in Table 6.4. All participants gave written informed consent prior to testing and ethical approval for the experiment was
granted by the University of Nottingham, School of Psychology Ethics Committee and was conducted in accordance with the ethical standards of the Declaration of

Table 6.4. Participant descriptives; p indicates the p-value of the independent samples t-test comparing the TD and ASD groups.

	TD	ASD	p
n	16	17	
Age in years	22.52 ± 6.60. (16.33-37.37)	23.22 ±6.46 (16.48-37.80)	.760
VIQ raw	89.50 ± 9.50 (74-110)	79.76 ± 24.022 (40-119)	.141
VIQ standardised	100.69 ± 13.00 (88-130)	92.41 ± 20.48 (61-131)	.179
PIQ raw	83.75 ± 12.32 (63-97)	76.12 ±22.05 (27-106)	.233
PIQ standardised	110.06 ±12.46 (90-126)	99.35 ±21.38 (61-132)	.091
FSIQ raw	173.25 ±12.20 (137-187)	15588 ±40.27 (76-203)	.108
FSIQ standardised	105.50 ±6.55 (87-114)	96.94 ±19.77 (65-124)	.110
AQ	21.20 ±7.96 (10-35)	27.47 ±6.99 (10-41)	.024*
ADOS	N/A	10.6 (5-19)	

Helsinki.

6.8.2. Procedure

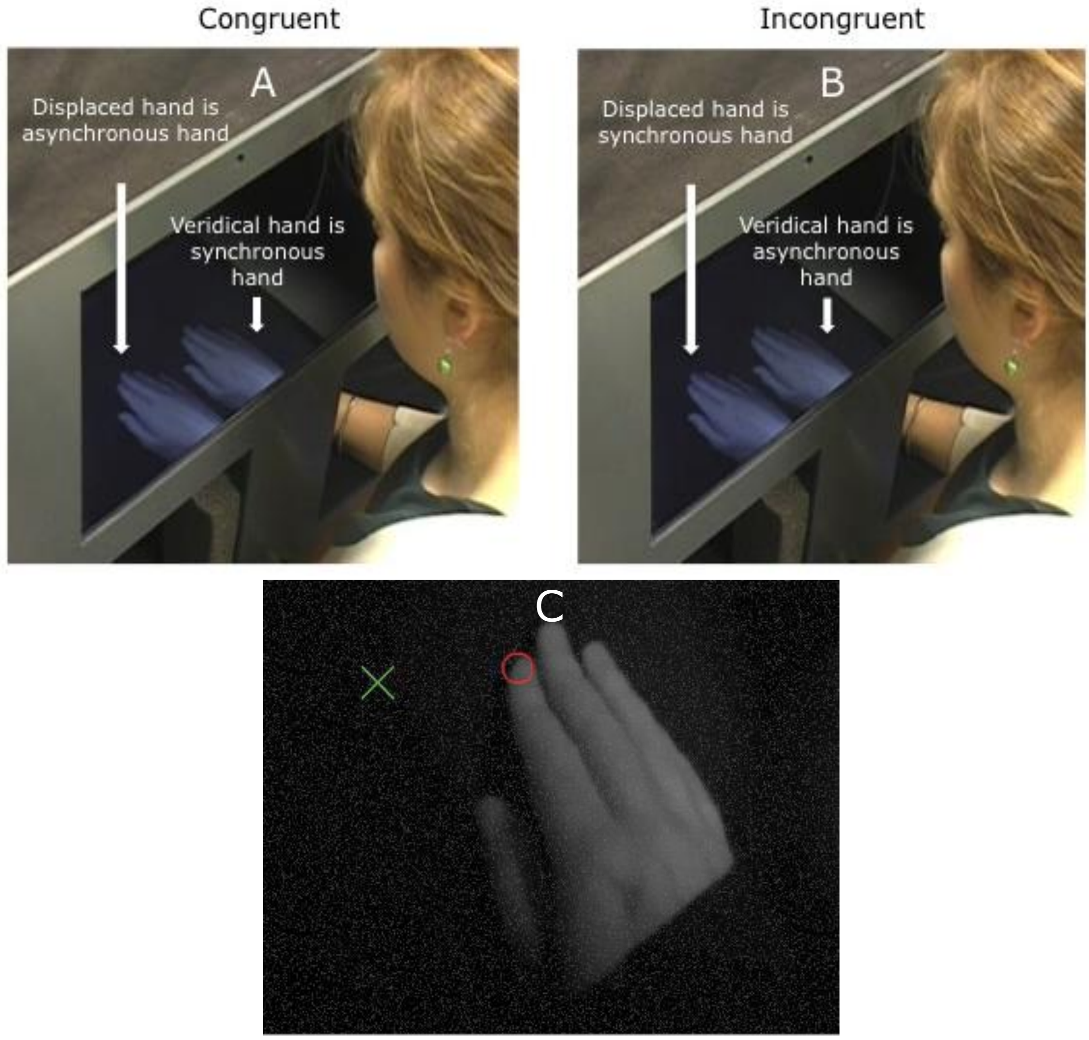


Figure 6.4. MIRAGE Task.
Participants placed their right hand into the MIRAGE and saw two live video images of the hand. The veridical hand was in the same location as the actual hand; the displaced hand was to the left or right of the veridical hand. In the experiment the arm was covered so that participants were unable to see the exact relationship between the limb and the images.
(A) In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300ms applied to it; the veridical hand did not (i.e. the veridical hand was the synchronous hand).
(B) In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300ms applied to it; the displaced hand did not (i.e. the displaced hand was the synchronous hand).
(C) After 10 seconds of brushing, the screen went blank and participants pointed at a target located between the previously presented hand images. Both the hand and target are shown here but in the experiment vision of the hand was occluded when the target was presented.

The participants in Experiment Seven also completed the current experiment as part of a half–day testing session conducted at the University, involving several different studies. All participants were tested in a quiet room and breaks were given every 30 minutes, or whenever they were needed. Participants completed the MIRAGE task described in Section 5.3.2 followed by the current MIRAGE task, which lasted approximately 15 minutes. Additionally, all participants completed the Autism Quotient (AQ; Baron-Cohen et al., 2001) and the short form of the WAIS-III (Wechsler, 1999). Participants in the ASD group also completed Module Four of the ADOS-2 (Rutter et al., 2012).

For the MIRAGE task, the initial procedure was identical to that used in Experiment Six (see Section 5.8.2). Adults placed their right hand into the MIRAGE and saw two virtual representations of their hand: the veridical hand was in the same location as the participant's actual hand while the displaced hand was immediately to the left or right of this (see Figure 6.4). Participants first completed practice trials, which were identical to experimental trials described below except that neither hand image showed a visual-tactile delay. These were included to ensure that participants were comfortable with the set-up and understood the task requirements.

The participant's right index finger was brushed at 1Hz for 10 seconds while he/she saw the brushstrokes on both right hands. In congruent conditions the displaced hand had a temporal delay of either 60, 180 or 300 ms applied to it; the veridical hand did not (i.e. the veridical hand was the synchronous hand). In incongruent conditions the veridical hand had a temporal delay of either 60, 180 or 300 ms applied to it; the displaced hand did not (i.e. the displaced hand was the synchronous hand). However, unlike the task used in Experiment Seven, after brushing, both hand images disappeared from view and a target (a green cross) was presented on the screen for five seconds. This appeared halfway between the two previously presented hand images, aligned horizontally with the tip of the index fingers (see Figure 6.4). For each condition, the displaced hand was presented once to the left of the veridical hand and once to the right of it (counterbalanced across conditions). The target was thus presented to the left of the participant's actual index finger in half the conditions and to the right in the remaining conditions. Participants were asked to point at the green cross, quickly and accurately, with their right index finger and to hold this position until the target disappeared (five-second duration). Vision of the hand remained occluded whilst the experimenter placed the participant's hand at the starting point for the next trial. The participant's hand movements were recorded and, as in Experiment Five, there were two trials for each of the six conditions; congruent 60 ms, 180 ms and 300 ms delay and incongruent 60 ms, 180 ms and 300 ms delay. These were presented in a randomised order.

6.9. Results

6.9.1. Data Analysis

Data was analysed in the same way as the data in Experiment Six. There were two trials per condition. For each trial, participant's hand movements were recorded during the five-second duration that the target appeared on the screen. For each video clip, the x-axis coordinates of three locations were recorded in pixels (1 pixel =0.75mm): 1) the tip of the index finger at the start of the video (baseline measurement), 2) the tip of the index finger at the end of the video (pointing measurement) and 3) the centre of the target. These values were entered into a Labview programme to calculate the distance and direction of reaches for each trial. For each condition, the target appeared once to the left of the veridical hand and once to the right of it. However, to facilitate analysis, errors were calculated as negative if participants pointed away from the target, regardless of whether the target was to the left or right of the veridical hand. A score of 100 equates to pointing exactly on the target, positive scores represent pointing in the direction of the target and negative scores represent pointing away from the target. A score of zero equates to pointing that is in line with the baseline position along the x-axis (see Figure 6.5). There was no missing data in the final sample.

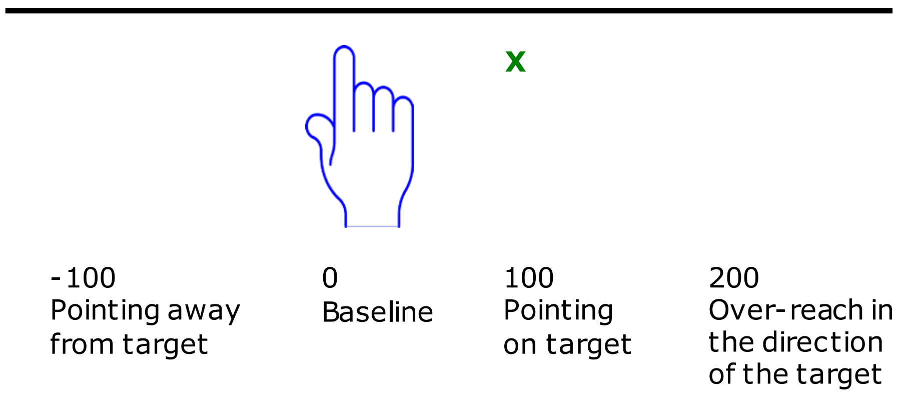


Figure 6.5. Reach values.
A score of 100 equates to pointing exactly on the target. Scores above 100 indicate over-reaches i.e. pointing in the direction of the target but beyond it. Scores below zero indicate pointing away from the target.

To assess accuracy, Bonferroni corrected ($p<.004$) one-sampled t-tests against 100 were conducted for each group, at each condition. To assess the extent that incongruent visuo-tactile inputs affected embodiment, scores in congruent conditions were subtracted from scores in incongruent conditions, for each group at each delay length. These congruency scores were entered into a repeated-measured ANOVA with group (ASD versus TD) as the between-subjects factor and delay (60 ms versus 180 ms versus 300 ms) as the within-subjects factor. Assumptions for normality, homogeneity and sphericity were met unless otherwise stated. All analyses were re-run without outliers as determined by the outlier labelling rule using 2.2 as a multiplier (Hoaglin & Iglewicz, 1987). The pattern of results remained the same thus the results reported below include outliers.

6.9.2. Results

Mean reach scores for each group in each condition are displayed in Figure 6.6. One-sampled t-tests (Bonferroni-corrected; $p<.004$) showed that scores were significantly lower than 100 (signifying reduced accuracy) for the TD group in the incongruent 60 ms ($t(15)=4.76$, $p<.001$), 180 ms ($t(15)=6.53$, $p<.001$) and 300

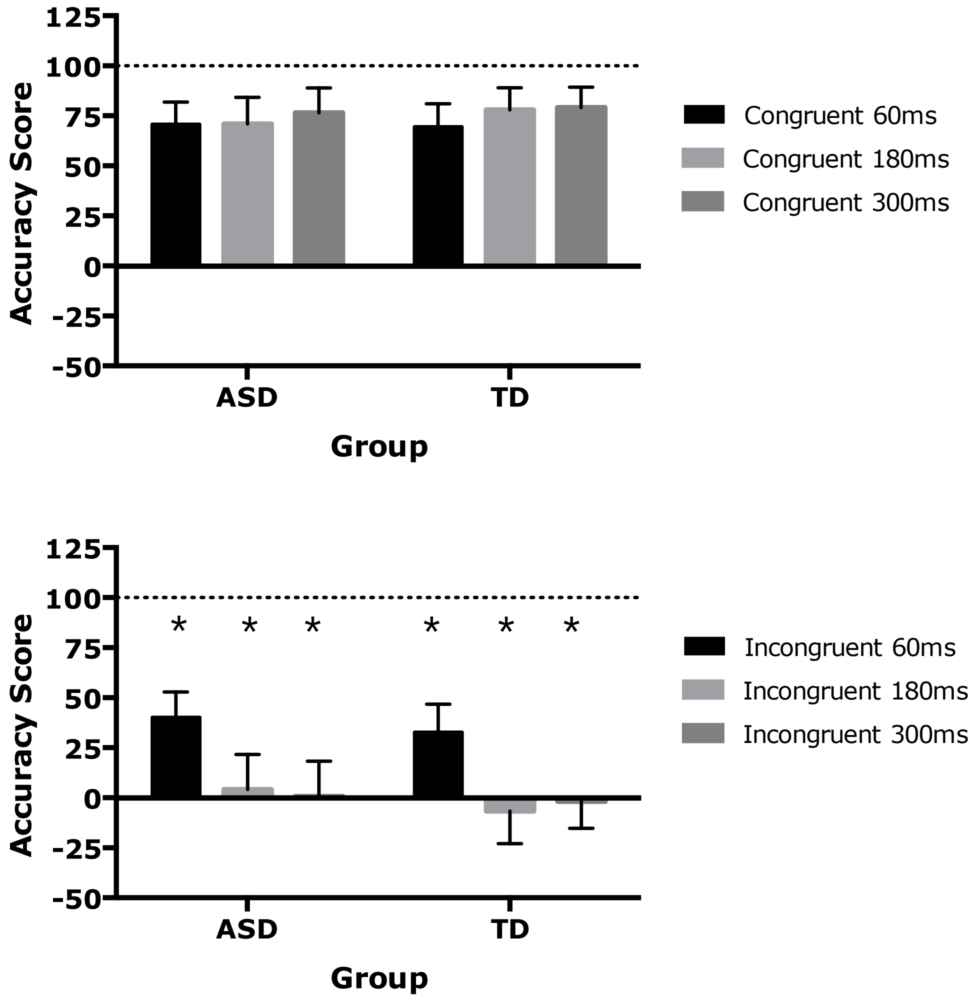


Figure 6.6. Mean reach scores for the autism spectrum disorder (ASD) group and typically developing (TD) control group. Error bars show standard error of the mean.
A score of 100 equates to pointing directly on the target (dotted line).
* Indicates scores that are significantly different from 100 at $p<.004$.

ms ($t(15)=7.61$, $p<.001$) conditions. For the ASD group, scores were also significantly lower than 100 in the incongruent 60 ms ($t(16)=4.72$, $p<.001$), 180 ms ($t(16)=5.49$, $p<.001$) and 300 ms conditions ($t(16)=5.64$, $p<.001$). No other results were significantly different from 100.

Congruency scores are shown in Figure 6.7. The repeated-measures ANOVA found a main effect of delay ($F(1.67, 51.9)=8.52$, $p=.001$). The assumption of sphericity was violated for this effect, as specified by Mauchly's test ($X^2(2)=.91$, $p=.034$), thus, degrees of freedom are reported using Greenhouse-Geisser estimates of sphericity. Pairwise comparisons (Bonferroni corrected) revealed no significant difference between the 180 ms and 300 ms congruency scores ($p=1$) but congruency scores were significantly lower at 60 ms delays compared to 180 ms ($p=.013$) and 300 ms delays ($p=.006$). There was no main effect of group or group by delay interaction.

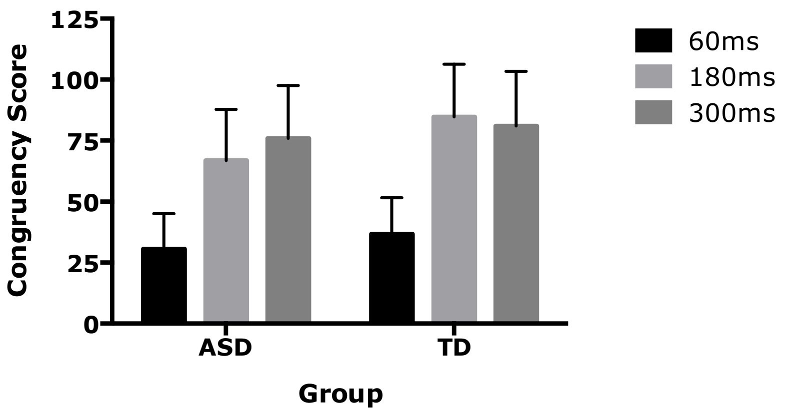


Figure 6.7. Congruency scores for the autism spectrum disorder (ASD) group and typically developing (TD) control group. Error bars represent standard error of the mean.

6.10. Discussion

The current experiment was designed to investigate whether MSI underlying body ownership is different in adults with ASD relative to TD controls and, if so, whether this is due to temporally extended visuo-tactile binding. Participants pointed to a target after presentation of synchronous visuo-tactile brushstrokes on one virtual hand image and asynchronous brushstrokes on a second, simultaneously presented, hand image. No significant performance differences between adults with ASD and an age- and IQ- matched TD control group were found (see Figure 6.6), which could suggest that the extended visuo-tactile temporal binding seen in children with ASD represents a developmental delay that normalises by adulthood.

In congruent conditions, participants in both groups consistently pointed in the direction of the target indicating that they had taken ownership over the synchronous, veridical hand. Performance in these conditions is similar to TD adults' performance in studies using comparable tasks (e.g. Newport & Preston, 2011) and indicates that the participants understood and were able to do the task. In incongruent conditions accuracy was reduced in both groups such that reach scores were significantly lower than 100 (which equates to pointing directly at the target) at all delay lengths. This indicates that participants were detecting and taking ownership over the synchronous hand in all conditions, even when it was not in the proprioceptively correct location. Importantly, this result was seen when the delay applied to the asynchronous hand was as small as 60ms. This performance is similar to that of the chronological-age-matched children in Experiment Six but is in contrast to children with ASD and younger TD children, whose reach scores were only significantly lower than 100 at medium (180ms) and long (300ms) delays.

To directly assess group differences, a repeated-measures ANOVA was run on congruency scores (i.e. the score in the congruent condition score minus the score in the incongruent condition, for each delay length). No between-group differences were found, however, across groups, scores were significantly lower in 60 ms compared to 180 ms and 300 ms conditions. This indicates that participants take ownership over the synchronous hand to a greater extent when the delay applied to the asynchronous hand is longer and, thus, the synchronous hand is easier to detect. In line with the previous experiments, no evidence was found for a fundamental over-reliance on proprioception. Accuracy was reduced when visuo-tactile synchrony and proprioception was incongruent, which would not be expected if the ASD group took ownership over the veridical hand across all conditions, as predicted by proprioceptive over-reliance. Instead, both ASD and TD groups appear to detect and distinguish synchronous from asynchronous visuo-tactile inputs, such that temporal synchrony influences subsequent reaching movements, even when the delay between asynchronous inputs is small (60ms).

Overall these results correspond with findings from Experiment Five and Seven, in which performance by children with ASD, but not adults, differs from age-matched TD participants. Together the findings from Experiment Six and the current study could indicate that temporally extended visuo-tactile binding underlying hand ownership in children with ASD represents a developmental delay that normalises by adulthood.

Alternatively, temporally extended sensory binding may continue into adulthood but the current sample may be unrepresentative of the ASD population. In Chapter One, I introduced the idea that atypical MSI, and temporally extended sensory binding, may underlie sensory sensitivities in ASD. Thus, it is possible that extended visuo-tactile temporal binding may only be seen clearly in adults with ASD if they have frequent and/or severe sensory sensitivities and this sample may have had uncommonly few of these. Indeed, only one of the participants with ASD showed evidence of abnormal sensory behaviour during the ADOS (a clinical assessment of ASD, administered prior to testing). However, this is not designed to be a reliable indicator of sensory atypicalities in general since these may only be present in certain contexts, for example, noisy environments. Nevertheless, a future study could assess this explanation by measuring sensory sensitivities using a validated questionnaire such as the Adult/Adolescent Sensory Profile (Brown, Tollefson, Dunn, Cromwell, & Filion, 2001) and assessing the relationship between these and performance on the MIRAGE task. However, sensory sensitivities are estimated to be present in over 90% of individuals with ASD (Leekam et al., 2007; Talay-Ongan & Wood, 2000), thus, it seems unlikely that the current sample does not experience these, at least to some extent. Instead, as discussed in Chapter Seven, I propose that sensory temporal binding may have normalised by adulthood but the consequences of this developmental delay may continue to have significant effects on social and sensory symptoms of ASD throughout the lifespan.

Additionally, the children with ASD in Experiment Six had, on average, greater cognitive impairments than the adults with ASD in the present study. It is possible that this is contributing to apparent age differences in temporally extended visuo-tactile binding. However, it is important to note that cognitive delay was still present in some of the adults in the current study, albeit to a lesser extent than the children in Experiment Six. Moreover, cognitive impairments do not necessarily cause atypical MSI. Instead, it has been suggested that improvements in top-down attentional mechanisms in individuals with ASD may be underlying improvements in multisensory temporal processing (Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). Therefore, temporally extended visuo-tactile processing may continue throughout the lifespan in low-functioning adults with ASD, due to a lack of improvements in attentional control. Thus, it is possible that increased sensitivity to the temporal constraints of MSI has a delayed onset and/or a slower rate of development, in *all* children with ASD, yet higher functioning individuals may 'catch up' with their peers sooner than those who are more cognitively delayed. In order to fully assess this claim, a future longitudinal study should be conducted, which can track changes in visuo-tactile temporal binding, cognitive ability and ASD characteristics from childhood through to adulthood.

6.11. General Discussion of Experiments Seven and Eight

Together the findings from Experiment Seven and Eight indicate that adults with ASD and TD adults show similar degrees of sensitivity to the temporal properties of visuo-tactile integration underlying body representation. This corresponds with findings from Poole et al., (2015), which showed that adults with ASD and an age-and IQ-matched TD control group had a similar temporal profile of visuo–tactile integration. This indicates that visuo-tactile temporal integration is similar not just in low-level tasks (e.g. detecting tactile pulses) but also tasks requiring higher-level processes known to be impaired in ASD, namely a sense of body ownership.

These findings are in contrast to those reported by Paton et al., (2012) and Palmer et al., (2015), which appeared to show reduced visuo-tactile-proprioceptive integration in adults with ASD. However, these studies employed the RHI and, as discussed in Chapter One, there are inherent limitations with this design. Specifically, it requires sustained attention to the fake hand over 3-minute blocks yet attention problems are common in ASD (Ames et al., 2010). Additionally, the classic RHI requires an individual to overcome the discrepancies in physical characteristics between the fake and real hand (i.e. texture, shape), which impact on the extent to which the rubber hand is embodied (Tsarkis and Haggard, 2005). Such differences may be more salient for individuals with ASD since detail-focused processing (Baron-Cohen et al., 2009; Happé and Frith, 2006) and imagination deficits (American Psychological Association, 2013) are common in ASD and may be underlying reduced ownership over the rubber hand. The MIRAGE tasks reported in this chapter avoided these shortcomings and found no differences between ASD and TD populations in MSI underlying hand ownership. However, as discussed in more detail in Chapter Seven, even if visuo-tactile temporal binding has normalised by adulthood in those with ASD, the effects of atypical binding in early childhood could continue to impact upon social, cognitive and behavioural functioning throughout the lifespan.

Chapter Seven: General Discussion

7.1. Overview of Research Background

This thesis had two main objectives. Firstly, I aimed to investigate the typical development of visual, tactile and proprioceptive integration underlying body representation. Adults integrate these sources in an optimal fashion, yet there is little research on how this ability develops in children. Moreover, findings across developmental studies are inconsistent, which could be due to differences in task designs and the ages of the children taking part. A greater understanding of how this ability matures in typically developing (TD) children can help us to discern how, and why, this development may differ in clinical populations. The second aim of this thesis was to investigate visuo-tactile-proprioceptive integration in individuals with autism spectrum disorders (ASD). A growing body of research indicates that multisensory integration (MSI) is atypical in ASD, yet the majority of this work focuses on visuo-auditory integration. It is important to examine visuo-tactile-proprioceptive integration, however, since this underpins body representation and the subject sense of self (Nava et al., 2014; Schütz-Bosbach et al., 2006). These, in turn, are necessary for social processes such as empathy and imitation (Schutz-Bosbach et al., 2006), which are impaired in ASD (American Psychological Association, 2013). Furthermore, it is estimated that over 90% of individuals with the disorder have sensory sensitivities, with tactile sensitivities being the most common (Tomchek & Dunn, 2007). It has been suggested that atypical MSI may be underlying both social and sensory differences in ASD, providing an explanatory mechanism that could account for both low-level and high-level components of the ASD behavioural profile (Bahrick & Todd, 2012). Importantly, understanding more about the processes underlying typical and atypical sensory integration could inform the design of effective interventions for individuals with ASD. This thesis focused specifically on examining the evidence for two prominent theories of atypical visuo-tactile-proprioceptive integration in ASD: 1) a fundamental over-reliance on proprioception and 2) temporally extended visuo-tactile binding. I will now summarise my experimental findings and examine how they correspond with, and contribute to, the existing literature.

7.2. Visuo-proprioceptive and visuo-tactile integration in typical development

Experiments One, Two and Three investigated visuo-proprioceptive and visuo-tactile integration underlying body representation in TD children. Research demonstrates that adults weight sensory inputs depending on their context-dependent reliability, in order to reduce the variance in the overall estimate (Ernst & Banks, 2004). When judging an object's size, for example, estimates derived from each sense are combined and averaged to create a coherent percept. Sensory estimates with less variance (or noise) are given greater weighting since they are deemed as more reliable (Landy et al., 1995). However, it is not clear when TD children are able to optimally integrate inputs in this way.

Experiment One used a MIRAGE multisensory mediated reality device (Newport et al., 2010) to investigate how the relative weightings of visual and proprioceptive inputs underlying hand localisation change over childhood. The task consisted of two control conditions and one experimental condition in which 4 to 11-year-olds were asked to estimate the location of their passive right index finger. In the first control condition, congruent visual and proprioceptive information regarding limb location were available and all children were highly accurate at locating their finger, indicating that they understood and were able to do the task. In the second control condition, only proprioceptive inputs were available (i.e. the hand was obscured from view). Accuracy remained high in this condition and no effect of age was found, suggesting that all children were able to use proprioception to locate their unseen hand. In the experimental condition, an adaptation procedure was used resulting in incongruent visual and proprioceptive input for hand location. In this condition, adults demonstrate visuo-proprioceptive integration but weight vision more heavily than proprioception (Bellan et al., 2015) since it is normally the more reliable sense (Mon-Williams et al., 1997). This results in significantly reduced accuracy in hand localisation compared to performance in the control conditions. The current results showed that children's accuracy was also significantly reduced compared to the control condition yet no participants showed complete unisensory dominance. Thus, in line with previous research, even by four years of age, children demonstrate an ability to integrate visuo-proprioceptive information when determining hand location. However, a significant effect of age was found such that estimates by younger children were closer to the true location of the hand than older children's estimates. This indicates that children's ability to flexibly re-weight sensory inputs depending on their context-dependent reliability improves with age. I propose that these findings indicate that throughout early childhood, visual input is increasingly integrated with proprioceptive information to determine hand location; developing from very little integration in 4-year-olds to almost adult-like ability in 10- to 11-year-olds.

The main aim of Experiment Two was to examine age differences in sensitivity to spatially incongruent visuo-proprioceptive information for hand localisation. Specifically, I tested whether children's ability to detect when visual and proprioceptive inputs should, and should not, be integrated together improves with age. To optimally integrate inputs originating from the same multisensory event and distinguish these from information originating from different stimuli, MSI in adults follow a spatial rule. Specifically, the likelihood that MSI occurs decreases as the distance between sensory inputs increases (Lewald et al., 2001). Sensitivity to spatial constraints of MSI underlying body representation may be reduced in younger children (Cowie et al., 2013, 2015); however, this has not been systematically assessed. Experiment Two employed a MIRAGE task but, unlike Experiment One, visual and proprioceptive inputs remained present throughout, to control for differences in visuo-spatial working memory ability. Children aged 4 to 11 years saw their hand in the same place as they felt it (congruent visuo-proprioceptive inputs) or displaced to the right by 0.5, 1, 1.5 or 2 hand widths. Results showed that the ability to detect a discrepancy between visual and proprioceptive inputs for hand localisation increased significantly with age in 4 to 11-year-olds. No evidence was found for an increased reliance on proprioceptive processing in younger children, instead, they were significantly more likely to integrate spatially separated visuo-proprioceptive information than older participants. Thus, no evidence was found to support the idea that the results of Experiment Two are due to a greater reliance on proprioception in younger children, or greater visuo-spatial working memory capacity in older children.

The findings from Experiment Two indicate that in typical development, spatial rules governing the occurrence of MSI become more refined with age. The MIRAGE task used in Experiment Three examined whether this development is also seen with regards to the temporal constraints of sensory binding. Children aged 4 to 11 years saw a pencil touch their hand at the same time as they felt it or 100, 150 200, 300 or 400 ms after the felt touch, and were asked whether the seen and felt touch occurred at the same time or not. Results showed that, in line with the findings from Experiment Three, children's ability to determine when visual and tactile inputs should and should not be combined, depending on their temporal properties, improves significantly with age.

Few studies have investigated when and how MSI underlying body representation becomes adult-like in typical development and inconsistent findings are common. Moreover, it is challenging to compare across studies due to variations in task designs and the different ages of the children involved. Some researchers have suggested that their study findings point to a clear unisensory dominance in younger children (e.g. Gori et al., 2008). In regards to MSI underlying body representation, Cowie et al., (2013) suggest that younger children show a visual dominance while Bremner et al., (2013) propose that they are dominated by proprioceptive inputs. However, based on the overall findings from Experiment One, Two and Three, I argue that younger children do not show a fundamental bias for either visual or proprioceptive information underlying body ownership and localisation. Instead, if visual information is more salient than proprioceptive information, then younger children will weight visual inputs more heavily than proprioception, while the opposite will be seen in a task in which proprioceptive information is more salient than visual information, regardless of the reliability of these inputs. As children age, the ability to re-adjust sensory weightings depending on their context-dependent reliability increases.

Additionally, Experiments Two and Three provide clear evidence that sensitivity to the spatial and temporal constraints of MSI underlying body representation increases with age in typical development. Though these developmental improvements have been shown for visuo-auditory integration (Mon-Williams and Wallace, 2014), these studies fill a notable gap in the literature by indicating that this protracted development also pertains to MSI underlying body representation.

7.3. Mechanisms for atypical visuo-tactile-proprioceptive integration in ASD

A growing body of research indicates atypical visuo-tactile-proprioceptive integration in individuals with ASD but the precise mechanisms underlying this have not been clearly established. Experiments Four to Eight examined the evidence for two prominent theories of atypical MSI in ASD: 1) a fundamental over-reliance on proprioception and 2) temporally extended visuo-tactile binding.

Support for proprioceptive over-reliance comes from a number of studies in which children learnt to control a robotic arm to capture objects. Using this procedure, Haswell et al., (2009) argued that children with ASD developed a much stronger association between their arm movements and corresponding proprioceptive feedback than typical children who, in contrast, showed greater visuo-proprioceptive integration. This finding was replicated by Gidley et al., (2008) and Izawa et al., (2012), who additionally reported a significant relationship between atypical sensory processing and social and motor impairments in participants with ASD. Moreover, Paton et al., (2012) reported that onset of the rubber hand illusion (RHI) was expedited when TD adults wore goggles which minimised proprioceptive discrepancy between the real and fake hand, thereby encouraging the visuo-tactile-proprioceptive integration underlying the illusion. However, this was not demonstrated in those with ASD. The authors propose that, unlike typical individuals, the ASD group weighted proprioceptive inputs more heavily than visuo-tactile inputs – regardless of the goggles – and, thus, may not have integrated multisensory inputs to the same extent.

However, Weimer et al., (2001) reported that children with ASD performed worse than TD children on tasks that depend on proprioceptive feedback alone, such as one-leg balancing with eyes closed. Additionally, many anecdotal reports indicate problems using proprioception in day-to-day tasks (e.g. pointing) and reduced awareness of body position in ASD (Biklen & Attfield, 2005). It is hard to align these findings with the idea of a fundamental proprioceptive over-reliance in this disorder.

An alternative leading theory of atypical MSI proposes that sensory binding is extended in individuals with ASD such that they are more likely to incorrectly bind together inputs that are temporally separated, compared to their peers. Preliminary evidence for temporally extended visuo-tactile binding comes from an RHI study by Cascio et al., (2013) in which synchronous and asynchronous conditions were conducted over two 3-minute blocks. After the first block, children with ASD showed similar levels of proprioceptive drift across the conditions, yet drift increased significantly after the second block in the synchronous condition only. The authors suggest that this represents a delay in illusion onset, and thus a delay in MSI, which could be due to extended temporal binding for visuo-tactile inputs. Specifically, individuals with ASD may have perceived asynchronous brushing as synchronous in the first block, if the delay between visual and tactile brushstrokes was within their temporal binding window (TBW). Consequently, synchronous and asynchronous conditions would be initially indistinguishable. The authors suggest that the TBW narrowed with continuous 'training' such that asynchronous events were no longer perceived synchronously after the second block of brushing. This interpretation fits within the broader MSI research indicating temporally extended visuo-auditory binding in children with ASD. Specifically, psychophysics studies (e.g. Foss-Feig et al., 2010; Kwakye et al., 2011; Stevenson e al., 2014) report that the ability to specify when visual and auditory inputs should (and should not) be integrated together either does not improve with age, or it shows a delayed improvement relative to typical populations.

However, support for both of these theories stems from studies using the RHI, which cannot distinguish the evidence for an over-reliance on proprioceptive processing over temporally extended visuo-tactile binding, as both accounts predict reduced illusion susceptibility. Experiments Four to Eight avoided the inherent limitations of the RHI by using the MIRAGE to directly tests the evidence for an over-reliance on proprioception and temporally extended visuo-tactile binding in ASD.

The MIRAGE task in Experiment Four assessed whether autistic traits in the normal population were associated with increased weighting of proprioceptive over visual inputs for hand localisation. Using a similar procedure to Experiment One, participants were asked to estimate the position of their passive right index finger after viewing congruent or incongruent visuo-proprioceptive information regarding hand position. Replicating previous findings in TD adults (Bellan et al., 2015), vision initially out-weighed proprioception in incongruent conditions, however, following continued visual occlusion, proprioception was up-weighted over time. Levels of autistic traits were not found to affect performance, thus, this experiment found no support for a relationship between autistic traits and an over-reliance on proprioception. However, traits were measured with the Autism Quotient (AQ; Baron-Cohen et al., 2001), a self-report questionnaire that may lack the reliability and validity necessary to place participants accurately along the non-clinical autism spectrum. Alternatively, over-reliance on proprioception may only be clearly seen in individuals with a clinical diagnosis of ASD, who may have autistic traits that are qualitatively different to those seen in sub-clinical populations. This explanation was assessed in the following experiments.

Experiment Five used a MIRAGE supernumerary limb illusion to test the evidence for 1) proprioceptive over-reliance and 2) temporally extended visuo-tactile binding in children with ASD, compared to TD children. Proprioceptive alignment and visuo-tactile synchrony were selectively manipulated to assess the extent that they impacted upon body ownership. 29 children with ASD aged 8-15 years, 29 chronological age-matched children and 29 (younger) verbal mental age-matched children placed their hand into the MIRAGE and saw two, identical live video images of their own hand. One virtual hand was proprioceptively aligned with the actual hand (the veridical hand), while the other was displaced to the left or right. Brushstrokes were applied to the participants' actual (hidden) hand while they observed the two virtual images of the hand also being stroked and were asked to identify their real hand. During brushing, a 60, 180 or 300 ms delay was applied to either the displaced hand or the veridical hand such that only one virtual hand had synchronous visuo-tactile inputs. When proprioceptive inputs were incongruent with visuo-tactile synchrony, none of the groups chose the proprioceptively correct hand significantly more than chance level. Thus, no evidence was found for a fundamental proprioceptive over-reliance in children with ASD. All groups chose the hand with synchronous visuo-tactile inputs when it was in the proprioceptively correct location and the delay applied to the asynchronous hand was large (180 ms or 300 ms). However, only the control groups did this when the delay was reduced to 60 ms; the ASD group performed at chance level. When proprioception and visuo-tactile synchrony were incongruent, only the chronological age-matched control group chose the synchronous hand significantly more than chance level. This indicates that the children with ASD have reduced sensitivity to the temporal constraints of visuo-tactile binding and consequently perform in line with younger TD participants.

It could be argued that Experiment Five did not test MSI abilities underlying body representation specifically since participants could have detected visuo-tactile synchrony without necessarily embodying the synchronous hand. Thus, Experiment Six tested whether temporally extended visuo-tactile binding was found in children with ASD compared to a chronological age-matched and verbal mental age-matched control group, in a task necessitating ownership over a virtual hand. The initial procedure was identical to that in Experiment Five: brushstrokes were applied to the two hand images and the participant's own, hidden hand. After brushing, though, vision of the hand images was obscured and children pointed at a target presented equidistant between the previously seen hand images. Results showed that, when visuo-tactile brushstrokes were applied to the proprioceptively correct hand, all groups were highly accurate at pointing to the target. Accuracy was significantly reduced in all groups when a visuo-tactile delay of 180 ms or 300 ms was applied to the proprioceptively correct hand image, indicating the influence of visual-tactile inputs on perceived hand position. However, only the chronological age-matched control group showed significantly reduced accuracy when the visuo-tactile delay was only 60 ms. This suggests that, as in Experiment Five, unlike an age-matched control group, a 60 ms delay seemed to be too small for the ASD group and younger control group to reliably detect and distinguish the synchronous hand from the asynchronous hand. This provides further support for the idea that visuo-tactile binding is temporally extended in children with ASD, which could, in turn, underlie atypical body representation.

The procedures used in Experiments Five and Six were used in Experiments Seven and Eight, respectively, with a group of adults with ASD and an age- and IQ-matched TD control group. Experiment Seven found that visuo-tactile temporal synchrony overrides proprioceptive inputs in both groups, such that no significant group differences were found in any condition. Similarly, no between-group performance differences were found in Experiment Eight. Instead, across groups, accuracy at pointing to the target was high when visuo-tactile synchrony and proprioception were congruent, but accuracy decreased significantly when these were incongruent, across all delay lengths. This indicates that both groups were sensitive to visuo-tactile delays of 60 ms or more.

Together, the results from Experiments Five and Six suggest that visuo-tactile binding underpinning body representation is temporally extended in children with ASD. This finding is in keeping with the visuo-auditory literature and extends the results from Cascio et al's (2013) RHI study. However, Experiments Seven and Eight found no evidence of this in adults with ASD, suggesting that, by adulthood, sensitivity to visuo-tactile temporal binding may have improved in individuals with ASD, such that it is in line with TD adults. Thus, temporally extended visuo-tactile binding in children may represent a developmental delay that normalises by adulthood, rather than a lifelong deficit.

As described above, studies have found evidence for a fundamental over-reliance on proprioception in individuals with ASD (Cascio et al., 2012; Palmer et al., 2015; Paton et al., 2012). Yet no evidence of this was found in the current experiments. Unlike in TD children, in those with ASD visuo-tactile synchrony does not override proprioception when the two are incongruent, suggesting the inputs may be more equally weighted. However, it is possible that temporally extended sensory binding may lead to an apparent proprioceptive dominance, but only in certain circumstances. Specifically, temporally extended sensory binding could increase the likelihood that inputs from separate events are erroneously integrated together. This could lead to the feelings of confusion and sensory overload experienced by many individuals with ASD (Rogers & Ozonoff, 2005). In an attempt to avoid this, and reduce the complexity of multimodal events, those with ASD may focus on inputs from one sensory modality instead of integrating these with other sensory information. This could lead to an increased reliance on unimodal processing (e.g. proprioception) over multimodal processing (e.g. synchronous visuo-tactile inputs), as reflected in RHI studies (e.g. Palmer et al., 2013, 2015, Paton et al., 2012). Nonetheless, this would not necessarily equate to *superior* proprioceptive processing, and indeed, no evidence has been found for this (Weimer et al., 2001; Biklen & Attfield, 2005). Moreover, a proprioceptive bias specifically would not be expected to occur in all situations, instead, the 'dominant' sense may vary within and between individuals with ASD, and across different circumstances, which could explain why no evidence for a fundamental proprioceptive over-reliance was found in participants with ASD in this thesis. Following on from this explanation, temporally extended sensory binding could contribute to the range and variation of sensory sensitivities seen in the disorder since an increased focus on one sensory channel at the expense of others could result in hypersensitivities to stimuli from this channel and hyposensitivities to the remaining, neglected sensory stimuli (Belmonte, 2004). Moreover, as discussed throughout this thesis, social processes such as empathy and imitation depend on the MSI that underpins body representation. If this integration is temporally extended it could disturb normal body representation and contribute to the socio-communicative impairments seen in ASD. Additionally, if synchrony detection is impaired, social events would be experienced as more complex and less cohesive, which may thus discourage social engagement.

7.4. Explanations for temporally extended visuo-tactile binding in ASD

This thesis found evidence for temporally extended visuo-tactile binding in children with ASD, which is consistent with findings of an extended visuo-auditory TBW (e.g. Kwakye et al., 2011) and suggests that atypical sensory processing in this clinical population may be seen across modalities. However, no evidence of atypical visuo-tactile processing was found in adults with ASD, yet throughout this thesis, I make the case that sensory symptoms seen in children and adults with the disorder could be due to atypical MSI. I will now discuss a possible cognitive and biological explanation for temporally extended sensory binding in children, and discuss how this could lead to autistic traits that are seen throughout the lifespan.

A cognitive theory of ASD developed by Bahrick and Todd (2012) proposes that there is reduced attention towards amodal information in ASD, which may lead to a delay in the experience-dependant narrowing of the TBW. Over the first six months of life, infants learn to selectively attend to relevant events and ignore irrelevant information, for example, they are drawn towards social stimuli such as voices and faces, over non-social stimuli (Flom & Bahrick, 2007). To do this, infants must accurately determine which inputs constitute unitary events and which are unrelated. Bahrick and Todd (2012) argue that infants achieve this by detecting amodal information (AI) before modal specific inputs. AI refers to information that is not specific to one sensory modality, for instance, shape and size can be determined by both vision and touch while synchrony, rhythm, and intensity can be specified by visual, tactile and auditory systems (Bahrick & Lickliter, 2002; Bahrick, 2009). Bahrick and Todd (2012) describe AI as the 'glue' that binds information across the senses, directing attention to unified, multimodal events and away from unrelated streams of sensory information. When the same AI is available concurrently to multiple senses, this promotes heightened neural responses (i.e. a multisensory facilitation effect) compared to when the same information is presented to each modality separately (Stein & Meredith, 1993). According to Bahrick and Lickliter (2002), this ensures that AI "pops out" as meaningful and guides attention towards multimodal events. They further suggest that, through repeated exposure to temporally synchronous multisensory inputs, TD children learn that AI is important and, over time, their ability to distinguish between synchronous and asynchronous multisensory inputs improves. This leads to an increased sensitivity to the temporal constraints of MSI and a gradual narrowing of the temporal binding window (TBW) over childhood.

The authors then propose that selective attention to AI, and the resulting multisensory facilitation effects, are reduced in individuals with ASD. This could lead to reduced sensitivity towards the spatial and temporal constraints of MSI. Additionally, though attending to synchrony may eventually aid experience-dependent narrowing of the TBW in those with ASD, this may occur at a much slower pace than in TD children. In this thesis, I found that while visuo-tactile temporal binding becomes more specific and sensitive with age in TD populations, this development is delayed in individuals with ASD. These results are in keeping with the concept of reduced attention to AI in ASD.

The idea that temporally extended sensory processing in ASD could be due to reduced attention towards amodal information is supported by findings from brain imaging studies. TD infants learn that when they move their hand (proprioceptive stimulation) they see it move simultaneously (visual stimulation). Over time, they come to understand that these inputs relate to the same event (von Hofsten, 2004; Von Hofsten, 2007). Using AI, therefore, helps infants to make sense of their environment and discover the relationship between perception and action, across time and space. Critically, studies indicate that learning about these multisensory perception-action loops underpins neural change and connectivity between sensory and motor systems (Ghazanfar & Schroeder, 2006; Sheya & Smith, 2010; Smith & Thelen, 2003). Thus, if children with ASD are not guided by AI, this could not only impede their ability to make sense of, and operate in, their environment but it could also lead to atypical brain development. In support of this, a growing number of brain imaging results indicate altered connectivity both within and between brain regions in individuals with ASD (Bertone, Hanck, Kogan, Chaudhuri, & Cornish, 2010; Kéïta, Mottron, & Bertone, 2010; Mottron et al., 2006). Moreover, a wide body of evidence demonstrates that seemingly minor differences in the timing of developmental processes can have significant and far-reaching effects on developmental outcomes (Knudsen, Heckman, Cameron, & Shonkoff, 2006; Mundy & Burnette, 2005). Thus, it is possible that delayed narrowing of the TBW could have cascading effects on key aspects of development, thereby contributing to sensory and social differences in ASD that endure throughout the lifespan, despite evidence of normal temporal processing in adults.

Bertone et al., (2010) present a theoretical framework that demonstrates how the core features of ASD, including social impairments, sensory sensitivities, and perceptual differences, could be explained by differences in local neural networks. Firstly, behavioural and physiological results imply that low-level perceptual differences in ASD, such as superior performance in visual search tasks (Caron et al., 2006), could be due to altered connectivity within specialised brain regions involved in intra-modal information processing (Belmonte et al., 2004; Bertone et al., 2010; Casanova, 2007; Milne, Scope, Pascalis, Buckley, & Makeig, 2009; Rubenstein & Merzenich, 2003; Vandenbroucke, Scholte, Engeland, Lamme, & Kemner, 2008). An electroencephalographic (EEG) study by Milne et al., (2009) for example, found that, when adults with ASD were shown a simple visual stimulus, differences in the neural correlates of visual perception, specifically in areas in or near the striate cortex, extrastriate cortex and cingulate gyrus, were seen, compared to a control group. Bertone et al., (2010) further propose that altered connectivity of local networks in early childhood would change the experience-dependent maturation of long-range neural connections between brain regions. These connections mediate sensory integration and shape the development of subsequent cognitive and behavioural skills. Thus, alterations would likely affect both low-level sensory processing and higher level socio-communicative functioning (Baron-Cohen et al., 2009; Belmonte et al., 2004; Chang et al., 2014). Evidence for this comes from a recent study by Chang et al., (2014) using diffusion tensor imaging (DTI) fiber tractography. Relative to control children, those with ASD showed reduced connectivity in parietooccipital tracts, which are involved in sensory perception and MSI. Bertone et al's (2010) theory is further supported by a number of brain imaging studies demonstrating reduced long-range connections between brain regions in individuals with ASD (e.g. Anderson et al., 2011; Thomas et al., 2009; Weinstein et al., 2011). Moreover, an EEG study by Russo et al., (2010) found that children with ASD combine sensory inputs at a later stage, and to a lesser degree than TD individuals. Thus, the atypical MSI demonstrated in this thesis in the form of temporally extended visuo-tactile binding, could be due to these early neurodevelopmental differences in brain connectivity (Driver & Noesselt, 2008), which in turn could be a result of reduced reliance on AI.

7.5. Limitations of the thesis and future research

Though this thesis found evidence of temporally extended sensory binding in younger compare to older TD children and in children with ASD compared to chronological age-matched TD controls, the width of each participant's TBW was not assessed. This limitation means that the degree to which visuo-tactile temporal binding is extended in younger children and those with ASD is not known. To establish this, a future study could employ a visuo-tactile cross-modal congruency task (CCT), similar to that used by Poole et al., (2015), with children with and without ASD.

The majority of research on MSI in ASD has focused on visuo-auditory integration, with several studies finding evidence of temporally extended visuo-auditory integration in children with the disorder (e.g. Foss-Feig et al., 2010; Kwakye et al., 2011; Stevenson et al., 2014; Woynaroski et al., 2013). This thesis adds to this literature by demonstrating that visuo-tactile temporal binding is also extended in this population. Together, this could suggest that extended and less precise sensory binding occurs across all sensory modalities in children with ASD (as proposed by Bahrick and Todd's (2012) theory of reduced attention towards amodal inputs in ASD. If this were the case then an intervention that narrows the visuo-auditory TBW may also narrow the TBW for other sensory inputs. Although this was outside the remit of this thesis, it would be useful to conduct a future study investigating the relationship between temporally extended sensory binding across different modalities. For instance, the same individuals could complete a visuo-tactile and a visuo-auditory temporal order judgment (TOJ) task. If there is a relationship between performances across the tasks, this could indicate that temporally extended sensory binding is domain-general.

A second main limitation of this thesis is that measures of sensory sensitivities were not taken in any study. Consequently, this work cannot directly assess whether temporally extended sensory binding is related to sensory symptoms in individuals with ASD. This is important to investigate to establish whether temporally extended sensory binding varies between individuals with ASD, in line with variations in the type and degree of sensory sensitivities seen across the disorder (Crane, Goddard, & Pring, 2009; Rogers & Ozonoff, 2005). An individual with an enlarged visuo-tactile TBW, for example, could have problems distinguishing synchronous from asynchronous visuo-tactile inputs, which could encourage unimodal processing of tactile information and hypersensitivities to these inputs. Yet, this same individual may show normal visuo-auditory temporal integration and consequently have no auditory sensitivities. To assess this claim, the study outlined in the preceding paragraph could incorporate measures of sensory sensitivities, using, for example, the Adult/Adolescent Sensory Profile (Brown et al., 2001). This is a self-report questionnaire, which assesses levels of sensory processing across visual, tactile, auditory, olfactory and proprioceptive systems. If for example, participants with tactile sensitivities show temporally extended sensory binding, but only when integrating tactile information, this would provide support for the idea that the width of the TBW may vary within individuals, depending on the sensory inputs being combined, and an enlarged TBW may underlie *specific* sensory sensitivities.

It should also be noted that sensory sensitivities vary within as well as between individuals with ASD, such that, for instance, a person may be intolerant to loud noises or touches only in certain circumstances, e.g. a new situation compared to a familiar one (Rogers & Ozonoff, 2005). This could be because sensitivity to the temporal (and/or spatial) constraints of MSI may vary depending on the sensory environment. For example, if an individual in a quiet room hears the 'click' of a light switch and simultaneously sees a lamp switching on, he/she may be able to integrate this information appropriately and understand that the two inputs came from the same source. However, in a noisy classroom, for instance, it may be much more challenging to correctly integrate sights and sounds originating from the same event (e.g. a teacher) and distinguish these from background noise, particularly if there is reduced reliance on AI in those with ASD. This may result in more extended and less precise visuo-auditory binding, leading to hyper- and/or hyposensitivities to sensory input in this latter circumstance only. A future study could investigate this hypothesis by conducting, for example, a multisensory temporal order judgment task in an environment with a large degree of background stimulation (for example a room with several other studies taking place simultaneously). The task could then be repeated on a different day in a quite environment with little competing sensory stimuli. If a correlation between sensory sensitivities and temporally extended binding is seen more strongly in the first condition, this would provide support for this theory.

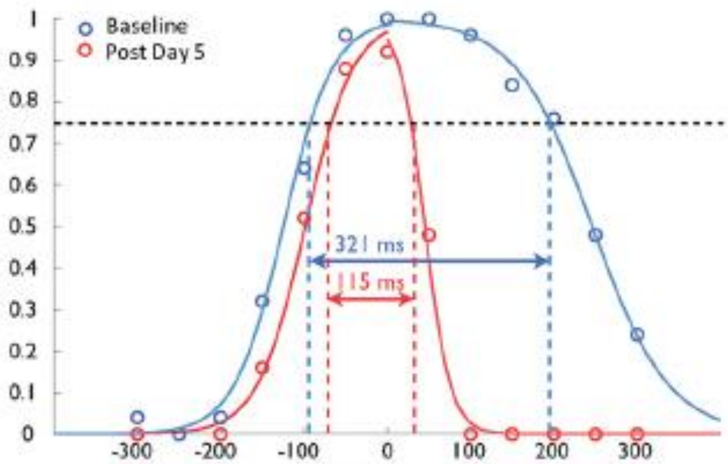
7.6 Clinical Implications

Knowing more about the underlying cause of sensory disturbances in ASD is important for informing evidence-based interventions to alleviate these (Mazurek et al., 2013; Reynolds, Lane, & Thacker, 2012). Indeed, sensory interventions are one of the most in-demand services for children with ASD (Green et al., 2006). Yet a recent systematic review concluded that current treatments are based on insufficient evidence and may not be effective (Case-Smith, Weaver, & Fristad, 2015). Interestingly, recent studies conducted with TD adults successfully demonstrated that the visuo-auditory TBW can be narrowed using multisensory perceptual feedback training (Powers, Hillock, & Wallace, 2009; Stevenson et al., 2013). In Powers et al., (2009), participants completed a simultaneity judgment (SOJ) task before and after training. In the task, participants in an experimental and a control group judged whether or not an auditory and a visual stimulus occurred simultaneously (forced-choice response). Stimulus onset asynchronies (SOAs) ranged from -300 (auditory stimulus presented first) to +300 ms (visual stimulus presented first) at 50 ms intervals. Participants completed training on the task for one hour a day for five days, before undergoing a follow-up assessment one week later. For the experimental group, feedback was given after responses (correct or incorrect) during training, but not during follow-up trials. A control group completed the same follow-up SOJ tasks as the experimental group, yet, instead of training, they were exposed to the same visuo-auditory pairings but were asked to respond when the visual stimulus was a red ring (thus, the task was not temporal in nature).

The estimated width of the TBW was set as the probability that the visual and auditory stimuli were judged as simultaneous ≥75% of the time. Results (see Figure 7.1) showed that for the experimental group, the mean width of the TBW narrowed significantly from 225 ms to 185 ms following training. Moreover, the group mean probability judgment of simultaneity decreased significantly following training in the 100 ms, 150 ms and 200 ms SOA conditions. In contrast, the width of the TBW for the control group actually increased, on average, following passive exposure to the identical stimuli, indicating that feedback is critical to the success of the training. Furthermore, the biggest differences in TBW width were seen in participants with the largest windows at baseline.

Since evidence suggests that individuals with ASD have atypically large TBWs, this presents an exciting avenue of research to investigate interventions to narrow the window in this clinical population. As outlined above, narrowing of the TBW would increase the ease with which synchronous inputs could be detected and

Probability of simultaneity judgment



Stimulus onset asynchrony

Figure 7.1. The visuo-auditory temporal binding window (TBW) narrows following training on a simultaneity judgment task.
The estimated width of the TBW was set as the probability that the visual and auditory stimuli were judged as simultaneous ≥75% of the time. In this participant, the TBW narrows from 321 ms to 115 ms after 5 hours of feedback training.
Adapted from "Perceptual Training Narrows the Temporal Window of Multisensory Binding," by A.R. Powers, A.R. Hillock and M.T. Wallace, 2009, *The Journal of Neuroscience 29 (39),* p. 12265–12274. Copyright 2009 by Society of Neuroscience.

distinguished from asynchronous inputs, which could reduce feelings of sensory overload and confusion. Future research could also investigate whether the visuo-tactile binding window is similarly malleable and if narrowing this TBW positively influences the development of body representation and the social processes that depend on this, such as empathy and imitation. Nonetheless, this type of intervention may not be suitable for children with ASD, particularly low-functioning individuals, since it appears to necessitate intensive training, over several consecutive days. Given the attention difficulties that are commonly seen in ASD (Ames & Fletcher-Watson, 2010), it is unlikely that this approach could be widely used in this population. Moreover, participants with certain sensory hypersensitivities may not tolerate continuous exposure to low-level sensory stimuli. However, it is possible that this task could be adapted into a simple game, which could be conducted on a computer or iPad. This may be suitable for at least some individuals with the disorder, particularly since repetitive behaviours and routines can be a source of enjoyment or relaxation for many with the disorder (American Psychological Association, 2013).

Interestingly, a recent study by Zmigrod & Zmigrod (2015) found that the audio-visuo TBW narrows significantly following transcranial direct current stimulation (tDCS) applied to the right posterior parietal cortex (PPC). TDCS is a painless, non-invasive brain stimulation method that can enhance cortical excitability by delivering a low-intensity electric current to the scalp. TD adults received anodal (positively charged electrode) or cathodal (negatively charged electrode) tDCS for 15 minutes while completing an audio-visual simultaneity judgment task. When the stimulus onset asynchrony (SOA) between the visual and auditory stimuli was 150ms, anodal tDCS over the right PPC reduced visuo-auditory simultaneity judgments by 30%, compared to conditions with cathodal or no stimulation. Importantly, this effect was seen after only a few minutes of non-invasive brain stimulation, indicating that this could be an effective and low-intensity way to narrow the TBW. Indeed, it requires no active or conscious involvement from the participant, suggesting that it could even be suitable for low-functioning individuals with ASD. Nonetheless, Zmigrod & Zmigrod (2015) did not assess if and when the TBW returns to its former width. This is essential to establish since the effects need to be long lasting for this to be a worthwhile intervention. Thus, to assess this, it is important to conduct a future study in which the task is repeated days, weeks and months after tDCS is applied. It may be that the brain stimulation needs repeating periodically to maintain improvements. However, the use of tDCS in clinical populations and children could carry potential ethical limitations.

One final avenue of future research could assess whether temporally extended sensory binding is also seen in individuals with sensory processing disorder (SPD). SPD is a developmental disorder characterised by over- and under- responding to sensory input, problems discriminating sensations and responding to sensory information atypically, in a way that impacts on day-to-day functioning (Miller & Schaaf 2008). Unlike ASD, though, fundamental social and language deficits are not seen. Interestingly, a brain imaging study by Chang et al., (2014) found that both children with ASD and those with SPD showed decreased connectivity in parietooccipital tracts relative to TD controls. However, only the children with ASD showed decreased connectivity in temporal tracts believed to be involved in social and emotional processing. This suggests that, while SPD and ASD should be viewed as two distinct developmental disorders, the sensory impairments that are seen in both may be due to the same underlying mechanisms. Thus, an intervention that improves sensory processing in ASD by narrowing the TBW may have the same beneficial effect for individuals with SPD. Further research could firstly assess whether the TBW is extended in SPD before exploring the efficacy of interventions designed to improve temporal integration of sensory inputs.

7.7. Conclusions

In summary, this thesis has found the following main findings. Firstly, children as young as four years are capable of integrating sensory inputs that underpin body representation (i.e. visual, tactile and proprioceptive information). However, optimal integration continues to develop over childhood, such that, under certain conditions, younger children may process unimodal over multimodal inputs. They do not, though, show a fundamental bias for information from one sensory system. Instead, the nature of the task dictates sensory processing. Thus, a task that relies on proprioception, for example, may lead to unimodal, proprioceptive processing instead of optimal MSI while unisensory, visual processing may be seen in a task that is more visual in nature. In contrast, older children (aged 10 to 11 years) and adults integrate multiple sensory inputs and up-weight information depending on its context-dependent reliability. In line with this protracted development of optimal integration, sensitivity to the temporal and spatial constraints of MSI underlying body representation also improves with age in TD children aged 4 to 11 years. Children with ASD, though, show reduced sensitivity to temporal visuo-tactile binding underlying hand ownership and localisation, compared to chronological age-matched controls. The participants with ASD perform in line with younger TD children, indicating a developmental delay in the narrowing of the TBW for visuo-tactile integration. Adults with ASD do not show this reduced sensitivity, which could indicate that, by adulthood, the width of the visuo-tactile TBW is similar for individuals with and without the disorder. Beyond understanding a prevalent developmental condition, the results reported in this thesis, and their interpretation, have important implications for future research, particularly the development of evidence-based interventions for alleviating sensory symptoms in individuals with ASD. Future research should explore the use of interventions to narrow the visuo-tactile TBW in individuals with ASD, such as perceptual feedback training (Powers et al., 2009) and tDCS (Zmigrod & Zmigrod, 2015). This could help to reduce sensory sensitivities and contribute to the development of accurate body representation, which underlies the development of social processes that are impaired in ASD, such as empathy as and imitation.

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