



Greenfield, Katie and Ropar, Danielle and Themelis, Kristy and Ratcliffe, Natasha and Newport, Roger (2017) Developmental changes in sensitivity to spatial and temporal properties of sensory integration underlying body representation. *Multisensory Research*, 30 (6). pp. 467-484. ISSN 2213-4794

Access from the University of Nottingham repository:

http://eprints.nottingham.ac.uk/48586/1/FINAL%20changes%20accepted%20Greenfield%20et%20al.%20DMI%20_Revised%20manuscript.pdf

Copyright and reuse:

The Nottingham ePrints service makes this work by researchers of the University of Nottingham available open access under the following conditions.

This article is made available under the Creative Commons Attribution licence and may be reused according to the conditions of the licence. For more details see: <http://creativecommons.org/licenses/by/2.5/>

A note on versions:

The version presented here may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the repository url above for details on accessing the published version and note that access may require a subscription.

For more information, please contact eprints@nottingham.ac.uk

**Developmental changes in sensitivity to Spatial and Temporal properties
of sensory integration underlying Body Representation**

Katie Greenfield¹, Danielle Ropar¹, Kristy Themelis¹, Natasha Ratcliffe¹, and
Roger Newport¹

Short title:

Developmental changes in sensory integration

Contact Information:

¹ School of Psychology, The University of Nottingham, University Park,
Nottingham, UK, NG7 2RD, UK

Katie Greenfield: lpxkg1@nottingham.ac.uk

Danielle Ropar: danielle.ropar@Nottingham.ac.uk (corresponding author)

Kristy Themelis: lpxkt6@nottingham.ac.uk

Natasha Ratcliffe: lpxnr2@nottingham.ac.uk

Roger Newport: roger.newport@nottingham.ac.uk

Summary

The closer in time and space that two or more stimuli are presented, the more likely it is that they will be integrated together. A recent study by Hillock-Dunn & Wallace (2012) reported that the size of the visuo-auditory temporal binding window - the interval within which visual and auditory inputs are highly likely to be integrated - narrows over childhood. However, few studies have investigated how sensitivity to temporal and spatial properties of multisensory integration underlying body representation develops in children. This is not only important for sensory processes but has also been argued to underpin social processes such as empathy and imitation (Schütz-Bosbach et al., 2006). We tested 4 to 11 year-olds' ability to detect a spatial discrepancy between visual and proprioceptive inputs (Experiment One) and a temporal discrepancy between visual and tactile inputs (Experiment Two) for hand representation. The likelihood that children integrated spatially separated visuo-proprioceptive information, and temporally asynchronous visuo-tactile information, decreased significantly with age. This suggests that spatial and temporal rules governing the occurrence of multisensory integration underlying body representation are refined with age in typical development.

Keywords

Multisensory integration; Development; Sensory processing; Visual-tactile; Visual-proprioceptive; Body representation

Introduction

The appropriate integration of visual, proprioceptive and somatosensory inputs underlies body representation and the subjective sense of self (Nava et al., 2014; Schütz-Bosbach et al., 2006). However, the likelihood that multisensory integration occurs depends on the nature of the sensory inputs being combined, in particular, the spatial and temporal distance between sensory inputs (Wallace et al., 2004). Evidence suggests that the probability of MSI decreases as the distance between sensory inputs increases. For example, 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 et al., 2001; Slutsky and 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 entities (Ernst and Banks, 2002). Similarly, a wide body of research indicates that the likelihood of multisensory integration follows a temporal rule (Hairston et al., 2006; Stevenson and Wallace, 2013; Wallace & Stevenson, 2014). For example, a visual and an auditory input separated by a large temporal delay are less likely to be integrated than inputs occurring simultaneously. However, 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). The period of time during which multisensory integration is very likely to occur has been referred to as the temporal binding window (TBW; Colonius and Diederich, 2004; Hairston et al., 2006; Hillock et al., 2011). This is thought to exist 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 30-40ms for information from the primary visual cortex to reach the brain while inputs from the primary auditory cortex take only around 10ms (Calvert et al., 2004). Thus, a TBW allows multisensory interactions to be flexibly specified.

The majority of research in this area has been conducted with adults and it is less clear how, and when, sensitivity to the spatial and temporal properties of MSI develops in children. However, a recent study by Hillock-Dunn and Wallace (2012) reported that the window of time in which visual and auditory inputs are perceived to be simultaneous narrows with age in 6 to 23 year-olds. Participants completed a simultaneity judgment task in which an audio and a visual stimulus were presented and participants judged whether they occurred at the same or different times. 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 binding window varied between participants, overall it narrowed with age and did not reach adult levels until well into adolescence. However, less is known about children's ability to decipher whether spatially and/or temporally separated visual, tactile and proprioceptive cues belong together. This is important to investigate since the capacity to compare and differentiate between the self and others depends on the normal integration of these inputs (Cascio et al., 2012). This ability and a sense of body ownership underlies the development

of social behaviours and skills including self-awareness, imitation and empathising (Schütz-Bosbach et al., 2006). A greater understanding of this development is important since a relationship between atypical visuo-tactile-proprioceptive integration and the severity of social impairments in children with autism spectrum disorders (ASD) has been reported (Casco et al., 2012). Thus, examining spatial and temporal aspects of sensory integration underlying body representation in typical development can help to provide a comparison point to assess if and how this may be atypical in ASD.

A number of preferential looking studies suggest that infants and even neonates can detect temporal and/or spatial incongruences between sensory inputs underlying body representation. In Rochat and Morgan (1995), 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. More recently, Zmyj et al., (2011) reported that neonates preferentially attend to synchronous compared to asynchronous visuo-tactile brushstrokes applied to the face. Though these findings suggest that infants are sensitive to spatial and temporal properties of multisensory integration relating to the self, it is not clear whether this ability is already adult-like or if it continues to develop and refine with age. Moreover, findings across infant studies appear to be inconsistent. 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, indicating that the infants were aware of when visual and proprioceptive for body localisation was incongruent. However, in a study by Rochat and Striano (2000), 1 to 5 month-olds were shown live videos of their legs or videos delayed by 0.5, 1, 2 or 3 seconds and showed no clear preference for any video. Additionally, non-linear findings within studies make interpretation difficult. In Collins & Moore (2008), for example, 6 to 11 month-olds distinguished live videos of their faces 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 or spatial incongruency detection in infants since they can only *infer* that detection has occurred.

Studies with children can avoid the issues inherent in infant studies since participants can verbally report their perceptions. Despite this, there is a lack of research investigating the development of sensitivity to temporal and spatial

properties of multisensory integration underlying body representation in children. A recent study by Jaime et al., (2014) however, reported 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 7 to 8 year-olds and adults, children aged 5 to 6 years were less likely to notice a visual delay of 100, 200 or 300ms. This suggests that, while the mechanisms for adult-like multisensory integration may be in place from birth, optimal integration continues to develop over childhood. It is not clear, though, whether this development continues beyond 8 years of age. Moreover, the authors separated children into age groups (5-, 6-, 7- and 8-year-olds) and between-groups analyses were conducted, which could mask important developmental changes within year groups.

The development of sensory integration underpinning body ownership was assessed by Cowie et al., (2013) and Cowie et al., (2016) across a wider age range of children. Both studies employed the rubber hand illusion (RHI; Botvinick and Cohen, 1998), in which brushstrokes are applied to a proprioceptively incongruent fake hand and the participant's unseen hand. In typical adults, this leads to embodiment of the fake hand when brushstrokes are temporally synchronous, but not when they are asynchronous (e.g. Botvinick, 2004). The illusion relies on integrating the visual and tactile inputs such that the observer experiences one multisensory event, as opposed to two separate unimodal events. Interestingly, in Cowie et al., (2013), after synchronous or asynchronous brushing, 4 to 9 year-olds' perceived hand position was closer to the fake hand than older children and adults. This suggests that younger children are more likely to integrate spatially and temporally incongruent visual, tactile and proprioceptive inputs. This could be because they are less sensitive to the spatial constraints of sensory integration. Alternatively, or as well as this, they may have temporally extended (or less precise) visuo-tactile binding. Thus, they may have perceived both synchronous and asynchronous brushing to be synchronous, leading to embodiment of the fake hand in both conditions. However, the classic RHI procedure cannot distinguish between these two explanations since visual and tactile inputs are spatially incongruent in both synchronous and asynchronous conditions.

Though infant studies suggest that the mechanisms for adult-like multisensory integration underpinning the sense of self and body ownership may be in place from birth, studies with older participants suggest that this ability continues to develop over childhood. Specifically, Cowie et al's (2013) RHI study suggests that

sensitivity to spatial and/or temporal properties of sensory integration matures with age. The current experiments were designed to separately assess the evidence for changes in sensitivity to the spatial (Experiment One) and temporal (Experiment Two) constraints of multisensory integration underlying body representation in typically developing children aged 4 to 11 years. In both experiments, instead of dividing children into arbitrary age groups, a developmental trajectory analysis was used to track age-related changes in sensory integration more precisely. Additionally, the experiments were conducted using a MIRAGE mediated reality device (see Fig. 1; Newport et al., 2010), which presents live video images of the participant's hand 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 to control visual presentation of the hand with millisecond precision. To investigate sensory integration, the MIRAGE has several advantages over the classic RHI. Firstly, the hand in MIRAGE looks exactly as the participants' own hand does and moves in real-time, thus, the current study does not rely on participants embodying a fake, static hand. Secondly, reported embodiment of the hand image is reliably quicker than embodiment of the fake hand 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 actual hand and the hand image can be removed.

In Experiment One, children 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. Based on the findings from Cowie et al., (2013), it was predicted that accuracy, i.e. the ability to determine which inputs should, and should not, be integrated together, based on their spatial proximity, would improve with age.

In Experiment Two, the same participants placed their right hand into the MIRAGE and saw it in the same spatial location as their actual hand. The experimenter touched the participants' 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 400ms 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 at a different time. Based on the results from studies by Hillock-Dunn and Wallace (2012) and Jaime et al., (2014), it was predicted that, as children age, they would be more accurate in detecting and distinguishing synchronous from asynchronous visuo-tactile inputs underlying body representation.

Experiment One

Method

Participants

60 typically developing children aged 5 to 12 years participated as part of a Summer Scientist Week event held at The University of Nottingham, in which children are 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. The British Picture Vocabulary Scale III (BPVS III; Dunn and Dunn, 2009), was used to assess verbal mental age to ensure that no children had a verbal developmental delay.

Data from three 5-year-olds was excluded, as these children did not keep their hands still during the tasks. Data from one 11-year-old was also excluded since this child had a diagnosis of ASD which is a condition that is commonly associated with sensory processing difficulties (American Psychiatric Association, 2013). This left 56 children (mean age=8.67 years, SD=1.65, 29 females) who were included in the analysis. In the remaining sample, data was missing for four participants 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.

Procedure

All participants were tested in a quiet room at the University. Children completed the current MIRAGE task and the f MIRAGE task presented in Experiment Two in one session which lasted 10 minutes. The order of the two tasks was counterbalanced, and the BPVS was administered after a break either before or after the MIRAGE tasks.

Figure 1

Children placed their hand into the 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. Children 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. They were instructed to keep their hand still with their fingers together 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. Children were then asked to make a fist and point out their index finger straight in front of them while resting their fist on the MIRAGE work surface (see Fig. 1 and Fig. 2). 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 on the screen in the same plane and 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 for approximately 2 seconds. The hand was then presented 2.5 hand widths to the right of the actual hand location (i.e. 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. Hand displacements were calculated and monitored online and did not require mechanical apparatus. Displacements were not made to the left of the child's midline as this would have suggested the arm would have had to be in a

physically awkward or impossible position giving additional top-down clues to whether the image was in the same location as their own hand.

Figure 2

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 HWs. Thus, for the current experiment, conditions were chosen that aimed to reveal potential age differences in performance, whilst avoiding ceiling and floor effects.

Results

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 HWs 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. This investigated firstly, the effect of displacement conditions on performance; secondly, the effect of age entered as a continuous variable on performance and lastly, whether there was an interaction between age and displacement condition. Trajectory analyses are akin to ANOVAs except that, instead of comparing group means, linear regressions characterised by an intercept and a gradient are compared instead. Intercepts specify when an ability begins to develop while gradients display the rate of development. Using this analysis, children do not need to be divided into arbitrary age groups, which could mask critical developmental changes within a group. Instead, trajectories reveal a more precise identification of the age at which, for example, children are able to detect a 0.5 HW discrepancy between visual and proprioceptive inputs for hand position. Moreover, using this analysis, a wider age range of children can be tested, instead of only testing children who fall within specified age groups.

To conduct the trajectory 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. This ensures that y-intercept of the trajectory occurs at the youngest age tested, such that the model only predicts performance from children in the age range tested. The within-subjects main effect of condition was assessed using a one-way ANOVA. This analysis was re-run as an ANCOVA, with rescaled age entered as a covariate, to test the interaction between condition and age. The main effect of condition was assessed separately from the condition by age interaction because the addition of a covariate alters the within-subjects main effect (Delaney and Maxwell, 1981) leading to an overly conservative estimate of the effect (Thomas et al., 2009).

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 to 11.64 years) in the 0, 1, 1.5 and 2 HW conditions (see Fig. 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 relative to younger children. A developmental trajectory was carried out to assess these findings in more detail.

Figure 3

Table 1. Mean percentage correct in each displacement condition across the sample.

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)

Developmental Trajectory

Table 1 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 in the 0 HW condition compared to the 0.5 HW ($p < .001$), 1.5 HWs ($p = .013$) and 2 HWs conditions ($p = .020$). Scores were also significantly higher in the 2 HWs condition compared to the 0.5 HW ($p < .001$) and 1 HW ($p < .001$) conditions and in the 1.5 HWs 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 0 HW condition). Secondly, this suggests that accuracy increases linearly as the space between the visual and proprioceptive inputs increases (i.e. with increased HW displacement).

The ANCOVA showed a main effect of age ($F(1, 54)=25.49$, $p < .001$, $\eta^2 < .353$). As demonstrated in Fig. 3, performance improves with age across conditions.

There was no significant interaction between age and condition ($F(1, 54) = .22$, $p = .64$, $\eta^2 = .004$), suggesting no strong difference in the rate of development between the HW displacement conditions.

Experiment Two

Method

Participants

Participants were the same as those in Experiment One.

Procedure

Children placed their right hand in the 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 seen touch followed the felt touch. Children's ability to detect and distinguish synchronous from asynchronous visuo-tactile inputs was measured.

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. Children 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 saw their hand on the screen in the same plane and spatial location as if he/she was viewing it directly. As in Experiment One, children were instructed to make a fist and point out their index finger, while resting their hand on the MIRAGE work surface (see Fig. 1 and Fig. 2). This hand position was 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 white-led pencil approximately 3cm perpendicular to the tip of the child's right index finger (see Fig. 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 the 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 400ms after the felt touch (400ms SOA). These trials were repeated if necessary until it was clear that the child understood and was able to complete the task. Delay rates were calculated and monitored online and did not require mechanical apparatus, instead, delays were calibrated using software 'probes.' These determine the number of milliseconds that have passed at any given stage within the program cycle. Importantly, even if the tactile stimuli do not occur at a fixed frequency, the seen delayed touch will always follow at a set time after the felt touch.

Experimental trials were identical to practice trials except that the visual and tactile stimuli were either synchronous (0ms SOA) or were separated by an SOA of 100, 150, 200, 300 or 400ms. 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 800ms were used. Results showed that children aged 5-12 could easily detect an SOA of ≥ 400 ms but performance decreased linearly with decreasing delay such that only one child (aged 12) could detect a 100ms 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.

Figure 4

Results

Data Analysis

For each child, the total number of times that the participant gave a correct answer (answering 'no delay' in the 0ms 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 100ms condition for four children and from one trial in the 400ms 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, as in Experiment One, a developmental trajectory was conducted to investigate the effect of SOA on performance, the effect of age (as a continuous variable) on performance and to assess whether there was an interaction between age and SOA. 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. 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 each participant's age entered as a covariate.

Accuracy

Accuracy was significantly above chance ($p < .001$) for the younger group (aged 5.5.2 to 8.67 years) and the older group (aged 8.84 to 11.64 years) in all conditions except for the 100ms SOA (see Fig. 5). No other results were significant. This indicates that children understood and could complete the task. Nonetheless, it is not clear from these results alone whether age effects performance.

Developmental Trajectory

Table 2 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 0ms SOA condition compared to the 100ms ($p = .015$) and 200ms ($p = .028$) SOA conditions. Accuracy was significantly greater in the 150ms, 200ms, 300ms and 400ms SOA conditions compared to the 100ms condition (all at $p < .001$). Lastly, accuracy was significantly higher in the 500ms SOA condition compared to the 400ms condition ($p = .002$) and in the 400ms SOA condition compared to the

150ms and 200ms 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 0ms SOA and 400ms SOA condition) and that accuracy in detecting a visuo-tactile SOA increases linearly with increased SOA.

 Figure 5

Table 2. Mean percentage correct at each visuo-tactile SOA (ms).

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 Fig. 5 indicates, accuracy improves with age across the conditions. There was no significant interaction between age and condition, ($F(1, 54) = 3.93, p = .053, \eta^2 = .028$), suggesting no strong difference in the rate of development between the SOA conditions.

Discussion

The results of the current study indicate that spatial and temporal rules governing the occurrence of multisensory integration underlying body representation are refined with age in typical development. Experiment One shows that even children as young as 4 years are highly accurate in correctly identifying when visual and proprioceptive inputs relating to hand localisation are spatially congruent. 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 between inputs increases. Performance is at chance level when the seen hand is displaced to the right by only 0.5 hand widths (HW), but accuracy is significantly above chance when visual displacement is increased to 1.5 or 2 HWs.

Importantly, performance across conditions improves significantly with age in 4 to 11 year-olds. Experiment Two investigated the effect of age on children's ability to detect whether visuo-tactile inputs for hand representation are temporally synchronous or asynchronous. All children were highly accurate in detecting when inputs were synchronous. When inputs were temporally asynchronous, accuracy at detecting a visuo-tactile delay of 100ms was at chance level but was significantly higher than chance when delays of between 150-400ms were used. Critically, as in Experiment Two, performance improved significantly with age in children aged 4 to 11 years.

Taken together, these findings suggest that spatially extended visuo-proprioceptive binding and temporally extended visuo-tactile binding reduces with age in 4 to 11 year-olds. This compliments and adds to Jaime et al's (2013) findings that sensitivity to the temporal properties of visuo-proprioceptive integration underlying body representation improves with age in 5 to 8 year-olds. This is also in line with Hillock-Dunn and Wallace's (2012) work showing that the visuo-auditory temporal binding window narrows with age across childhood.

If visuo-proprioceptive and visuo-tactile binding are less tightly constrained in younger children, as the results suggest, this would increase the likelihood that inputs from separate events are mistakenly integrated together, which could explain Cowie et al's (2013; 2015) findings. These studies showed that while proprioceptive drift in the RHI is seen in 4 to 13 year-olds and adults following synchronous brushing, 4 to 9 year-olds also show proprioceptive drift after asynchronous brushing. According to the current study, the younger children may have integrated temporally incongruent visuo-tactile inputs and spatially incongruent visuo-proprioceptive inputs to embody the fake hand, due to extended, or less precise, visuo-proprioceptive and visuo-tactile binding. The current study also suggests that the age differences seen in Cowie et al., (2013) were not due to differences in susceptibility to the illusion since an effect of age was also seen in the current experiments, which did not require participants to overcome physical differences between a real and a fake hand. A future study could conduct the tasks used in the current study alongside the traditional RHI to assess if one of these abilities is predominantly underlying the development differences found by Cascio et al (2013, 2015) or if they contribute equally to performance.

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 One and the 100ms condition in Experiment Two, 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 number of conditions in each experiment was limited to help children maintain concentration and attention throughout the procedure. All children expressed significant enjoyment in interacting with the MIRAGE system, thus potentially a future study could be conducted that includes additional HW displacements of 0.25 and 0.75 (in Experiment One) and SOAs of 250ms and 350ms (in Experiment Two), to achieve a more precise identification of developmental changes in task performance. Further research could administer these tasks to adults to specify the age at which children's sensory integration abilities in this domain reach maturity. Despite these limitations, the current findings show that multisensory integration underlying body representation is less tightly constrained in younger children, such that sensitivity towards spatial and temporal properties of sensory integration develops with age in 4 to 11 year-olds. These findings provide a comparison point to assess the nature of atypical visuo, tactile and proprioceptive integration in children with autism spectrum disorders.

Acknowledgements

KG was supported by an Economic and Social Research Council (ESRC) PhD studentship (grant number ES/J500100/1). The funders had no role in the study design, data collection, analysis, decision to publish or preparation of the manuscript.

References

- American Psychiatric Association. (2013). *Diagnostic and Statistical Manual of Mental Disorders: DSM-V 5th ed.* American Psychiatric Association, Washington, D.C.
- Bahrack, L.E., Watson, J.S., 1985. Detection of intermodal proprioceptive–visual contingency as a potential basis of self-perception in infancy. *Dev. Psychol.* 21, 963–973. doi:10.1037/0012-1649.21.6.963
- Botvinick, M., 2004. Probing the Neural Basis of Body Ownership. *Science* 305, 782–783. doi:10.1126/science.1101836
- Botvinick, M., Cohen, J., 1998. Rubber hands ‘feel’ touch that eyes see. *Nature* 391, 756. doi:10.1038/35784
- Calvert, G., Spence, C., Stein, B.E., 2004. *The Handbook of Multisensory Processes.* MIT Press.
- Cascio, C.J., Foss-Feig, J.H., Burnette, C.P., Heacock, J.L., Cosby, A.A., 2012. The rubber hand illusion in children with autism spectrum disorders: delayed influence of combined tactile and visual input on proprioception. *Autism* 16, 406–419. doi:10.1177/1362361311430404
- Colonus, H., Diederich, A., 2004. Multisensory Interaction in Saccadic Reaction Time: A Time-Window-of-Integration Model. *J. Cogn. Neurosci.* 16, 1000–1009. doi:10.1162/0898929041502733
- Cowie, D., Makin, T.R., Bremner, A.J., 2013. Children’s Responses to the Rubber-Hand Illusion Reveal Dissociable Pathways in Body Representation. *Psychol. Sci.* 24, 762–769. doi:10.1177/0956797612462902
- Cowie, D., Sterling, S., Bremner, A.J., 2016. The development of multisensory body representation and awareness continues to 10 years of age: Evidence from the rubber hand illusion. *J. Exp. Child Psychol.* 142, 230–238. doi:10.1016/j.jecp.2015.10.003
- Delaney, H.D., Maxwell, S.E., 1981. On Using Analysis Of Covariance In Repeated Measures Designs. *Multivar. Behav. Res.* 16, 105–123. doi:10.1207/s15327906mbr1601_6
- Dunn, L.M., Dunn, D.M., 2009. *The British picture vocabulary scale.* GL Assessment Limited.
- Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415, 429–433. doi:10.1038/415429a

- Hairston, W.D., Hodges, D.A., Burdette, J.H., Wallace, M.T., 2006. Auditory enhancement of visual temporal order judgment: *NeuroReport* 17, 791–795. doi:10.1097/01.wnr.0000220141.29413.b4
- Hillock, A.R., Powers, A.R., Wallace, M.T., 2011. Binding of sights and sounds: Age-related changes in multisensory temporal processing. *Neuropsychologia* 49, 461–467. doi:10.1016/j.neuropsychologia.2010.11.041
- Hillock- Dunn, A., Wallace, M.T., 2012. Developmental changes in the multisensory temporal binding window persist into adolescence. *Dev. Sci.* 15, 688–696. doi:10.1111/j.1467-7687.2012.01171.x
- Jackson, C.V., 1953. Visual factors in auditory localization. *Q. J. Exp. Psychol.* 5, 52–65. doi:10.1080/17470215308416626
- Jaime, M., Longard, J., Moore, C., 2014. Developmental changes in the visual–proprioceptive integration threshold of children. *J. Exp. Child Psychol.* 125, 1–12. doi:10.1016/j.jecp.2013.11.004
- Lewald, J., Ehrenstein, W.H., Guski, R., 2001. Spatio-temporal constraints for auditory–visual integration. *Behav. Brain Res.* 121, 69–79. doi:10.1016/S0166-4328(00)00386-7
- Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C.A., Haggard, P., Iannetti, G.D., 2014. Whole-body mapping of spatial acuity for pain and touch. *Ann. Neurol.* 75, 917–924. doi:10.1002/ana.24179
- Nava, E., Steiger, T., Röder, B., 2014. Both developmental and adult vision shape body representations. *Sci. Rep.* 4, 6622. doi:10.1038/srep06622
- Newport, R., Pearce, R., Preston, C., 2010. Fake hands in action: embodiment and control of supernumerary limbs. *Exp. Brain Res.* 204, 385–395. doi:10.1007/s00221-009-2104-y
- Rochat, P., Striano, T., 2000. Perceived self in infancy. *Infant Behav. Dev.* 23, 513–530. doi:10.1016/S0163-6383(01)00055-8
- Schütz-Bosbach, S., Mancini, B., Aglioti, S.M., Haggard, P., 2006. Self and Other in the Human Motor System. *Curr. Biol.* 16, 1830–1834. doi:10.1016/j.cub.2006.07.048
- Slutsky, D.A., Recanzone, G.H., 2001. Temporal and spatial dependency of the ventriloquism effect. *NeuroReport Rapid Commun. Neurosci. Res.* 12, 7–10. doi:10.1097/00001756-200101220-00009
- Stevenson, R.A., Wallace, M.T., 2013. Multisensory temporal integration: task and stimulus dependencies. *Exp. Brain Res.* 227, 249–261. doi:10.1007/s00221-013-3507-3

- Thomas, M.S.C., Annaz, D., Ansari, D., Scerif, G., Jarrold, C., Karmiloff-Smith, A., 2009. Using Developmental Trajectories to Understand Developmental Disorders. *J. Speech Lang. Hear. Res.* 52, 336. doi:10.1044/1092-4388(2009/07-0144)
- Tsakiris, M., Haggard, P., 2005. The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 80–91. doi:10.1037/0096-1523.31.1.80
- Wallace, M.T., Roberson, G.E., Hairston, W.D., Stein, B.E., Vaughan, J.W., Schirillo, J.A., 2004. Unifying multisensory signals across time and space. *Exp. Brain Res.* 158, 252–258. doi:10.1007/s00221-004-1899-9
- Wallace, M.T., Stevenson, R.A., 2014. The construct of the multisensory temporal binding window and its dysregulation in developmental disabilities. *Neuropsychologia* 64, 105–123. doi:10.1016/j.neuropsychologia.2014.08.005
- Zmyj, N., Jank, J., Schütz-Bosbach, S., Daum, M.M., 2011. Detection of visual–tactile contingency in the first year after birth. *Cognition* 120, 82–89. doi:10.1016/j.cognition.2011.03.001

Figure Captions

Figure 1. Children 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. 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.

Figure 2. Children pointed their index finger straight in front of them while resting their fist on the MIRAGE work surface. The hand was either seen in the same spatial location as their actual hand or displaced to the right by 0.5, 1, 1.5 or 2 hand widths.

Figure 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%). All other analyses were run using age as a linear covariate.

Figure 4. Children pointed their index finger straight in front of them while resting their fist on the MIRAGE work surface. The experimenter held a white-led pencil approximately 3cm perpendicular to the tip of the child's right index finger. 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 the original position. The visual touch occurred at the same time as the felt touch or 100, 150, 200, 300 or 400ms after the felt touch. In order to show the hand positions clearly, the hand is not shown inside MIRAGE in this figure.

Figure 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.