Psychological SCIENCE Research, Theory, & Application in Psychology and Related Sciences aps ASSOCIATION FOR PSYCHOLOGICAL SCIENCE

The development of a crossmodal sense of body ownership

Journal:	*Psychological Science*
Manuscript ID	PSCI-15-0753.R4
Manuscript Type:	Research article
Date Submitted by the Author:	n/a
Complete List of Authors:	Nava, Elena; University of Milan-Bicocca, Dep. of Psychology Bolognini, Nadia; University of Milano Bicocca, Psychology Turati, Chiara; University of Milano Bicocca, Psychology
Keywords:	Childhood Development, Cognitive Development, Human Body

THE DEVELOPMENT OF A CROSSMODAL SENSE OF BODY OWNERSHIP

Elena Nava[1], Nadia Bolognini[1,2], Chiara Turati[1]

[1] Department of Psychology & Milan Center for Neuroscience - University of Milano Bicocca (Italy)

[2]Laboratory of Neuropsychology, IRCCS Istituto Auxologico Italiano (Italy)

Abstract

In this study, we investigated the contribution of tactile and proprioceptive cues to the development of the sense of body ownership by testing the susceptibility of 4-5- and 8-9-year-old children, and adults to the Somatic Rubber Hand Illusion (SRHI). We found that feelings of owning a rubber hand, as assessed by means of explicit reports (i.e., questionnaire), are already present by age 4 and do not change throughout development. On the contrary, the capture of the sense of hand position by the illusion, as assessed by a pointing task, is only present in 8-9 year-olds and adults, but not younger children, and the magnitude of such capture increases with age.

Our findings reveal that tactile-proprioceptive interactions differently contribute to the two aspects characterising the SRHI: while their contribution to an explicit sense of self is already adult-like by age 4, their contribution to a more implicit recalibration of hand position are still developing by age 9.

1. Introduction

The sense of body ownership is intrinsically linked to bodily self-awareness. Several studies have shown that the way we perceive our body arises from the efficient integration of bodily signals coming from different sensory modalities, among which touch, proprioception, and vision play a major role (Bolognini & Maravita, 2007; Ehrsson, 2012). One of the most famous paradigms that has contributed to the notion of multisensory sense of self is the Rubber Hand Illusion (RHI, Botvinick & Cohen, 1998), in which synchronous strokes performed on the (hidden from view) participant's hand and a (visible) artificial rubber hand induce the participants to report that the rubber hand is their hand. Interestingly, the feeling of owning a rubber hand is also induced without the contribution of vision (Ehrsson, Holmes & Passingham, 2005; Nava, Steiger & Röder, 2014). Indeed, in the so-called Somatic Rubber Hand Illusion (SRHI, Ehrsson et al., 2005; Nava et al., 2014; Petkova et al., 2012), blindfolded adult participants touch a rubber hand while their hand is being synchronously touched. This gives rise to the illusory feeling that participants are actually touching their own hand. The RHI and SRHI are commonly measured through a questionnaire and a pointing task, which respectively assess two aspects of the illusion: a more explicit, conscious feeling of owning a rubber hand (i.e., self-evaluation in the questionnaire), and a more implicit, sensorimotor measure, consisting in a mis-localisation of the perceived location of the own hand towards the rubber hand (i.e., proprioceptive drift in the pointing task). Notably, these two measures do not always correlate (Nava et al., 2014; Rohde, Di Luca & Ernst, 2011), suggesting that the explicit feelings of ownership and the recalibration of hand position reflect two separate mechanisms subtending body representation.

To date, the development of the sense of body ownership has received very little attention, notwithstanding the importance for the construction of a unitary and coherent representation of the body and for self-awareness. Two studies have directly investigated children's susceptibility to the RHI in children aged 4 to 9 (Cowie, Makin & Bremner, 2013) and in children aged 10 to 13 (Cowie, Sterling & Bremner, 2016). The first study showed that in children there is a dissociation between reported feelings of ownership and recalibration of hand positon toward the rubber hand. Indeed, while both children and adults similarly reported feelings of owning a rubber hand (as indexed from a questionnaire), children up to 9 years of age showed larger proprioceptive drifts compared to adults. The authors proposed that these two components at the basis of the RHI may be supported by different mechanisms. In particular, while the similar scores provided in the questionnaire across age groups could indicate an early maturation of visuo-tactile integration processes linked to the explicit perception of ownership over one's own body, the larger proprioceptive drift could index a later maturing visuo-proprioceptive process, which is more implicit. Interestingly, Cowie et al. (2016) found that proprioceptive drifts reach adult-levels by age 10-11, suggesting that some aspects of multisensory body representation undergo a protracted period of development.

The contribution of visual and proprioceptive cues to the perception of bodily illusions in young children (i.e., 5- to 7-year-olds) has also been investigated by Bremner and colleagues (2013), by means of the Mirror Illusion (Holmes, Crozier & Spence, 2004). In this crossmodal illusion, a mirror is placed between the participant's arms, facing one hand (e.g., left) and covering the other hand (i.e., right). The mirror presents an apparent visual location of the (right) hand, which is in conflict with its real position, perceived through proprioception. In adults, reaching responses made with the unseen right arm are biased by the mirror reflection of their left hand. Children were overall sensitive to the visual capture of hand position (indexed by the reaching bias); nonetheless, the visual capture increased substantially up until 6 years of age.

Overall, current evidence indicates that particularly visuo-tactile-proprioceptive interactions for body representation undergo relevant changes during early childhood (whose development is protracted up to 11 years of age; see Cowie, Sterling & Bremner, 2016). However, it is still unknown whether and how tactile and proprioceptive modalities interact in the absence of vision, and contribute to the development of the sense of body ownership and position.

Touch and proprioception alone, as well as their interactions, are foundational to self-perception from birth. Indeed, proprioceptive and somatosensory anatomy and functions are in place very early in prenatal development (along with chemosensation, see Turkewitz & Kenny, 1982). From birth, infants systematically explore themselves and the world primarily through touch and proprioception (e.g., by moving their limbs, sucking, etc., Rochat & Striano, 2000). In particular, infants experience tactile-proprioceptive interactions when they bring their hands towards their mouth or other parts of their body, thus learning the contingency of this multisensory stimulation (Butterworth & Hopkins, 1988). This behaviour may predict and shape a sense of body ownership which largely involves tactile-proprioceptive cues. Furthermore, infants are able to reach to objects even if deprived of vision of their own hands, as shown in a study (Clifton, Muir, Ashmead & Clarkson, 1993), in which infants succeeded grasping an object both in light and in darkness, suggesting that proprioceptive cues drive the development of reaching in early infancy.

In light of these considerations, this study explores, for the first time, the role of proprioceptive and tactile cues in the development of the sense of bodily self, without any visual contribution, by testing the susceptibility of children aged 4-5 and 8-9 to the SRHI. Two hypotheses could be made. First, because the tactile and proprioceptive modalities develop very early in ontogeny and are early integrated, children could already present an adult-like susceptibility to the illusion. Alternatively, because the tactile information needs to be properly calibrated by vision (see Gori, Del Viva, Sandini & Burr, 2008), children may show a weaker or even no illusion as compared to adults.

2. Method

2.1 Participants

Informed by developmental studies on comparable topics (e.g., Cowie et al., 2013), we set our sample size at 18 per condition for the groups of children, all right-handed. Our final sample comprised 72 children: thirty-six 4-5 year-olds (20 females, mean age = 5.0, ±0.5) and thirty-six 8-9 year-olds (19 females, mean age = 5.1, ±0.6), and 40 adults (25 females, mean age = 23.8, ±5.3). Four additional children aged 4-5 years were tested but excluded from the final sample because they had difficulties understanding the task. All age groups were further split into two groups, with half of the participants performing the synchronous condition (4-5 years: N = 18; 8-9 years: N = 18; adults: N = 20), and the other half the asynchronous condition (4-5 years: N = 18; 8-9 years: N = 18; adults: N = 20). This between-subject design aimed at minimizing testing time particularly for children. The children were tested after obtaining the signed informed consent by their parents. The study was approved by the Ethical Committee of the University of Milan-Bicocca.

2.2 Experimental design

2.2.1 Induction of the SRHI

A life-sized plastic left hand served as stimulus to induce the SRHI. The rubber hand was placed between the participant's hands, at a distance of 15 cm between the participant's left index finger and the rubber hand's index finger. The stimulation consisted in having the experimenter moving the index finger of the participant's right hand on the rubber hand. At the same time, the experimenter stroked the same part of the left hand of the participant, synchronizing the stroking of both hands as closely as possible in the synchronous condition, while providing sequential stroking (i.e., one stroke to the rubber hand, one stroke to the participant's hand) in the asynchronous condition. The participants were stroked in a proximal-distal direction, randomly across all fingers, knuckles, and parts of the hand, at a rate of approximately 0.5-1.5 Hz. The stroking velocity was also randomly changed. Similarly to other studies (see e.g., Rohde et al., 2011), a pilot study conducted with adults had shown that randomly changing spatial and temporal pattern during tactile stimulation increases sense of ownership over the rubber hand.

Each stimulation lasted ≈ 60 seconds (one trial), and was repeated three times (i.e., overall 180 seconds of stimulation). Short breaks between trials (≈ 10/15 seconds) served the experimenter to ask the participants (particularly the children) if everything was all right.

2.2.2 Measurement of the pointing task

To document whether the felt position of the participant's left hand would change after the stroking session, participants performed a pointing task before and after the induction of the SRHI. The task consisted in pointing, with the right-hand index finger, towards the middle finger of the left hand, which was placed under a cardboard box (length= 60 cm; width= 30 cm; height= 40 cm), designed to resemble a small table. Participants had to make the pointing movement over the table, on which a measuring tape was placed. After each pointing, the experimenter manually took the response by typing the number of cm in the computer.

2.2.3 Measurement of the sense of body ownership through a questionnaire

At the end of the experiment, participants were asked to rate two statements. The first one was designed to reflect the strength of the embodiment of the rubber hand: "I felt as if I were touching my own hand". The other statement was unrelated to the illusion and served as control statement for suggestibility: "I felt as if I had three hands"[1].

All participants were asked to rate each single statement on a continuous rating scale, by pointing to the appropriate position on a continuous line (adults were asked to mark with a pencil the rating scale). The extreme left of the line indicated "I strongly disagree" and corresponded to -5, while the extreme right of the line indicated "I strongly agree" and corresponded to 5. A mark in the middle of the line, corresponding to 0, indicated "I neither agree nor disagree".

For children, the statements were repeated and rephrased until the experimenter thought they were fully understood. Also, the scale was adapted for children to be more easily understood, so that +5 corresponded to "yes, a lot", -5 to "not at all" and 0 to "in between".

2.2.4 Experimental procedure

All participants were tested individually in a quiet room and were informed about the study and the material used (i.e., rubber hand, blindfold). Participants were then blindfolded and their left hand placed palm down on the table. To familiarise the participant with the pointing task, the experimenter took the participant's right index finger and moved it towards the left middle finger over the top of the cardboard box. Once the participant had understood the task, the actual pointing task started and the experimenter recorded (in cm) the three trials performed by the participants. After the pointing task, the experimenter placed the rubber hand next to the participant's left hand and started with the illusion induction.

After the induction of the SRHI, participants were re-tested on the pointing task, which consisted in 3 pointing trials. At the end of the task, the blindfold was removed and participants were presented with the questionnaire.

3. Results

3.1 Pointing

Analyses on the pointing were aimed at answering two main questions: 1) do children and adults recalibrate their hand position after the SRHI induction? 2) Is there a developmental change in the SRHI?

To answer the first question, we entered the average pointing into a repeated-measure Analysis of Variance (rmANOVA), with Session (pre- SRHI and post- SRHI) as a within-subjects factor, and Age (the two groups of children and the adults) and Synchrony (synchronous and asynchronous stroking) as between-subjects factors. The analysis revealed main effects of: Age, $F(2, 106) = 3.35$, $p = 0.04$, Synchrony, $F(1, 106) = 17.01$, $p < 0.001$, and Session, $F(1, 106) = 51.34$, $p < 0.001$. We also found the following significant interactions:

[1] We only included a single illusion statement because in a pilot study with ten 4-5 year-old children (who were different from the sample included in the final analysis) we assessed that other classical questions (adapted from the Botvinick & Cohen questionnaire, 1998, i.e., "It seemed as if I were feeling the touch on my hand in the location where I was touching the rubber hand") were too difficult for this particular age group to be reliably understood.

Session x Age, F(2, 106) = 14.43, p < 0.001, Session x Synchrony, F(1, 106) = 43.73, p < 0.001, and, most importantly, a Session x Synchrony x Age interaction, F(2, 106) = 3.62, p = 0.03. To further explore the triple interaction, we conducted other two rmANOVA separately for the two synchrony conditions, given that the SRHI is reliably induced by synchronous stroking (Botvinick & Cohen, 1998; Ehrsson et al., 2004).

The 2 (Session) x 3 (Age) rmANOVA for the synchronous condition revealed a main effect of Session, F(1, 53) = 97.77, p < 0.001, and a significant interaction between Age and Session, F(2, 53) = 12.00, p < 0.001. Post-hoc Bonferroni-corrected comparisons showed that only 8-9 year-old children and adults had a significant difference between pre- and post-illusion scores (both p < 0.001); on the contrary, 4-5 year-olds did not present such difference (p = 0.09). That is, only older children and adults proved to be sensitive to the SRHI, as indexed by recalibration of their hand position toward the rubber hand (see Fig. 1A).

Additionally, post-hoc tests also showed that pre-illusion scores differed between 4-5 year-old children and adults (p = 0.01) because of younger children biasing their pointing toward the left side with respect to their hand position. Note however that 4-5 year-olds did not differ from 8-9 year-olds (p = 0.99) and the latter did not differ from adults (p = 0.22).

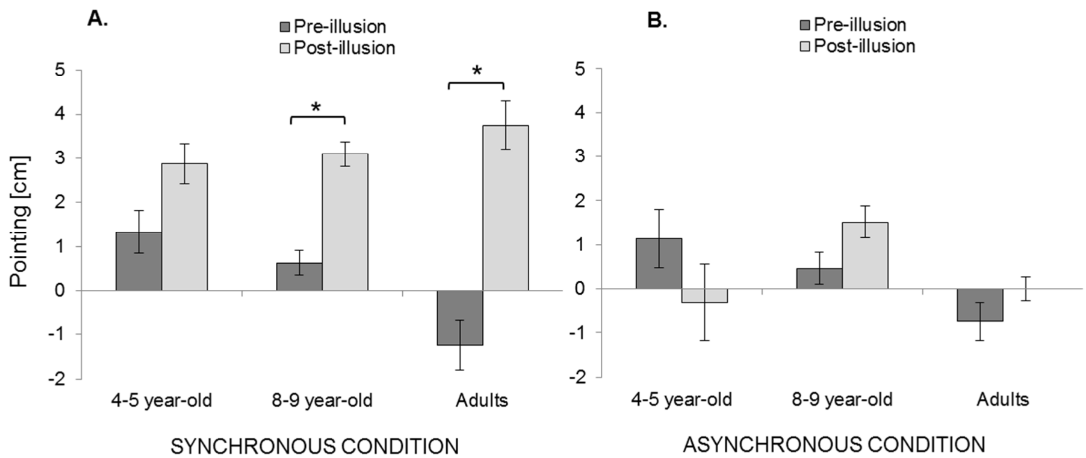
In the asynchronous condition, the same rmANOVA model showed a significant Age x Session interaction, F(2, 53) = 621, p = 0.003. However, post-hoc comparisons did not reveal any significant difference related to the SRHI: indeed, there was no difference among groups and between pre- and post-illusion scores (all ps > 0.20, see Fig. 1B).

This evidence was further verified by analysing changes in the SRHI magnitude across age. To this aim, we calculated the difference between post- and pre- illusion scores, in turn computing the so-called proprioceptive drift, which was then entered in a 2 x 3 ANOVA, with Synchrony and Age as between-subject factors. The analysis showed main effects of Age, F(2, 106) = 14.43, p < 0.001, and of Synchrony, F(1, 106) = 43.73, p < 0.001, and a significant Age x Synchrony interaction, F(2, 106) = 3.62, p = 0.03. The interaction was then analysed with two separate 1-way ANOVAs (between-subject factor: Age) for synchronous and asynchronous conditions.

The 1-way ANOVA of the synchronous condition revealed a main effect of Age, F(2, 53) = 12.00, p < 0.001: Bonferroni-corrected comparisons showed a larger proprioceptive drifts in adults as compared to both 4-5 (p < 0.001) and 8-9-year-old children (p = 0.003), with no differences between the two groups of children (p = 0.68).

The 1-way ANOVA of the asynchronous condition revealed a main effect of Age too, F(2, 53) = 6.21, p = 0.004: the effect was caused by 4-5 year-old children having a different directional pointing drift compared to both 8-9 year-olds (p = 0.006) and adults (p = 0.02): indeed, younger children showed a proprioceptive drift in the opposite direction of the rubber hand, hence they did not show the typical directional bias featuring the SRHI. No difference emerged between 8-9 year-old children and adults (p = 0.99).

Fig. 1



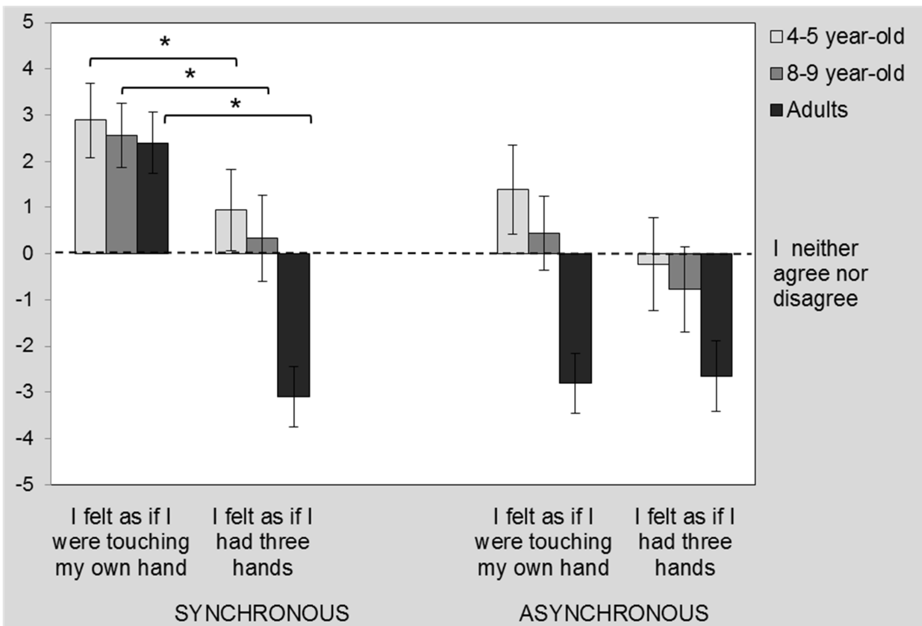
3.2 Questionnaire

Because the scores for the illusion and control question were not normally distributed, they were analysed with non-parametric tests to observe differences between groups (Kruskal-Wallis test) and within groups (Wilcoxon Signed Rank Test).

Following the rational of the data analysis performed on the pointing data, we first explored whether children and adults perceived the illusion at all, by comparing the illusion against the control question, separately for group. Higher scores to the illusion (than control) question following synchronous stroking would indicate a sensitivity to the illusion. This analysis indeed revealed a general sensitivity to the illusion in all age groups, in that all participants rated more positively the illusion than the control question in the synchronous condition (all ps < 0.03, see Fig. 2). On the contrary, no difference emerged between the illusion and the control question in the asynchronous condition in all age groups (all ps > 0.20).

Having established that all participants subjectively experienced the illusion, we then explored the developmental changes in the magnitude of the perceived illusion in the synchronous and the asynchronous condition across groups. A Kruskal-Wallis test did not reveal any difference across age groups in the synchronous condition, $H(2, 56) = 1.29$, $p = 0.52$. On the contrary, there was a difference across age groups in the asynchronous condition, $H(2, 56) = 12.29$, $p = 0.002$. Post-hoc comparisons showed that this was caused by adults providing stronger negative responses to the illusion question than children. No difference was found between children (p = 0.99). Overall, these findings show that no developmental change was observed in the subjective report of the illusion.

Fig. 2



Inspection of Fig. 2 suggests that the difference observed between younger children and adults in the magnitude of perceived illusion may have been the result of difficulties for younger children to understand the questions, rather than the consequences of genuinely perceiving the SRHI.

To rule this possibility out, and in turn to assess whether younger children are genuinely sensitive to the illusion, we ran a new experiment with a new sample of younger children (N = 33), to whom 4 questions (two illusion and two control questions) were given before and after the induction of the illusion. We reasoned that if children are genuinely experiencing the illusion, we would see differences in rating the questions selectively for the illusion than the control questions.

Furthermore, we also changed the way of recording children's response: instead of indicating their response on the scale, the child was asked to rate his/her experience on a 7-point scale similar to the one used by Cowie et al. (2013). The pointing task followed the same procedure of Experiment 1, so that we also had the opportunity to replicate our findings on the proprioceptive drift.

4. Experiment 2

4.1 Participants, stimuli and procedure

Eighteen new 4-5 year-old children (8 females, mean age = 5.0, ± 0.60) were tested on the SRHI in the synchronous condition, while fifteen 4-5 year-old children (5 females, mean age = 4.8, ± 0.60) were tested in the asynchronous condition. The stimuli and the procedure mimicked Experiment 1, with the following differences: the questionnaire consisted of 4 questions, 2 items referring to the illusion, and 2 items used as control questions. We therefore added one additional illusion question and one additional control question to those used in the previous experiment (Experiment 1), and we also presented them in a different form. The two illusion questions were "While you were touching the rubber hand, did you feel as if you were touching your own hand?" (like in Experiment 1) and "While you were touching the rubber hand, did you feel as if the rubber hand were your own hand?". The two control questions were "While you were touching the rubber hand, did you feel as if you had three hands?" (like in Experiment 1) and "While you were touching the rubber hand, did you feel as if your own hand had disappeared?". In this new experiment, instead of pointing on the response line, the children were asked to rate the perception on a 7-point scale, similar to Cowie et al. (2013), with "0" corresponding to "absolutely no" and "6" to absolutely yes". Contrarily to Experiment 1, the child gave a verbal response that the experimenter typed into the computer. By simply adding two new questions to the ones used in Experiment 1 (and not changing them all), we aimed at verifying whether possible difference between Experiment 1 and Experiment 2 would arise from the difficulties of the questions (i.e., children overall not understanding them) or by the way children were instructed to answer them.

To prove that the younger children really understood the questions and could discriminate between illusion and control questions, we posed them not only after, but also prior to the illusion induction with the rubber hand. We reasoned that if for the children illusion and control statements were not distinguishable, they would provide the same answer to each of the items irrespective of the induction of the illusion. In this baseline test, each child was blindfolded and the experimenter stroked the child's finger over the rubber hand. That is, there was no illusion induction, only the experience of touching the rubber hand alone. Following the baseline test, the experiment would proceed exactly as Experiment 1, thus including the measurement of the proprioceptive drift.

5. Results

5.1 Pointing

The pointing data of the new sample of 4-5 year-old children was entered into a 2x2x4 rmANOVA, with Session (pre- and post-illusion pointing) as within-subjects factor, and Synchrony (synchronous vs. asynchronous condition), and Group (the new sample of 4-5 year-old children and the three groups of Experiment 1) as between-subjects factors.

The analysis revealed the following main effects: Synchrony, $F(1, 137) = 10.30$, $p = 0.002$, and Session , $F(1, 137) = 41{,}58$, $p < 0.001$; and interactions: Session x Group, $F(3, 137) = 10.25$, $p < 0.001$, Session x Synchrony, $F(1, 137) = 35.05$, $p < 0.001$, and, most importantly, a triple Session x Synchrony X Group interaction, $F(3, 137) = 3.56$, $p = 0.02$. Separate 2 x 4 ANOVA on condition showed that in the synchronous condition, there was a main effect of Session, $F(1, 70) = 65.94$, $p < 0.001$, and a significant interaction between Session and Group, $F(3, 70) = 8.58$, $p < 0.001$. Post-hoc Bonferroni-corrected comparisons showed that the pre- and post-illusion pointing of the two 4-5 year-old groups did not differ (both $p > 0.45$).

As in Experiment 1, in the asynchronous condition we also found a significant Session x Group interaction, $F(3, 67) = 4.77$, $p = 0.004$, but again, post-hoc comparisons did not reveal any significant difference related to the SRHI (all ps > 0.17).

Finally, a 2 x 4 ANOVA with Drift as within-subjects factor, and Synchrony and Group as between-subjects factor showed a main effect of Group, $F(3, 137) = 10.25$, $p < 0.001$, and Synchrony, $F(1, 137) = 35.05$, $p < 0.001$, as well as a significant Group x Synchrony interaction, $F(3, 137) = 3.56$, $p = 0.02$. Separate ANOVA on the two stroking modes confirmed the pattern of Experiment 1. Indeed, there was a main effect of Group in the synchronous condition, $F(3, 70) = 8.58$, $p < 0.001$, caused by larger drifts of adults in comparison to all the other groups of children (all ps < 0.03). Furthermore, the two groups of 4-5 year-old children had comparable drifts with respect to the 8-9 year-old children (both ps > 0.63). In the asynchronous condition, we found a main effect of Group too, $F(3, 67) = 4.77$, $p = 0.004$, but it was not caused by the drift of the new sample of 4-5 year-olds. Indeed, the new sample of 4-5 year-old children did not differ from any other group (all ps > 0.30).

Overall, results of Experiment 2 successfully replicated data of Experiment 1, corroborating the finding that the illusion does not show in 4-5 year-old children.

5.2 Questionnaire

As in Experiment 1, the questions were analysed using non-parametric tests. Because Experiment 1 served specifically to observe whether 4-5 year-old children understand the questions related to the illusion, and because they were presented in a different fashion with respect to Experiment 1, we analysed them without making further comparisons with Experiment 1. First, we compared all four questions in the synchronous and the asynchronous conditions before illusion induction (i.e., baseline) but did not find any difference, in that the children rejected all of them in both stroking modes (all ps > 0.73). In contrast, we did find a difference between questions following the SRHI induction selectively for the illusion questions. In other words, the children gave higher ratings to the two illusion questions following synchronous (illusion question 1: mean = 4.72, SD = 1.18; illusion question 2 = 3.89, SD = 2.11) but not asynchronous stroking (illusion question 1: mean = 0.80, SD = 1.52; Z = 4.42, p < 0.001; illusion question 2 = 0.33, SD = 1.29; Z = 3.69, p < 0.001, see Fig. 3). Furthermore, there was no difference between the control questions following synchronous and asynchronous stroking (all ps > 0.44).

A significant difference was observed between the illusion and the control questions following synchronous (both p < 0.001) but not asynchronous stroking (both p > 0.10), revealing that the children experienced the illusion.

6. Discussion

In this study we investigated, for the first time, the contribution of tactile and proprioceptive cues and their interaction in the development of the sense of body ownership brought about by the SRHI. Results showed that the subjective feeling of owning a rubber hand, as assessed by means of explicit reports (i.e., questionnaire), is already present by age 4 and does not change throughout development. This evidence is in line with previous studies conducted on both adults (Ehrsson et al., 2005; Nava et al., 2014), and children (Cowie et al., 2013; 2016) and suggests that the conscious perception of the body does not rely upon constant visual feedback. It is also in line with the perspective that the questionnaire reflects a sort of 'default' representation of the body image: this internal body representation controls, in a top-down fashion, incoming new bodily sensory signals, monitoring their inclusion in the body image (Costantini & Haggard, 2007). In other words, children, as well as adults, are aware that they possess a certain number of body parts possessing specific characteristics; based on such implicit knowledge the incoming multisensory cues (here induced by the synchronous SRHI) are processes and included in the body image.

By contrast, results from the pointing task show that a reliable capture of the sense of hand position by the SRHI, which is a more unconscious, bottom-up, measure with respect to the questionnaire, was only present in 8-9 year-old children and adults. Indeed, while older children and adults showed a difference in pre- and post-illusion pointing selectively in the synchronous SRHI, 4-5 year-old children did not show the recalibration of hand position toward the rubber hand after both stroking modes. Furthermore, the changes in the magnitude of the drift in the synchronous condition, i.e., larger drifts in adults compared to both 4-5- and 8-9- year-olds, further confirms that, although the integration of tactile and proprioceptive cues necessary to experience the SRHI, is in place by 8-9 years, such multisensory process is not yet adult-like.

The absence of capture of hand position by 4-5 year-old children could have two, non-mutually exclusive reasons. First, there are studies suggesting that tactile spatial abilities appear late in development. In this regard, Begum Ali, Cowie and Bremner (2014) showed that 4 year-old children are worse than 6 year-old children at localising tactile stimuli applied to their hands. This disadvantage increased mainly when 4 year-old children were given visual feedback about the position of their hands, and disappeared when the sight of their hands was covered. This means that vision strongly enters in conflict with proprioception at a younger age. In this perspective, it could be claimed that our children 'took advantage' from being blindfolded to fully rely on the tactile cue, that is, on their hand being stroked.

Another possibility is that younger children have yet not developed optimal integration abilities, upon which both the SRHI as well as the RHI strongly rely (see Ehrsson et al., 2004; 2005). If children do not integrate tactile and proprioceptive cues, the illusory tactile capture of the hand position is prevented. Indeed, crossmodal illusion in general, and the SHRI in particular, arises when the brain is capable of fusing together multisensory inputs, namely the real self-touch of the rubber hand and the position of the participant's hand being stroked in the SHRI, based on their temporal correlations. At the neural level, the emergence and maturation of multisensory integration critically depend on cross-modal experience (stein et al., 2014). Thus, on the same line, it could be claimed that the experience made with tactile-proprioceptive cues, necessary for optimally integrating them, is still not sufficient by age 8-9.

Overall, our findings appear to corroborate previous studies that showed that integration across different sensory pairings (e.g., visual and haptic, Gori, Del Viva, Sandini & Burr, 2008; auditory and haptic, Petrini, Remark, Smith & Nardini, 2014) are "late bloomers" (Ernst, 2007), suggesting that tactile and proprioceptive interactions are still developing by age 8-9.

Because Cowie et al. (2013) tested 4- to 9- year-old children on the visual RHI, it is important to highlight the common findings, as well as the differences. First, both Cowie et al (2013) and our study revealed that the subjective feeling of owning the rubber hand is already adult-like by age 4. This suggests that an explicit, conscious experience of owning a rubber hand is not modulated by types of sensory modalities involved: both the RHI and the SRHI demonstrate that visuo-tactile and tactile-proprioceptive cues, respectively, contribute to the explicit sense of body ownership, and, ultimately, to a sense of self.

However, the comparison of the proprioceptive drift dramatically changes in the two illusions. Indeed, at variance of our findings with the SRHI, Cowie et al. (2013) found that all children experienced the visual RHI, and that the magnitude of the illusion decreased with age. Since the most evident difference between our paradigm and that of Cowie and colleagues (2013) is the preclusion of vision - allowed in the RHI but precluded in the SRHI - the different performance of younger children is suggestive of a special role of vision in shaping the multisensory representation of the body in space during development. Among the other senses, vision predominantly contributes, and likely guides, multisensory experiences that constantly update the brain about current postures of the body and its parts. Indeed, vision provides a default use of an external coordinate frame for multisensory control of action (Röder, Kusmierek, Spence & Schicke, 2007; Bolognini & Maravita, 2007). Because touch is automatically remapped onto an external frame of reference, it could be that younger children are still developing an adult-like automaticity in remapping touch in external frames and, in the absence of vision, they tend to switch frames of reference in favour of an anatomical one.

Finally, we should discuss why there are differences in the explicit and implicit sense of body ownership, as observed in the difference between subjective reports and proprioceptive drift. Our interpretation is that an overt, explicitly reported (as derived from the questionnaire) sense of body ownership may derive from from an early-developing representation of the body (Berlucchi & Aglioti, 1997; Costantini & Haggard, 2007). Conversely, the ability to spatially remap the hand position may need constant multisensory experiences in order to fine-tune to adult-like levels (Gori, Del Viva, Sandini & Burr, 2008; Nardini, Jones, Bedford & Braddick, 2008; Stein, Stanford & Rowland, 2014). The difference between an explicit and implicit body representation is also suggestive of the historical difference between the body image and the body schema put forward by the neuropsychological literature in brain-damaged patients (Head & Holmes, 1911; Paillard, 1999; Berlucchi & Aglioti, 1997). While the body image represents the knowledge of possessing different body parts in their actual layout and occurs at a conscious level, the body schema registers one's body parts in space and updates them – unconsciously - while the body moves. In this perspective, it could be speculated that while the body image develops early in life, the body schema adjusts as the body rapidly changes in size through development.

In conclusion, our findings show that tactile-proprioceptive interactions differently contribute to emerging aspects underlying the development of body representation. While these interactions underlie an earlier development of a subjective sense of self, they still need to fine-tune in determining the position of the body parts.

Acknowledgments

We would like to thank Viola Brenna, Giulia Corasaniti, Marica Corvetti and Elisa Frigerio for helping in recruiting and testing the children. We would also like to thank all the children and families that participated in the experiment. This study was supported by a European Research Council Starting Grant to C.T. on a project entitled 'The origins and development of the human mirror neuron system' - ODMIR. No. 241176.

Authors' contribution

E.N. and C.T. developed the study concept; testing and data collection were performed by E.N.; E.N. and N.B. performed the data analysis and interpretation under the supervision of C.T. E.N. drafted the manuscript, and C.T. and N.B. provided critical revisions. All authors approved the final version of the manuscript for submission.

References

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

Berlucchi, G, & Aglioti, S. (1997). The body in the brain: neural bases of corporeal awareness. *Trends in Neuroscience, 20*, 560-564.

Bolognini, N., & Maravita, A. (2007). Proprioceptive alignment of visual and somatosensory maps in the posterior parietal cortex. *Current Biology*, *17*, 1890-1895.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel'touch that eyes see. *Nature*, *391*, 756-756.

Bremner, A.J., Hill, E.L., Pratt, M., Rigato, S., & Spence, C. (2013). Bodily illusions in young children: developmental change in visual and proprioceptive contributions to perceived hand position. *PloS One*, *8*, e51887.

Butterworth, G., & Hopkins, B. (1988). Hand-mouth coordination in the new-born baby. *British Journal of Developmental Psychology*, *6*, 303-314.

Clifton, R. K., Muir, D. W., Ashmead, D. H., & Clarkson, M. G. (1993). Is visually guided reaching in early infancy a myth?. *Child Development*, *64*, 1099-1110.

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*, 229-240.

Cowie, D., Makin, T.R., & Bremner, A.J. (2013). Children's responses to the rubber-hand illusion reveal dissociable pathways in body representation. *Psychological Science*, *24*, 762-769.

Cowie, D., Sterling, S., & Bremner, A. J. (2016). The development of multisensory body representation and awareness continues to 10years of age: Evidence from the rubber hand illusion. *Journal of Experimental Child Psychology*, *142*, 230-238.

Cowie, D., Sterling, S., & Bremner, A.J. (2016). The development of multisensory body representation and awareness continues to 10years of age: evidence from the rubber hand illusion. *Journal of Experimental Child Psychology*, *142*, 230-238.

Ernst, M. O. (2008). Multisensory integration: a late bloomer. *Current Biology*, *18*, R519-R521.

Ehrsson, H. H., Spence, C., & Passingham, R.E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, *305*, 875-877.

Ehrsson, H. H. (2012). The concept of body ownership and its relation to multisensory integration. In B. E. Stein (Ed.), *The New Handbook of Multisensory Processes* (pp. 775–792). Cambridge, MA: MIT Press.

Ehrsson, H.H., Holmes, N.P., & Passingham, R.E. (2005). Touching your own body: self-attribution is associated with activity in multisensory brain regions. *Journal of Neuroscience*, *25*, 10564-10573.

Gori, M., Del Viva, M., Sandini, G., & Burr, D.C. (2008). Young children do not integrate visual and haptic form information. *Current Biology*, *18*, 694-698.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, *34*, 102-254.

Holmes, N. P., Crozier, G., & Spence, C. (2004). When mirrors lie: "visual capture" of arm position impairs reaching performance. *Cognitive, Affective & Behavioral Neuroscience*, *4*, 193-200.

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, *18*, 689-693.

Nava, E., Steiger, T., & Röder, B. (2014). Both developmental and adult vision shape body representation. *Scientific Reports*, *4*, 1-8.

Paillard, J. (1999). Body schema and body image – a double dissociation in deafferented patients. In Gantchev, G.N., Mori, S., & Massion, J. (Eds.). *Motor control, Today and Tomorrow*, pp. 197-214. Sophia: Academia Publishing House.

Petkova, V.I., Zetterberg, H., & Ehrsson, H.H. (2012). Rubber hands feel touch, but not in blind individuals. *PloS One*, *7*, e35912.

Petrini, K., Remark, A., Smith, L., & Nardini, M. (2014). When vision is not an option: children's integration of auditory and haptic information is suboptimal. *Developmental Science*, *17*, 376-387.

Rochat, P., & Striano, T. (2000). Perceived self in infancy. *Infant Behavior and Development*, *23*, 513-530.

Rohde, M., Di Luca, M., & Ernst, M. O. (2011). The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. *PloS One*, *6*, e21659.

Röder, B., Kusmierek, A., Spence, C., & Schicke, T. (2007). Developmental vision determines the reference frame for the multisensory control of action. *Proceedings of the National Academy of Sciences*, *104*, 4753-4758.

Stein, B.E., Stanford, T.R., & Rowland, B.A. (2014). Development of multisensory integration from the perspective of the individual neuron. *Nature Reviews Neuroscience*, *15*, 520-35.

Turkewitz, G., & Kenny, P. A. (1982). Limitations on input as a basis for neural organization and perceptual development: a preliminary theoretical statement. *Developmental Psychobiology*, *15*, 357-368.

Figure captions

Fig. 1. Mean pre- and post-illusion pointing, separately for the synchronous (A) and asynchronous condition (B). The asterisks indicate significant differences between the pre- and post-illusion pointing. Note that only 8-9 year-old children and adults showed such difference.

Fig. 2. Mean responses for the illusion and control question for all age groups, separately for synchronous and asynchronous stroking. Asterisks indicate significant differences between the illusion and the control question. Note that all participants experienced the illusion following synchronous stroking.