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05 October 2015

Version of attached file:

Accepted Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

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

Further information on publisher's website:

<http://dx.doi.org/10.1016/j.jecp.2015.10.003>

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The development of multisensory body representation and awareness continues to ten years of age: evidence from the rubber hand illusion.

Dorothy Cowie¹, Samantha Sterling² & Andrew J. Bremner²

¹Department of Psychology, Durham University

²Sensorimotor Development Research Unit, Department of Psychology, Goldsmiths,
University of London

ACKNOWLEDGEMENTS: We acknowledge support from the European Research Council (FP7/2007-2013; grant no. 241242; awarded to AJB). Thanks to Thames View Junior School, the Jo Richardson Community School and Goldsmiths Casting Laboratory.

ABSTRACT

Recent research using the Rubber Hand Illusion shows that the multisensory processes underlying body representations are markedly different in children of 4-9 years and adults. In representing the position of their own hand in external space, children of this age rely more on the sight of the hand, and less on its proprioceptively felt position, than adults do. The present study investigates when in later childhood the balance between visual and proprioceptive inputs reaches an adult-like weighting. After inducing the Rubber Hand Illusion in 10- to 13-year-olds, we asked participants to point with eyes closed to the perceived position of their hand. We found that pointing responses reached adult levels at 10-11 years, showing that at this age children perceive hand location using an adult-like balance of sensory cues. We conclude that the multisensory foundations of the bodily self undergo a protracted period development through early and mid-childhood, reaching an adult state by 10-11 years.

Keywords: Rubber Hand Illusion; Development; Body representation; Multisensory

Perceiving one's own body is a complex task, for which adults use many different sources of information. Recent neurophysiologically-inspired models suggest that multisensory processing from vision, touch and proprioception is an integral part of own-body perception (Makin, Holmes & Ehrsson, 2008; Tsakiris, 2010). For example, neurons in premotor cortex integrate visual and tactile stimuli positioned near the hand, and both visual and proprioceptive cues to hand posture can set the receptive field locations of these cells (Graziano, 1999). Understanding the childhood development of body-representation systems is crucial for understanding diverse functions including the establishment of a sense of body location and identity, the perceived separation of one's own body from others, and the control of action.

In development, own-body processing appears to start early, but develop over a long period. Infants are able to perceive many relevant multisensory relations. For example, 5 month old infants are sensitive to visual-proprioceptive congruency (seeing a limb move at the same time as you feel it move): they preferentially attend to nonsynchronous movement over synchronous (Bahrick & Watson, 1985). Likewise, very young infants detect visual-tactile synchrony between brush strokes applied to a viewed body, and strokes applied to their own face (Filipetti, Johnson, Lloyd-Fox, Dragovic & Farroni, 2013) or limbs (Zmyj, Jank, Schütz-Bosbach & Daum, 2011). These sensitivities reflect infants' early abilities to detect common properties of stimuli – in this case, temporal and spatial properties of stimulation across the senses – what has been referred to in the literature as amodal perception (Bahrick & Lickliter, 2012). These abilities are argued to form the developmental building blocks for the identification of self (Bahrick, 2013) and the distinction between self and other. However, in addition to “amodal” multisensory processing, infants also use unisensory featural information about their own bodies. They are no longer sensitive to visual-tactile synchrony on the face when the visual face which they are inspecting is

inverted. Similarly, they are no longer sensitive to visual-proprioceptive synchrony (Morgan & Rochat, 1997) or visual-tactile synchrony (Zmyj *et al.*, 2011) when the form of the legs is changed. Thus, both multisensory and unisensory featural cues seem to be used by infants in processing information about their own bodies.

Despite these early competencies, recent work suggests that the development of multisensory processing for own-body perception may follow a particularly protracted time course (Begum Ali, Cowie & Bremner, 2014; Cowie, Makin & Bremner, 2013; Bremner, Hill, Pratt, Rigato & Spence, 2013; Pagel, Heed & Röder, 2009; Nardini, Begus & Mareschal, 2012). These studies differ from infant work in that they much more explicitly require participants to locate or identify the self – information which preferential looking studies of course cannot provide. Thus, the development of multisensory processing for own-body perception is not complete during infancy nor during childhood. At what point does it develop? Few studies have systematically measured the transition from childhood immaturity into adult-like processing. Here we use the Rubber Hand Illusion, a classic paradigm for investigating the multisensory basis of body representations (Botvinick & Cohen, 1998). Our aim is to find the age at which own-body perception reaches its adult state.

The Rubber Hand Illusion specifically allows the study of multisensory processing in the context of a subjective sense of body ownership (Ehrsson, Spence & Passingham, 2004; Longo, Schüür, Kammers, Tsakiris & Haggard, 2009; Tsakiris & Haggard, 2005). In this illusion, the sight of a fake hand being stroked, combined with synchronous stroking on the participant's real hidden hand, causes adults to feel as if the fake hand is their own, and to perceive the touch they feel as occurring on the fake hand. As well as these subjective sensations, assessed by questionnaire, the perceived position of the participant's hand can change following illusion induction. After the stroking (induction) period, participants, with eyes closed, are asked to point with the unstimulated hand underneath the index finger of the

stimulated hand (intermanual pointing). When stroking on real and fake hands is synchronous, these intermanual points ‘drift’ significantly towards the fake hand (Botvinick & Cohen, 1998). Susceptibility to the illusion requires the perception of temporal and spatial visuotactile synchrony between the strokes delivered to the real and fake hands. In the standard illusion, it is also affected by featural information specifying whether or not the fake hand looks similar to one’s own (Haans, Ijsselstein & De Kort, 2008, though see Armel & Ramachandran, 2003). Based on the evidence reviewed above from looking duration studies, even infants should be capable of this. However, feeling the rubber hand illusion also requires links to be made between this multisensory information and a sense of limb ownership and location, aspects of bodily perception which have not yet been made available from looking time measures.

Interestingly, Cowie *et al.* (2013) showed that children of 4 – 9 years differ markedly from adults in their responses to this illusion, demonstrating a long period of development in own-body perception and suggesting that these connections between multisensory information and aspects of self-perception may not be fully developed in infancy or even early childhood. Like adults, children’s questionnaire and pointing responses were stronger in the synchronous condition. Thus by 4 years at the latest, visual-tactile cues are used in an adult-like fashion to determine perceived hand location, a sense of hand ownership, and the location of a viewed touch. However, and of particular interest here, for both stroking modes intermanual pointing responses (though not questionnaire items) showed a much stronger illusory effect for 4- to 9-year-olds than for adults. Thus, vision of an appropriately oriented hand¹ is a powerful cue to perceived hand location at 4-9 years. While our data (Cowie *et al.*,

¹ In Cowie *et al.* 2013, vision of an appropriately oriented hand is referred to as ‘visual-proprioceptive processing’. This is because the effects it has might result from seeing a fake hand, and/ or seeing an object that it is oriented in the same way as one’s own felt hand. In this paper, for simplicity, vision of an appropriately oriented hand is termed ‘vision’.

2013) show that this effect is much less in adults, the developmental trajectory of the illusion between 9 years and adulthood is not yet known. As the effect is three times as large in children as in adults, and given the importance of the adolescent period for the development of the self (Sebastian, Burnett & Blakemore, 2008) it is important to understand when the illusion declines to adult levels. That is the aim of this paper.

It is during early adolescence that the hand typically reaches adult size (Bee, 2000) and so in this period perception of the hand might be expected to become less plastic and more mature. There is also evidence that at this age multisensory processing develops to an adult-like state, in that children begin to combine and weight multisensory cues optimally (Nardini, Jones, Bedford & Braddick, 2008; Nardini, Bedford & Mareschal, 2010; Gori, del Viva, Sandini & Burr, 2008). Indeed, one study (Nardini *et al.*, 2013) suggests that this adult-like optimal cue weighting did not occur for weighting of visual and proprioceptive cues to hand position until at least 10-12 years. Thus, the present study investigates responses to the illusion during early adolescence (10-11 years and 12-13 years) using methods described in Cowie *et al.* (2013). This allows us to determine the age at which visual reliance on the sight of the hand develops to adult levels, and to examine how this impacts on perceived hand position, perceived touch location, and a subjective sense of ownership of the hand.

Method

Participants

Research was approved by the local research ethics committee. We tested 60 children: thirty 10- to 11-year-olds (M 10.8 yrs, sd 0.3 yrs) and thirty 12- to 13-year-olds (M 13.0 yrs, sd 0.4 yrs). Data are compared with those from Cowie *et al.* (2013), which includes adults and 3 age groups of children (4- to 5-year-olds; 6- to 7-year-olds; 8- to 9-year-olds). While that study identified broad differences between children (4-9 years of age) and adults, here

we expect to find finer-grained developmental changes in the responses to the illusion (i.e., differences between age groups of children).

Experimental procedure

The procedure consisted of pointing training trials, baseline trials, test trials, and questionnaire items. We equated postural and motor demands for all participants by using each participant's arm length to scale setups and measure responses. To start each trial, the right hand was placed on a tray under the table, at 50% of the participant's arm length to the right of the body midline.

On two training trials, the left hand was visible and rested on the table surface. The participant slid their right index finger along a horizontal groove under the table, so that it was underneath their left index finger. The use of this groove meant that for all trials, points were measured in the mediolateral axis only. After training trials, a screen was positioned to the left of body midline. This blocked the participant's view of their left hand in all subsequent trials.

We consider it particularly important that the effect of the illusion is referenced to baseline pointing in developmental studies of the Rubber Hand Illusion, in order to account for potentially confounding developmental effects of pointing performance (Hay, Bard, Fleury & Teasdale, 1991). In four baseline trials, the right hand was positioned as before, with the left hand resting on the table at 25% arm length to the left of body midline. With eyes closed, the participant was asked to point with their right index finger underneath their left index finger. The position of each point was marked; the mean and standard deviation of these four points were analysed. In order to encourage participation and introduce hand movement between trials, participants then chose a sticker reward from a box.

In visual-tactile stimulation ('test') trials, the participant's eyes were closed and hands placed as in baseline trials. A fake left hand (painted, plaster-cast, and appropriately-sized for

each age group) was placed on the table at body midline. A cloth was placed over the left arm. The participant watched for two minutes while the experimenter stroked the fake and real left hands with paintbrushes. In a between-subjects design, stroking on the fake hand was either synchronous or asynchronous with stroking on the real hand. Strokes were given on all fingers as well as on the back of the hand. Synchronous strokes were given at approximately 1-2Hz, at the same time, in the same place, and for the same duration on the real and fake hands. Asynchronous strokes were given as alternate strokes to the real and fake hands, in different places, and again at a rhythm of approximately 1-2Hz. This design minimized testing time, ensuring that even young participants would provide data of good quality. As in baseline trials, with eyes closed the participant was asked to point with their right index finger under the left index finger of their own hand. The right hand was repositioned, the participant opened their eyes, the stroking was repeated for 20 seconds, and the participant closed their eyes and pointed again. Each participant made four points. We measured whether the mean of these “post-induction” points shifted with respect to baseline points. In a fifth "catch" trial, the participant was asked to point first under the fake finger, then under their own finger. These catch trials demonstrated that all participants understood the task, because points to the fake hand were always far to the right of points to the real hand. Results from these trials are not analysed further.

To finish, the participant was asked two questions: 1. “When I was stroking with the paintbrush, did it sometimes seem as if you could feel the touch of the brush where the fake hand was?” and 2. “When I was stroking with the paintbrush, did you sometimes feel like the fake hand was your hand, or belonged to you?”. The answer scale was: “No, definitely not”/ “No”/ “No, not really”/ “In between”/ “Yes, a little”/ “Yes, a lot”/ “Yes, lots and lots”. These responses were coded from 0 (“No, definitely not”) to 6 (“Yes, lots and lots”).

Statistical analyses

From baseline trials we calculated *constant error* as the difference between mean pointing position and actual hand position in the mediolateral axis, scaled as a percentage of arm length. Errors towards the body midline from actual hand position were scored as positive. *Variable error* was calculated as the within-participant standard deviation of baseline points.

We next calculated *proprioceptive drift* towards the fake hand by subtracting, for each participant, their mean baseline pointing position from their mean test pointing position. This difference was converted to a percentage of each participant's arm length. This measure therefore provides an estimate of the effects of visuotactile stimulation which is independent of differences in baseline accuracy or body size.

ANOVA was used to assess the effects of age and stroking mode on proprioceptive drift, and on each of the two questionnaire items. No statistical tests presented here repeat those presented in Cowie *et al.* (2013). Unless otherwise stated, these analyses include the age groups tested in the present experiment (10-11 and 12-13 years old) as well as those reported previously in Cowie *et al.* (2013) (4-5 years, 6-7 years, 8-9 years, and adults).

Results

Baseline (no fake hand present): ANOVA on constant error (Fig. 1A) showed a main effect of Age, $F(5,174) = 3.60$, $p = .004$, $\eta_p^2 = .094$. Post-hoc Tukey HSD tests revealed significant differences between the 4-5 years group and the 8-9 years group only ($p = .001$), describing an increase in constant error towards the midline across this period. These baseline differences are corrected for in our measure of proprioceptive drift.

Test (after visual-tactile stimulation): Baseline-corrected proprioceptive drift was greatest with synchronous stroking, and at the youngest ages (Fig. 1B). ANOVA revealed main effects of Stroking mode (synchronous vs. asynchronous; $F(1,168) = 33.55$, $p < .001$,

INSERT FIG 1 ABOUT HERE

$\eta_p^2 = .166$) and Age (6 age groups; $F(5,168) = 2.65$, $p = .025$, $\eta_p^2 = .073$), and no significant interaction between these factors, $F(5,168) = 0.67$, $\eta_p^2 = .020$. In contrast to Cowie *et al.* (2013), which examined broad group difference between children and adults, here we conducted planned contrasts comparing adults with each of the younger groups to show the age at which responses reach maturity. Responses were different from adults' at 4-5 years ($t(168) = 2.53$, $p = .012$, $d = 0.61$), 6-7 years ($t(168) = 2.39$, $p = .018$, $d = 0.62$) and 8-9 years ($t(168) = 2.64$, $p = .009$, $d = 0.66$) but importantly not at 10-11 years ($t(168) = 1.48$, $p = .141$, $d = 0.49$) or 12-13 years ($t(168) = 0.38$, $p = .702$, $d = 0.13$). Stroking mode had significant effects on proprioceptive drift at 10-11 years, $t(28) = 2.11$, $p = .044$, $d = 0.77$, and 12-13 years, $t(28) = 2.13$, $p = .043$, $d = 0.62$, as well as at 6-7 years, 8-9 years and adult (Cowie *et al.* 2013).

INSERT FIG 2 ABOUT HERE

Questionnaire data: For these responses (Figure 2), ANOVA revealed main effects of stroking mode (synchronous vs. asynchronous) for Question 1 (Touch), $F(1,168) = 24.10$, $p < .001$, $\eta_p^2 = .125$, and Question 2 (Ownership), $F(1,168) = 17.38$, $p < .001$, $\eta_p^2 = .094$. There were no main effects of age for Question 1 (Touch), $F(1,168) = 1.15$, $\eta_p^2 = .033$, or Question 2 (Ownership), $F(1,168) = 0.46$, $\eta_p^2 = .014$. There was no significant interaction between these factors for Question 1, $F(5,168) = 0.71$, $\eta_p^2 = .021$, or Question 2, $F(5,168) = 1.41$, $\eta_p^2 = .040$. Stroking mode had significant effects on Question 1 responses at 10-11 years, $t(28) = 3.38$, $p = .002$, $d = 0.62$, and 12-13 years, $t(28) = 4.25$, $p < .001$, $d = 0.78$, as well as younger ages and in adults (Cowie *et al.* 2013). Stroking mode had significant effects on Question 2 responses at 10-11 years, $t(28) = 2.82$, $p = .009$, $d = 0.51$, and 12-13 years, $t(28) = 6.00$, $p < .001$, $d = 1.10$, as well as younger ages and in adults (Cowie *et al.* 2013).

Discussion

The present study used the Rubber Hand Illusion to assess hand localisation, a subjective sense of hand ownership, and a subjective sense of touch localisation. The data reported here show that multisensory mechanisms for own-hand perception develop to adult levels by 10 years of age. While the subjective senses of hand ownership and touch localisation are adult-like in early childhood, localisation of the hand is dominated by vision until 10-11 years. The findings have implications for our understanding of sensorimotor development and for our understanding of the developing bodily self. These are discussed in turn below.

Sensorimotor development

Synchronous visual-tactile cues caused greater mean drift than asynchronous cues, as well as causing stronger reported sensations of limb ownership and visual capture of touch. This role of visual-tactile synchrony in perceiving the bodily self is constant across ages. In contrast, overall drift was higher in children and dropped to adult levels around 10-11 years. Thus, the data suggest that the sight of an appropriately-oriented hand is a strong cue to body location for children, but becomes less important in early adolescence. Because of the constant difference between synchronous and asynchronous conditions, visuotactile stimulation per se does not immediately seem to make a difference to perceived hand location. An interesting test of whether visuotactile stimulation contributes to the larger drift effect in children would be a condition in which participants simply view the hand with no stimulation. Certainly in adults, the sight of a fake hand with no stroking can cause the illusion (Hohwy & Paton, 2010). Likewise for adults in the analogous full body illusion, viewing the body with asynchronous stimulation can elicit a sense of body ownership (Maselli & Slater, 2013). We therefore suggest that independent of synchrony, viewing the hand plays a role in the illusion.

The idea that the sight of the hand is more strongly weighted than its felt position complements findings from non-illusory studies of hand localisation (e.g. von Hofsten & Rösbald, 1988; Nardini *et al.*, 2013). Even at 10-12 years, these have often been unable to show that proprioception contributes significantly to perceived hand position when vision is also available. However, these studies rely on measuring small effects – tiny shifts in pointing position between trials on which target position is cued by vision alone, and trials on which it is cued by both vision and proprioception. In contrast, the conflict method of the rubber hand illusion (see also King, Pangelinan, Kagerer, & Clark, 2010) pulls apart visual and proprioceptive influences. The observed position of pointing estimates, between the real and fake hands, shows that both visual and proprioceptive information are used to perceive hand position at all ages tested. This in fact shows a developmental continuity from infancy, where the conflict method of viewing asynchronous displays also shows integration of visual and proprioceptive information (Bahrick & Watson, 1985; Morgan & Rochat, 1997).

By 10-11 years, the contribution of vision relative to proprioception in hand localisation is down-weighted in comparison with younger children. Thus a fundamentally adult-like sensory weighting for hand position is achieved only late in childhood. An interesting point is what is meant by ‘vision of the hand’. Here, children view a hand which resembles their own in both posture and form. While we know that infants are sensitive to body form information (Morgan & Rochat 1997), it would be interesting to know whether, as for adults (Tsakiris, 2010; Costantini & Haggard, 2005; Makin *et al.*, 2008), these factors are important determinants of embodiment in children. The present data delineate the development of the basic sensory foundations of the body representation system, providing the appropriate background from which to answer questions about more specific postural or form constraints on the visual cues to the bodily self during childhood and adolescence.

The development of the bodily self

The underpinnings of own-body perception are present in the first six months of life. By this age, infants are able to detect synchrony between visual and proprioceptive information (Bahrick & Watson, 1985), as well as to locate touch in an external (visual) frame of reference (Bremner, Holmes & Spence, 2008). Results from Cowie *et al.* (2013) show a robust use of synchronous visual-tactile information by four years, but there are recent suggestions that this is present in infancy (Zmyj *et al.*, 2011) and even in neonates (Filippetti *et al.*, 2013). It has also been argued that infants have an awareness of own-body form early in the first year of life (Morgan & Rochat, 1997; Zmyj *et al.*, 2011; Filippetti *et al.*, 2013). Finally a recent NIRS study suggests that identifying with a body is achieved through the same neural mechanisms in infants and adults (Filippetti, Lloyd-Fox, Longo, Farroni & Johnson, 2014).

Despite these suggestions of early competency in own-body perception, it is increasingly clear that significant developments in own-body perception occur well into childhood. Major developments occur in the second year of life, when increased self-awareness can be seen in the form of language use and mirror recognition (Lewis, 2011). Simple body perception tasks develop between 20 and 30 months, with major errors still occurring at this later age (Brownell, Nichols, Svetlova, Zerwas & Ramnani, 2010). The use of vision in locating a reaching (Hay *et al.*, 1991; Contreras-Vidal, Bo, Boudreau & Clark, 2005) or static (Bremner *et al.*, 2013; King *et al.*, 2010; Begum Ali *et al.*, 2014) hand changes markedly in mid-childhood. Thus, there is almost continuous development in own-body perception from infancy until late childhood.

The current study reinforces that view of a long developmental trajectory in own-body perception. However, the data suggest that the ability to identify a hand as one's own based on sensory information (here assessed by a question on hand ownership) demonstrates no significant development between 4-5 years and adulthood, compared to an ability to

localize one's own hand (here assessed by drift) which continues to develop up to at least 10 years of age. Given that a subjective sense of hand ownership and perceived location of the hand appear to develop according to different timelines, this suggests that the bodily self is not a unitary construct developing in a unitary manner, but rather consists of several processes which unfold at different rates. Brownell, Zerwas & Ramani (2007) suggest that "body self-awareness may serve as a developmental bridge between the kinaesthetically based awareness and discrimination of one's own body evident in infancy and the more complex psychological self that develops over childhood and adolescence". In contrast, our data demonstrate no evidence that body identification or self-awareness, which can be gained from visual-tactile signals, develops after 4 years of age. We thus tentatively propose that body identification or self-awareness matures earlier than the proprioceptively-based sense of limb location, which in fact takes a strikingly long time to reach a mature state. However, the idea that these various self-representations consolidate with age, providing foundations for the next stage of development, remains appealing. Sebastian *et al.* (2008) point out that adolescence sees the development of much more complex forms of self-awareness – in particular the ability to relate the self to the social environment. Our results suggest that 10-11 years may mark the end of a long period of flux in the sensory perception of one's own body. Adult-like use of multisensory information by this age may provide the necessary sensory foundation for the new conceptions of the self which emerge in adolescence.

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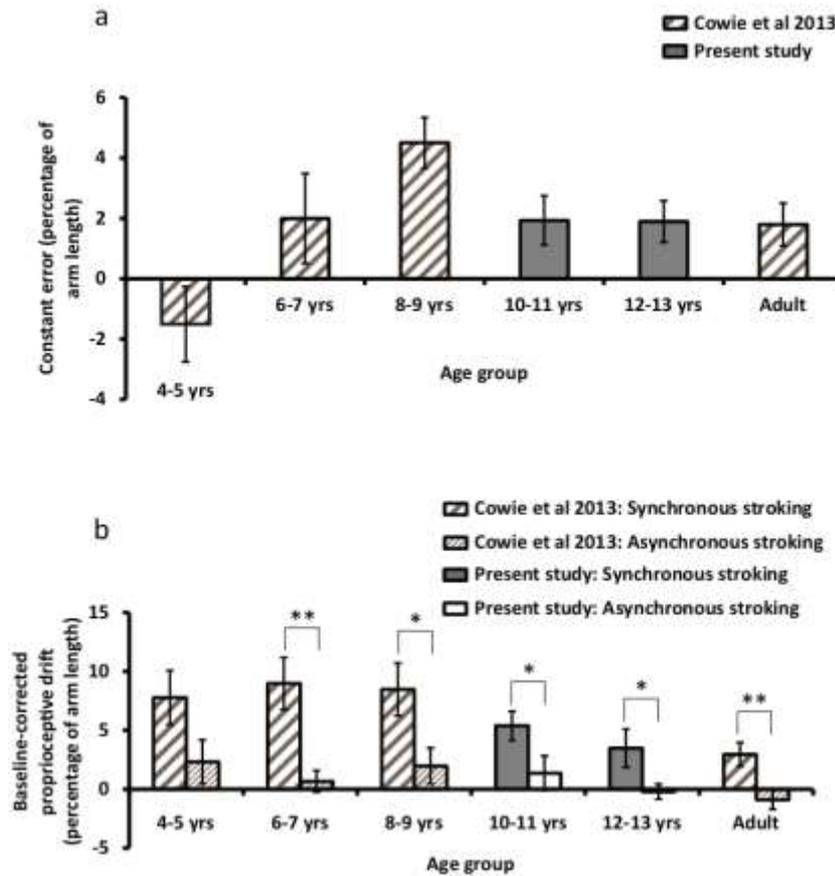


Figure 1: Pointing responses. (A) Constant error of baseline points towards the midline, as a percentage of arm length. Means and standard errors across participants are shown. (B) Proprioceptive drift toward the midline, calculated by subtracting for each participant their baseline pointing position from their pointing position after visual-tactile stimulation. Means and standard errors across participants are shown. Asterisks indicate significant effects of stroking mode within age groups, compared using t-tests (* = $p < .05$; ** = $p < .01$). Data from the present study are shown alongside data from Cowie et al. (2013).

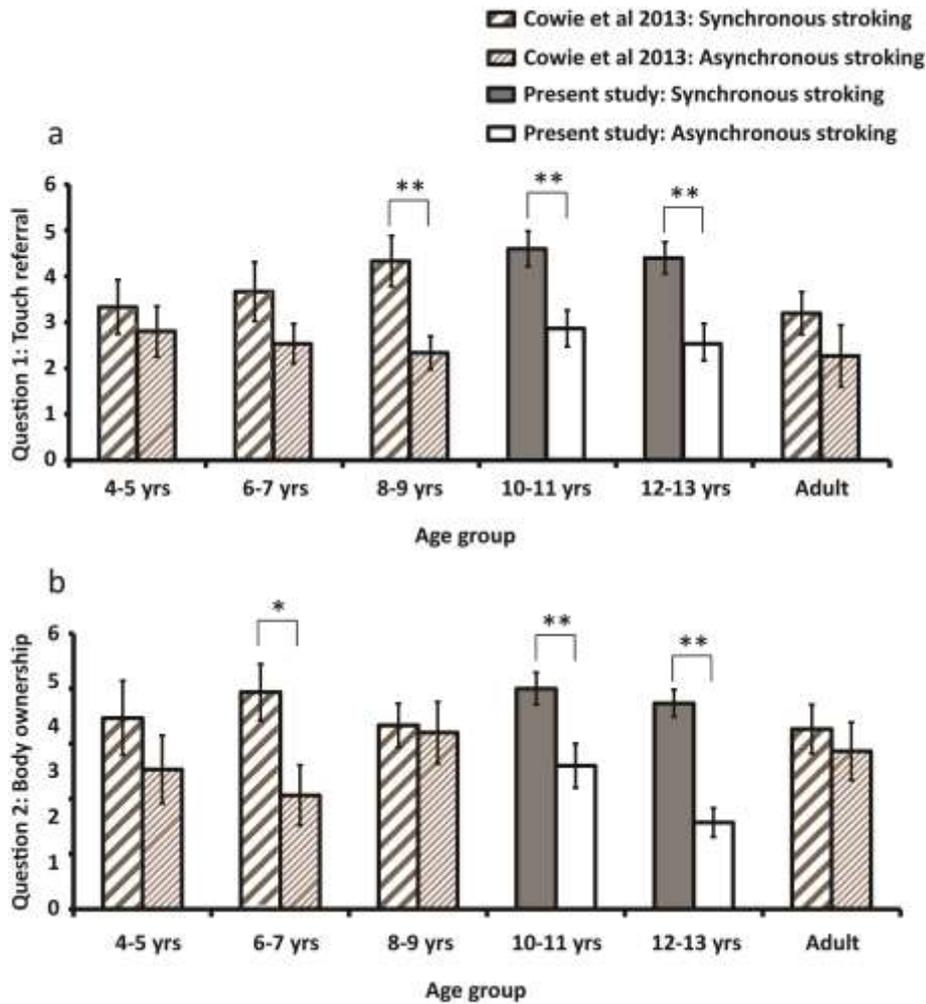


Figure 2: Questionnaire responses. (A) Responses to question on perceived touch referral to the fake hand. Means and standard errors across participants are shown. (B) Responses to question on perceived ownership of the fake hand. Means and standard errors across participants are shown. Asterisks indicate significant effects of stroking mode within age groups, compared using t-tests ($* = p < .05$; $** = p < .01$). Data from the present study are shown alongside data from Cowie et al. (2013).