Developing body representations in early life: combining somatosensation and vision to perceive the interface between the body and the world

ANDREW J BREMNER

Sensorimotor Development Research Unit, Department of Psychology, Goldsmiths, University of London, London, UK.

Correspondence to Andrew J Bremner, Department of Psychology, Goldsmiths, University of London, New Cross, London SE14 6NW, UK. E-mail: a.bremner@gold.ac.uk

PUBLICATION DATA
Accepted for publication 2nd August 2015.
Published online

ABBREVIATIONS

CHD	Crossed-hands deficit
SEPs	Somatosensory evoked potentials

This article lays out the computational challenges involved in constructing multisensory representations of the body and the interface between the body and the external world. It then provides a review of the most pertinent empirical literature regarding the ontogeny of such representational abilities in early life, focussing especially on ability to make spatiotemporal links between bodily events transduced by vision and somatosensation (cutaneous touch and proprioception), and the ability to use multisensory bodily cues to locate tactile stimuli. Findings from infants, children, and blind adults point towards a trajectory of development in early life in which infants and children, as a result of sensory experience, learn new ways of combining cues concerning the body arising from vision and somatosensation, in order to best represent the layout of their limbs and sensory events occurring on their limbs in relation to the external environment.

We need to perceive our bodies accurately in order to move around the environment in a physically competent manner. And so the development of multisensory representations of the spatial disposition of our body and limbs underpins emerging sensorimotor competence. Furthermore, multisensory body representations are involved in all of our mental processes, by providing an 'embodied' point of reference to the external world.[1]

Perhaps the most direct sensory information concerning the body arises from cutaneous touch and proprioception, with signals from the vestibular system also providing direct information about the body's positioning with respect to the environment. Nonetheless, as adults our representations of limb and body position result from the combination and integration of information from these direct (and largely somatosensory) receptors with the visual and even auditory information which is more particularly suited to providing information about the external world.[2,3] Body representations are thus reliant on multisensory cortical and sub-cortical areas, including particularly premotor cortex, posterior parietal cortex, and the putamen.[2] The multisensory nature of body representations gives rise to a number of computational challenges for the developing child. Not only do the senses convey information about the body and limbs in different neural codes and reference frames, but the spatial and temporal relationships between sensory modalities can vary dramatically from moment to moment. For instance, each time our arm changes posture the relations between tactile coordinates on the hands and locations in the external environment are realigned (Fig. 1).

Whilst adults dynamically and automatically remap spatial correspondences among the senses across changes in the posture of the limbs,[2] we cannot necessarily infer that the same is the case earlier in development. Indeed, these computational problems are amplified during infancy and childhood. The number and variety of postural changes that a child makes in the service of purposeful skilled movement increases substantially in the first years of life. Furthermore, the spatial distribution of the limbs and the body also changes profoundly. Such physical and behavioural changes necessitate continuous adaptation of multisensory body representations in early life.[4,5]

In the following sections, I will review findings from studies addressing the development of an ability to form links between somatosensory cues and vision, multisensory processes that enable us to perceive our bodies in the external world. Evidence from these studies indicates that such multisensory body representations develop gradually in early life as a result of sensory experience.

MULTISENSORY BODY REPRESENTATIONS AT BIRTH?

A number of early behaviours of the infant at birth (and in utero) indicate the presence of primitive body representations.[6] Some clearly multisensory reactions are also present, such as the vestibular–ocular reflex, in which vestibular signals concerning bodily movement are used to stabilise the

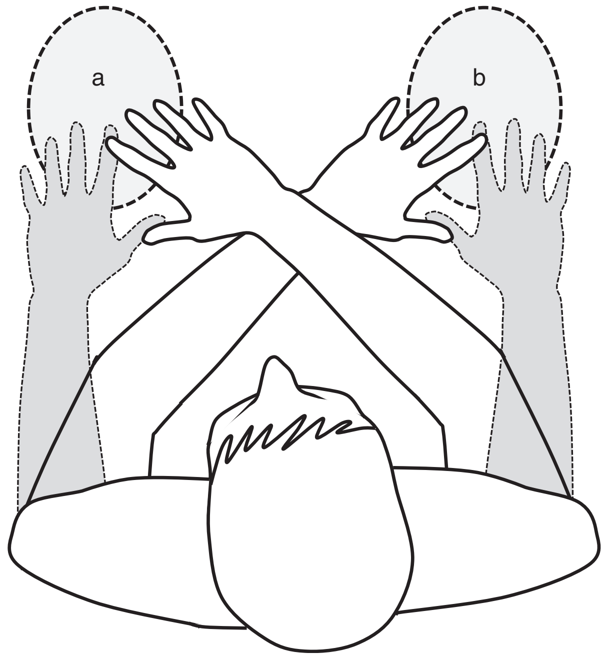

Figure 1: Crossing the hands confuses the mind. When the arms are crossed, intrinsic tactile locations on the skin come to occupy less familiar places in the external environment. Whereas a touch on the left hand would usually occur in a particular area in the external environment (a), when the arms are crossed it now occurs in a less familiar external area (b). For this reason, in order to locate a touch to the hand in the external environment when our arms are in a novel posture, we have to take account of the positions of our arms in external space.[2,24] Despite an ability to achieve this,[20,21] several studies now show that adults, children, and even infants demonstrate poorer tactile localization performance when the arms are crossed than when they are uncrossed.[15,16,18,19,24] A touch on a hand which is crossed over the midline summons conflicting representations of where the touch is currently in the external world and where it would usually be if the arms were arrayed in a more canonical (uncrossed) layout (indicated in this figure by the shaded arms). For this reason the crossed-hands deficit can be used as an index of an ability to perceive tactile events in the external environment. Improvements in the ability to localize touches in external space across changes in body posture are seen in the first year of life.[13,14,22] Figure adapted from Bremner and van Velzen.[24]

visual image via eye movements.[7] Newborn head-turning to tactile stimulation has also been observed.[8] Could it be that multisensory body representations are largely available to the newborn? Studies using infants' looking preferences as an index of multisensory perception (discussed in 'Crossmodal matching' section), have been used to confirm this view. However, I shall raise what I think is an important limitation of these studies, and present findings from alternative methods (see 'Locating touches' and 'Keeping track of touch' sections) which show that there are some important ways in which multisensory body representations are restructured and refined across development.

What this paper adds

- A review of findings from studies addressing the development of an ability to form links between somatosensory cues and vision, the multisensory processes that enable us to perceive our bodies in the external world.
- A demonstration that there are significant postnatal developments in the ways in which typical infants and even young children perceive their bodies, and particularly the relationship between their bodies and the external world.

CROSSMODAL MATCHING OF VISUAL BODILY CUES WITH SOMATOSENSORY INFORMATION

Several studies using infants' looking preferences have investigated an early ability to make crossmodal links between cues about the body coming from somatosensation (proprioception, cutaneous touch) and vision. These studies typically examine infants' preferences for visual movements of limbs projected on a screen which are either congruent or incongruent with their own limb movements perceived proprioceptively (Fig. 2).[9,10] From as early as 3 months, infants' looking behaviour demonstrates that they are able to differentiate multisensory bodily events on the basis of visual–proprioceptive (temporal and spatial) congruency. More recently researchers have examined whether infants can detect if a visually perceived stroke to the skin occurs at the same time as a felt (tactile) stroke.[11] Even newborn infants are able to do this.[12] Such early crossmodal competence has fuelled speculation that an ability to perceive the bodily self is well specified from birth.[10]

One important limitation of the crossmodal matching studies just described (Fig. 2) is that they present visual bodily information on a screen well outside of personal space (sometimes as far as 1 m distant). Thus, any crossmodal links that infants make in this context are necessarily abstracted from spatial frames of reference centred on the body and limbs. This prompts the question of whether an ability to link this screen-based visual information to somatosensory input is of relevance to spatial representations of the body and limbs that could provide the basis for sensorimotor coordination, and body representations more generally.[6] This concern is amplified when we consider that the picture of early competence does not always resonate with other evidence. For instance, there are important developmental changes in the way multisensory information is used to guide reaching behaviours, with infants and even young children neglecting to make use of visual cues to hand position.[13] Infants are also initially rather limited in the way they can make crossmodal links between touch and vision: although head-turning to tactile stimuli is present at birth,[8] orienting responses that bring visual fixation to bear on a tactile stimulus develop late in the first year of life.[14] In the next two sections I will describe research demonstrating substantial changes in the ways infants and children combine multisensory cues concerning the body.

LOCATING TOUCHES IN THE EXTERNAL WORLD

As well as informing us about what is happening on the skin, touch also tells us about the ways in which the sur-

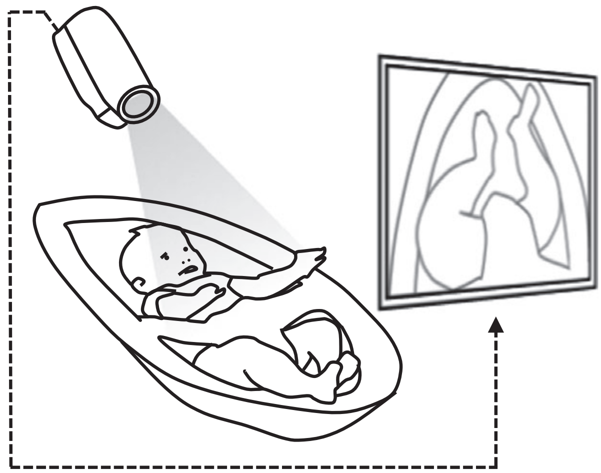

Figure 2: Crossmodal matching studies of multisensory body perception in infancy. Researchers have measured infants looking preferences for visual movements of limbs projected on a screen which are either congruent or incongruent with their own limb movements perceived proprioceptively.[9,10] Differentiation of congruent and incongruent displays is typically demonstrated by a looking preference for the incongruent presentation, but preferences for the congruent presentation are also observed under some circumstances, and are equally as diagnostic of differentiation. Young infants' abilities to respond to temporal and spatial correspondences between somatosensory (cutaneous touch, proprioception) and visual cues in these kinds of studies have been used as evidence of an ability to form multisensory representations of the body in early life.[9,10,12]

face of our body interfaces with objects in the external spatial world. Thus, an important question concerns how and when infants become able to locate touches and thus their bodies and limbs in external space. We can trace the emergence of external spatial coding of touch by examining effects of body posture on tactile localization. For instance, under certain circumstances, when adults are asked to localize touches on their hands they make more mistakes when their hands are crossed than when they are uncrossed.[15] This 'crossed-hands deficit' (CHD) arises because adults are obliged to encode the location of tactile events in the external world (Fig. 1).

Work with blind adults demonstrates that external spatial coding of touch arises out of multisensory interactions. Congenitally blind participants show no CHD even though blindfolded sighted and late blind adults (even those with only a few years of visual experience in early life) show the same CHD as sighted adults.[16] More recently, no CHD was found in an individual who was born congenitally blind, but whose sight was restored at the age of 2 years through the removal of congenital cataracts.[17] These findings indicate that visual experience, specifically in early life, is important in the typical development of external spatial coding of touch.

Developmental studies indicate that external spatial coding of touch (as demonstrated through the CHD) is present early in development. Two studies have demonstrated the presence of the CHD in early childhood.[18,19] One study of infants, measuring manual responses elicited by tactile stimuli on the hand, has found the CHD at the young age of 6.5 months.[14] Thus, it seems that an ability to go beyond simple anatomical coordinates and represent the location of a touch on the hand in the external world is available in early infancy. However, as described earlier, evidence from blind individuals in adulthood shows that external coding of touch emerges primarily out of multisensory interactions with visual experience in early life.[16,18] It thus seems a plausible prediction for future investigations that external coding of touch (and thus the CHD) will not be present in individuals with less visual experience (i.e. infants <6.5 months of age).

KEEPING TRACK OF TOUCH ACROSS CHANGES IN LIMB POSTURE

Irrespective of when infants or children learn to locate touches and their limbs in the external environment, a further hurdle involves developing an ability to update the location of a touch (and a limb) when the body moves into unfamiliar postures. Studies with adults demonstrate that when locating a touch in an unfamiliar posture we rapidly incorporate visual and proprioceptive information about limb position in order to remap the touch to its location in the external world.[20,21] But how does the developing brain come to solve this task as the infant gradually builds up an increasingly complex repertoire of purposeful skilled movements across the first year of life? The 6.5-month-olds tested in a study by Bremner et al.[14] showed some limitations in this regard: they demonstrated a tendency to respond manually to touches as if those touches were occurring in the external locations where their limbs would normally rest in a familiar (uncrossed) layout. This led to a higher proportion of mistakes in the crossed-hands posture. But by 10 months of age, infants maintained a consistent level of accuracy across both familiar and unfamiliar postures. It seems that an ability to incorporate sensory information about limb posture into representations of the external location of tactile events develops significantly during the second half-year of life.

What processes underlie the improvements in behavioural performance just described? One question here is whether developmental improvements in postural remapping reflect improvements in the spatial perception of bodily events across different postures or whether we are seeing improvements in the infants' coordination of their orienting responses. The second question concerns what sensory information infants are making use of to update their representations of limb position and remap their behavioural responses. A recent brain-imaging study of tactile processing in infancy helps address both of these matters.

Rigato et al.[22] investigated modulatory effects of arm posture on somatosensory evoked potentials (SEPs) recorded from the scalp in 6.5- and 10-month-old infants (Fig. 3). When presented with tactile stimuli, the 6.5-

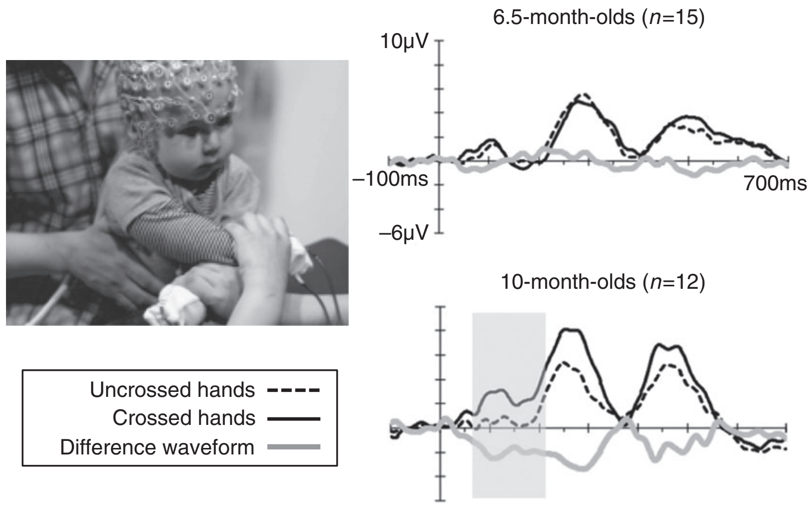

Figure 3: Researching the early development of body representations via somatosensory evoked potentials (SEPs). Rigato et al.[22] examined the effect of arm posture on SEPs. The infants (as pictured on the left) received 200ms vibrotactile stimuli to the hand in either an uncrossed- or a crossed-hands arm posture (the crossed-hands posture is shown). As in adults,[21] 10-month-old infants SEPs were modulated by posture from early in somatosensory processing, indicating a somatosensory postural remapping. Younger (6.5mo) infants however, demonstrated SEPs that were unaffected by arm posture suggesting that in the first months of life, somatosensory spatial representations are strongly anchored to the usual positions of the limbs.

month-old infants showed no reliable effect of posture on their SEPs; it was as if these younger infants processed tactile events in the same way irrespective of the posture of their limbs, mirroring the findings from behavioural studies that this age group tended to respond to the same external location irrespective of limb posture.[14] However, the older 10-month-old infants, like adults,[21] showed significant postural modulations of somatosensory processing. Thus, improvements in tactile localization across limb postures may well be underpinned by the increased role of postural information in somatosensory processing seen in event-related potentials. Importantly, the modulatory effects of posture seen at 10 months occur (as they do in adults[21]) early in somatosensory processing (~60–120ms). In answer to the first question raised above, this suggests that improvements in somatosensory processing and postural remapping at 10 months of age occur largely at the early feed-forward (perceptual) end of neural processing in somatosensory cortex.

In addressing the second question raised above, a further experiment[22] investigated what sensory information concerning limb position drives the postural modulation of somatosensory processing seen at 10 months. Tactile stimuli were presented again, but this time with the infants' arms obscured from view by a cloak. In this case, the 10-month-old infants showed no effect of posture on their SEPs. It seems that, at this point in development, visual cues to hand posture are required to remap tactile space.

Thus, by 10 months of age, infants appear to be able not just to represent the location of touches in the external environment, but also to dynamically update tactile localization across changes in limb posture. Nonetheless, it is important to note that changes continue beyond the first year in the ways infants and even children combine multisensory cues to localize touches. For instance, in contrast to adults and older children, 4-year-old children are actually worse at determining which hand felt a touch when they can see their hands.[18] It seems that visual cues to hand posture actually interfere with the process of localizing touches in early childhood. Indeed, an adult-like weighting of visual relative to proprioceptive hand position cues does not appear to mature until after 9 years of age.[23]

CONCLUSIONS AND FUTURE DIRECTIONS

Given the variety of postures through which our limbs move from moment to moment, our ability to assemble coherent representations of the body and the world from the multisensory stream of information presented to the nervous system is fairly miraculous.[24] Whilst adults seemingly manage this with ease,[2] the ways in which multisensory information concerning the body is combined change substantially in early life, as a result of sensory experience. This review has described the findings from a number of studies of infants' and children's responses to tactile information (in both behaviour and brain) which make it clear that we cannot assume that infants and even young children perceive their bodies – and particularly the relationship between their bodies and the external world – in as coherent a way as we do in adulthood. A clear goal for future research is to understand better the ontogenetic processes underlying the development of multisensory body representations, considering both the experiential and maturational factors that give us a sense of our own bodies, and the relationships between our bodies and the external world. To this end it will be important to consider the development of the whole range of sensory inputs that contribute to these processes, including – as well as vision and somatosensation – audition, the vestibular system,[7,25] and even olfaction.[26]

Further research into the development of multisensory body representations should provide useful clues in helping us understand not just typical development, but also patterns of perceptual and sensorimotor ability and impairment in atypically developing groups. Whilst there is still a relatively limited understanding of multisensory processes in developmental disorders, a number of studies indicate atypicalities across several disorders.[27] Particularly relevant to the current article are findings demonstrating that there are differences in the way atypically developing individuals process somatosensory information. As mentioned above, an absence of vision in early life leads to differences in the way congenitally blind people represent touch spatially, with a less automatic referral of tactile events to locations in external space.[16,17] Recent research with individuals with autism spectrum disorder also finds a similar reduction in the influence of external space on tactile representation,[28] and also differences in the way visual, tactile, and proprioceptive cues are weighted in multisensory representations of hand position.[29] As discussed in this article, one of the main messages from research on the typical development of body representations, is that changes in the ways sensory cues are combined to form multisensory body representations are the rule rather than the exception in early life. Thus, it will be important to consider not just the nature of developmental disorders of multisensory processes, but how such impairments emerge across developmental time. Furthermore, because multisensory processing is influenced by multisensory processes and vice versa, future studies will need to trace the developmental trajectories of both unisensory and multisensory deficits, and attempt to identify the causal developmental relationships between them.[27]

ACKNOWLEDGEMENTS

The author is supported by an award from the European Research Council under the European Community's Seventh Framework Programme (FP7/2007–2013) (ERC Grant agreement no. 241242). The author states that he has no interests that could constitute a real or perceived conflict or bias.

REFERENCES

1. Varela FJ, Rosch E, Thompson E. The Embodied Mind: Cognitive Science and Human Experience. Cambridge, MA: MIT press, 1992.
2. Holmes NP, Spence C. The body schema and multisensory representation(s) of peripersonal space. *Cogn Process* 2004; **5**: 94–105.
3. Makin TR, Holmes NP, Ehrsson HH. On the other hand: dummy hands and peripersonal space. *Behav Brain Res* 2008; **191**: 1–10.
4. Adolph KE, Avolio AM. Walking infants adapt locomotion to changing body dimensions. *J Exp Psychol Hum Percept Perform* 2000; **26**: 1148.
5. Burr D, Binda P, Gori M. Multisensory integration and calibration in adults and children. In: Trommershauser J, Landy MS, Kording KP, editors. Sensory cue Integration. New York: Oxford University Press, 2011: 173–94.
6. Bremner AJ, Cowie D. Developmental origins of the hand in the mind, and the role of the hands in the development of the mind. In: Radman Z, editor. The Hand: An Organ of the Mind. What the Manual Tells the Mental. Cambridge, MA: MIT Press, 2013: 27–55.
7. Rosander K, von Hofsten C. Visual-vestibular interaction in early infancy. *Exp Brain Res* 2000; **133**: 321–33.
8. Moreau T, Helfgott E, Weinstein P, Miller P. Lateral differences in habituation of ipsilateral head-turning to repeated tactile stimulation in the human newborn. *Percept Mot Skill* 1978; **46**: 427–36.
9. Bahrick LE, Watson JS. Detection of intermodal proprioceptive–visual contingency as a potential basis of self-perception in infancy. *Dev Psychol* 1985; **21**: 963–73.
10. Rochat P. The innate sense of the body develops to become a public affair by 2–3 years. *Neuropsychologia* 2010; **48**: 738–45.
11. Zmyj N, Jank J, Schütz-Bosbach S, Daum MM. Detection of visual–tactile contingency in the first year after birth. *Cognition* 2011; **120**: 82–9.
12. Filippetti ML, Johnson MH, Lloyd-Fox S, Dragovic D, Farroni T. Body perception in newborns. *Curr Biol* 2013; **23**: 2413–6.
13. Bremner AJ, Holmes NP, Spence C. Infants lost in (peripersonal) space. *Trends Cogn Sci* 2008; **12**: 298–305.
14. Bremner AJ, Mareschal D, Lloyd-Fox S, Spence C. Spatial localization of touch in the first year of life: early influence of a visual spatial code and the development of remapping across changes in limb position. *J Exp Psychol Gen* 2008; **137**: 149–62.
15. Yamamoto S, Kitazawa S. Reversal of subjective temporal order due to arm crossing. *Nat Neurosci* 2001; **4**: 759–65.
16. Röder B, Rösler F, Spence C. Early vision impairs tactile perception in the blind. *Curr Biol* 2004; **14**: 121–4.
17. Ley P, Bottari D, Shenoy BH, Kekunnaya R, Röder B. Partial recovery of visual–spatial remapping of touch after restoring vision in a congenitally blind man. *Neuropsychologia* 2013; **51**: 1119–23.
18. Begum Ali J, Cowie D, Bremner AJ. 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. *Dev Sci* 2014; **17**: 935–43.
19. Pagel B, Heed T, Röder B. Change of reference frame for tactile localization during child development. *Dev Sci* 2009; **12**: 929–37.
20. Azañón E, Soto-Faraco S. Changing reference frames during the encoding of tactile events. *Curr Biol* 2008; **18**: 1044–9.
21. Rigato S, Bremner AJ, Mason L, Pickering A, Davis R, Velzen J. The electrophysiological time course of somatosensory spatial remapping: vision of the hands modulates effects of posture on somatosensory evoked potentials. *Eur J Neurosci* 2013; **38**: 2884–92.
22. Rigato S, Begum Ali J, van Velzen J, Bremner AJ. The neural basis of somatosensory remapping develops in human infancy. *Curr Biol* 2014; **24**: 1222–6.
23. Cowie D, Makin TR, Bremner AJ. Children's responses to the rubber-hand illusion reveal dissociable pathways in body representation. *Psychol Sci* 2013; **24**: 762–9.
24. Bremner AJ, van Velzen JL. Sensorimotor control: retuning the body-world interface. *Curr Biol* 2015; **25**: R159–61.
25. Bremner JG, Hatton F, Foster KA, Mason U. The contribution of visual and vestibular information to spatial orientation by 6- to 14-month-old infants and adults. *Dev Sci* 2011; **14**: 1033–45.
26. Schaal B, Durand K. The role of olfaction in human multisensory development. In: Bremner AJ, Lewkowicz DJ, Spence C, editors. Multisensory Development. Oxford, UK: Oxford University Press, 2012: 29–62.
27. Hill EL, Crane L, Bremner AJ. Developmental disorders and multisensory perception. In: Bremner AJ, Lewkowicz DJ, Spence C, editors. Multisensory Development. Oxford, UK: Oxford University Press, 2012: 273–300.
28. Wada M, Suzuki M, Takaki A, Miyao M, Spence C, Kansaku K. Spatio-temporal processing of tactile stimuli in autistic children. *Sci Rep* 2014; **4**: 5985.
29. Cascio CJ, Foss-Feig JH, Burnette CP, Heacock JL, Cosby AA. The rubber hand illusion in children with autism spectrum disorders: delayed influence of combined tactile and visual input on proprioception. *Autism* 2012; **16**: 406–19.