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Development of body representations in human infancy

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Abstract
Perceiving one's own body underpins skilled interactions with the external world and plays a fundamental role in the sense of self. Findings across experimental psychology and neuroscience show that body perception depends on integrating bodily information across multiple senses. However, the emergence of such multisensory abilities in early human development is just starting to be investigated. It is now generally established that human infants are sensitive to the spatiotemporal congruency between cues about the body coming from different senses, even with only a few months or even days of postnatal experience. Conversely, other abilities appear to have a more protracted development, such as the ability to make the crossmodal links required to locate tactile stimuli in external space, i.e., the "remapping problem" (Driver & Spence, 1998; Heed, Buchholz, Engel, & Röder, 2015), which develops gradually in the first year of life. This article briefly reviews the scientific literature concerning body representations in early infancy, highlighting the important role of visual experience in the development of these fundamental representational abilities.

1. Introduction

Our representations of our body and limbs are essential components of our sense of self. The body is our interface with the external world, and consequently our perceptions continuously provide us with bodily-related information (e.g., Bermúdez, Marcel, & Eilan, 1995). To act in a skilled way in our daily lives, we need to perceive our bodies and limbs and locate them accurately with respect to the environment. Even beyond these fundamental roles for body representations, embodied cognition accounts (Goldman & de Vignemont, 2009; Borghi & Cimatti, 2010) have it that bodily perception and action are the foundations of higher-level cognitive functions, such as memory, reading, and writing, learning, and reasoning.

But what perceptual abilities underpin our body representations and how do they develop? As we will explain later in this article, the developmental integration of the multiple sensory systems which specify the body (e.g., touch, vision, and hearing) are of fundamental importance here. An important study in this area by Filippetti and colleagues (2013) has shown that even newborn infants are sensitive to some forms of multisensory correspondences related to their bodies. Evidence such as this has been used to make the argument for an innate sense of the body in early life (e.g., Rochat, 2010). Nonetheless, it is not until 10 months of age that infants' will reliably look with their eyes towards a tactile stimulus presented to their hand (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008), indicating that the development of multisensory body representations does not unfold in a straightforward manner.

2. Somatotopy in the infant's brain

The body is represented in an orderly somatotopic manner in primary somatosensory cortex (S1). Adjacent areas on the skin are also largely adjacent within certain regions of SI (Grodd, Hülsmann, Lotze, Wildgruber, & Erb, 2001). This somatotopic organization is likely to be fundamental to bodily perception and is pervasive throughout the mammalian nervous system (Erzurumlu & Gaspar, 2012; Luhmann & Khazipov, 2018). Hence, studying the development of infant somatotopic body maps in the nervous system is one potential avenue to understanding how infants develop an ability to represent their own body (Marshall & Meltzoff, 2015; Meltzoff & Marshall, 2020).

A recent study with macaques has demonstrated somatotopy in the somatosensory and motor systems at birth (Arcaro, Schade, & Livingstone, 2019). Evidence of somatotopic organization in even preterm newborns has been demonstrated using neuroimaging techniques. Using electroencephalographic (EEG), Milh et al. (2007) have reported that hand and foot movements triggered off "delta-brush" oscillations in the corresponding areas of the cortex in premature newborns (29-31 weeks gestational age). Recently, Dall'Orso et al. (2018) have shown that the spatial cortical responses in preterm infants induced by movements of the wrists, ankles, and mouth touch are similar to those observed in adults. Moreover, a series of studies using EEG have shown that the somatotopic response elicited by tactile stimulation of infants' limb and lip emerges as early as two months of age (Saby, Meltzoff, & Marshall 2015; Meltzoff, Saby, & Marshall, 2019). Overall, these findings suggest that an intrinsic somatotopic map could be available from a very early age. However, we cannot ignore the possibility that early prenatal experience (e.g., of somatosensory feedback following spontaneous fetal movement) shapes the development of the somatotopic map (for a review of what is known of the role in somatotopy of early experience in rodents see Erzurumlu & Gaspar, 2012).

Our body's skin is continuous; however, adults tend to divide it into several parts, which are named by linguistic labels such as head, shoulder, chest, arm, and leg. Studies have demonstrated that the perception of tactile stimulation is modulated by this high-level representation of the body (for a review, see Tamè, Azañón, & Longo, 2019). For example, adults perceive the more tactile distance between two points across body-part boundaries than within body-part boundaries on the skin, even though pairs of points have the same length (de Vignemont, Majid, & Haggard, 2009). Recent studies have reported this categorical effect in body processing in infants aged 6–7 months (Shen, Weiss, Meltzoff, & Marshall, 2018; Shen, Meltzoff, Weiss, & Marshall, 2020), indicating that it may have some biological basis across cultures and can be independent of language. It is reasonable to suggest therefore that the body's categorical representation that exists before language can scaffold the acquisition of the body parts' linguistic labels. Indeed, a recent study has shown that cross-linguistic variations in the application of body part nouns do not appear to influence the nature of tactile category boundaries between body parts in adults (Le Cornu Knight, Bremner, & Cowie, 2020).

3. The early origins of the multisensory links involved in body perception

As we have seen, somatotopic organization of cortical representations of the body are present at birth and likely earlier. However, we might have reasonable doubt about whether somatotopic structure alone is sufficient to support the body's rich and dynamic representations required for self-representation and skilled action (see, Bermúdez, Marcel, & Eilan, 1995). Certainly, multisensory integration with other external environmental signals, which is thought to underpin bodily perception (for reviews, see Tsakiris, 2010; Ehrsson, 2013), is not immediately indicated via somatotopy. Indeed, studies of adults have demonstrated that perception of one’s body depends extensively on integrating information across multiple senses (Tsakiris, 2010; Ehrsson, 2013). Signals from across touch, vision and hearing inform us about many different properties of our bodies and body parts (Azañón et al., 2016), from their spatial extents to their internal states. The integration of such signals helps us construct a variety of body representations (Schwoebel & Coslett, 2005). For instance, the body schema, which enables a dynamic sensorimotor representation of the relative positions of body parts, is thought to stem from the integration of proprioceptive, tactile, visual, vestibular and motor inputs. On the other hand, the presentation of the structure of the body is postulated to be derived mainly from vision (Buxbaum & Coslett, 2001). Therefore, studies on the development of multisensory links involved in body perception (e.g., visual-proprioceptive and visual-tactile links; for a review, see Bremner, 2016) provide an important additional source of information about the ontogeny of body representations in early life.

Generally, it has been established that even with only a few months (or even days) of life experience, human infants can detect the spatiotemporal congruency between cues about the body coming from different modalities. In these studies, infants’ competence to discriminate between congruent and incongruent multisensory events has been evaluated. The idea is that if infants can detect congruency, it would indicate that infants can make crossmodal links across modalities. For example, in a pioneering study exploring the ability to detect visual-proprioceptive congruency (Bahrick & Watson, 1985), the infants were presented a live video of their legs and feet movement (i.e., congruent display) and a video of others’ legs and feet movement (i.e., incongruent display) simultaneously. The results showed that 5-month-old infants preferred to look longer at the incongruent display, indicating that these infants could differentiate between a congruent and incongruent visual-proprioceptive event. Moreover, by using a similar paradigm, Rochat and Morgan (1995) observed that 3-month-old infants could discriminate the visual-proprioceptive events between first-person and third-person perspectives (see also Schmuckler & Fairhall, 2001; Miyazaki & Hiraki, 2006; Schmuckler & Jewell, 2007).

Another string of studies has reported that newborn infants have a striking ability to differentiate multisensory bodily events based on visual-*tactile* congruency (Zmyj, Jank, Schütz-Bosbach & Daum, 2011; Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Filippetti, Lloyd-Fox, Longo, Farroni, and Johnson, 2015; Filippetti, Orioli, Johnson, & Farroni, 2015). These studies typically investigate infants’ preferences for videos in which a visual stroke to the face or the limbs is congruent or incongruent with the tactile stroke applied to their own face or limbs. Filippetti et al. (2013) demonstrated that even newborn infants could detect temporal congruency based on visual-tactile cues. Interestingly, newborns did not show this when the visual stimulus was inverted, suggesting that this multisensory was only applied when the infants were processing body relevant stimuli. Furthermore, Filippetti et al. (2015) have shown that newborn infants can also detect visual-tactile spatial congruency on the face. In sum, it is reasonable to conclude that early multisensory processing can register correspondences across the interceptive and exteroceptive receptors to generate a representation of the body from early in life. This might be taken to support the speculation of an innate ability to bodily self available at birth (e.g., Rochat, 2010).

The studies reviewed above show that the newborn infant has a clear ability to detect multisensory congruency related to the body. Nonetheless, there are a number of limitations to this evidence. The findings with newborns demonstrate a perception of spatiotemporal visual-tactile congruency only on the face, and not on other parts of the body. And all of this variety of studies investigate an apprehension of visual-tactile and visual-proprioceptive congruency between the body and a screen in external space, which may not bear an equivalence to the kinds of multisensory abilities required to perceive the body in bodily space. Indeed, several studies have reported that bodily multisensory integration in adults only occurs within the peripersonal space (in the context of the Rubber hand illusion; for a review, see Tsakiris, 2010; Ehrsson, 2013). Thus, it is essential to investigate situations in which multisensory events occur within the personal space of the body. This has been recently undertaken in a series of studies examining infants' sensitivity to visual-tactile and auditory-tactile colocation on their hands and feet, where both visual, auditory and tactile stimuli were presented on the infants' bodies themselves (e.g., Begum Ali, Thomas, Mullen, & Bremner, 2021; Freier, Mason, & Bremner, 2018; Thomas et al., 2018). In one recent study by Begum Ali et al. (2021), 4-month-old infants were presented with stimuli pairs comprising a visual flash and a vibrotactile stimulus across where the tactile and visual stimuli were presented on the same or different feet. The infants showed a preference for the condition in which the visual-tactile stimuli were colocated on the same feet, indicating that infants as early as four months of age are sensitive to visual-tactile colocation on their feet. Similarly, Thomas et al. (2018) reported that infants of the same age could detect auditory-tactile colocation on the body. Given that the first skilled reaching does not typically occur until five months of age (e.g., Galloway & Thelen, 2004), and in line with the findings from newborns (e.g., Filippetti et al., 2013), it therefore seems likely that infants develop an ability to detect visual-tactile colocation before the acquisition of skilled reaching.

4. Refining and reconstructing multisensory body representations across early development

Despite evidence discussed in the preceding section pointing to the conclusion that infants by birth or shortly after perceive the multisensory basis of the body, an increasing number of studies challenge the idea that infants are born with a full-fledged body perception before extensive postnatal experience (as has been argued by, e.g., Rochat, 2010). For instance, the competence of tactile localization in external space develops gradually across the first year of life (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008; Rigato, Begum Ali, van Velzen, & Bremner, 2014; Begum Ali, Spence, & Bremner, 2015).

Imagine being about to swat an unseen mosquito biting your left arm. Whilst it may feel automatic and straightforward for an adult to locate the mosquito, this act requires complex dynamic multisensory integration of tactile, proprioceptive, and sometimes visual information about the stimulus location on the body (Heed, Buchholz, Engel, & Röder, 2015; Longo, Azañón, & Haggard, 2010). Given potential changes in the body's posture, we need to consider the current position of the limbs, update the location of the touch "remapping" its coordinates in external space. This remapping needs to be dynamic and flexible, so that, for instance, we do not make mistakes when our limbs are crossed in our waking life. Though the process of tactile remapping is essential for our daily life, according to recent developmental studies, human infants do not develop this competence until 6 months of age (Begum Ali et al., 2015; Bremner et al., 2008). Infants younger than 6 months old appear to perceive touches in anatomical coordinates, rather than code them to external spatial locations.

In order to examine the coding of touches in external space, researchers have tended to focus on a special phenomenon, the crossed-hand deficit (CHD, Yamamoto & Kitazawa, 2001; Shore, Spry, & Spence, 2002; Azañón & Soto-Faraco, 2008), in which tactile localization performance is impaired when the limbs cross the body midline. Evidence of the CHD in infants would demonstrate the influence of external spatial representation on young infants' tactile localization. Begum Ali et al. (2015) found an adult-like CHD in 6-months-olds but not in 4-months-olds. They compared infants' foot orienting responses made with the foot receiving the vibrotactile stimulus across uncrossed-feet and crossed-feet postures. 6-month-old infants showed significantly more correct foot orienting responses in the uncrossed than in the crossed posture. In contrast, the 4-month-old infants performed equivalently across postures. More surprisingly, the 4-month-old infants had a better performance in the crossed posture than the 6-month-old infants. These striking results suggest that, in the younger 4-month-olds, touches are just perceived as touches on the body, but are not related to locations in external space.

The crossed-hands deficit, when it emerges at 6 months of age, demonstrates that infants start to locate touches in external space by rule of thumb. They orient towards the place in external space where their hand or foot would usually rest. But of course, we require more sophisticated abilities than this if we are to keep up with the configuration of our body parts when they move into different postures. Bremner et al. (2008) showed a picture of how infants gradually develop the competence to locate touches and their limbs in the external space across different postures between 6.5-month-olds and 10-month-olds. Infants were presented with vibrotactile stimuli to either hand in crossed- or uncrossed-hand postures. 6.5-month-olds demonstrated a higher proportion of mistakes in the crossed-hands posture because they tended to respond manually to the side where the hand would naturally rest, regardless of the hand posture. Conversely, 10-month-old infants showed equivalent accuracies across both crossed- and uncrossed-hand postures. These results demonstrated that the ability to realign tactile coordinates to locate touches in external space develops significantly during the second half-year of life.

What sensory information infants utilize to update their representations of limb posture? Rigato et al. (2014) addressed this question by investigating modulatory effects of hand posture on somatosensory evoked potentials (SEPs) in 6.5-, 8-, and 10-month-old infants. The infants received vibrotactile stimuli to the hand in crossed- or uncrossed-hand postures. The 10-month-old infants showed significant postural modulation of somatosensory processing: larger SEP responses were observed from the electrodes contralateral to the stimulated hand in the crossed-hands posture. However, this modulation was not observed in the younger groups. These results were consistent with the findings from behavioral studies (i.e., Begum Ali et al., 2015; Bremner et al., 2008) that this age group has a bias in locating the touches in the typical location irrespective of limb posture. Interestingly, when a cloth obscured the sight of arms and hands, the 10-month-old infants showed no SEP response between the two postures. Thus, it is reasonable to assume that visual cues to hand posture are indispensable for remapping touches to external coordinates at 10 months of age.

Taken together, the ability to remap crossmodal links between vision and touch across postural changes and represent the location of a touch on the limb in the external space emerges in the first half-year of life, and is refined to become more flexible and dynamic towards the first birthday. These findings place strong qualifications on the idea that human infants are innately endowed with an ability to perceive their own bodies (e.g., Rochat, 2010), and highlight the limitations of the important early abilities which have been so far established (e.g., Filippetti et al., 2013). A particular challenge in early life seems to be developing a coherent representation of the body across tactile and external space. This conclusion is in accord with other studies showing that body representations in the service of purposeful actions also undergo significant spatial tuning that continues well into late infancy (e.g., D'Souza, Cowie, Karmiloff-Smith, & Bremner, 2017).

5. The role of visual experience in developing body representations

Research with blind people provides some important clues to the role of visual experience in shaping multisensory body representations. Röder, Rösler, and Spence (2004) have reported that congenitally blind adults show no CHD. Conversely, the performance of late blind adults was impaired by crossing the hands. These findings indicate that visual experience plays a vital role in developing multisensory body representations. More importantly, the fact that late blind adults show similar CHD as sighted adults indicated that re-weighting of multisensory integration after the sight loss would not influence the CHD in blind adults. More evidence supporting the view that visual experience is crucial in tactile spatial perception comes from the studies that take a closer look at the relationship of the age of sight loss and the CHD. One particular blindfolded adult, born congenitally blind, but whose eyesight was restored at the age of two years by removing congenital cataracts, shows no CHD (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013). More recently, Azañón, Camacho, Morales, and Longo (2018) demonstrated a sensitive period after the first five months where visual experience is dispensable: So long as sight was restored before five months of age, tactile remapping developed typically. Combining evidence from CHD studies in typically developing infants (i.e., that 4-month-old infants show no somatosensory remapping in tactile space), we think it likely that visual experience involved in remapping touch in external space between 5-months and 2-years old is crucial in the development of tactile remapping.

The notion that visual experience of the limbs is crucial to the typical development of body representations is consistent with the complementary change in the availability of faces and hands in vision in the first year of life: the visual input of hands becomes more and more available, whereas the visual input of faces shows a reverse pattern (Fausey, Jayaraman, & Smith, 2016). Furthermore, a series of studies highlights the critical role of visual input in reaching the tactile targets on the body in infants (Chinn, Noonan, Hoffmann & Lockman, 2019; Chinn, Hoffmann, Leed & Lockman, 2019; Leed, Chinn & Lockman, 2019). Chinn and colleagues found that manual localization performance to a tactile target improves substantially during the first year of life. The ability to reach tactile stimuli is limited to the face, head, and arms initially and then gradually extends to the body's entire surface. More importantly, infants were more likely to look at the target before reaching it than the reverse, indicating that visual information can help code the external space's target location.

How does visual experience aid somatosensory remapping? Though there is little literature on this topic, the studies investigating the ability to perceive visual-tactile and auditory-tactile colocation on the body provide some hints about this question (Begum Ali et al., 2020; Freier, Mason, & Bremner, 2018; Thomas et al., 2018). In these studies, tactile stimuli were presented concurrently with the visual stimuli. The 4-month-old infants, who do not demonstrate the ability of somatosensory remapping, can colocate visual-tactile and auditory-tactile stimuli on their bodies. It seems likely that 4-month-old infants utilize visual information as an anchor to localize the concurrent multisensory stimulation in external space. However, if the visual cues are absent, perceiving touches is only related to anatomical coordinates and not to external space (i.e., no CHD found in 4-month-old infants; Begum Ali et al., 2015). Visual experience may be indispensable for building a spatial representation crucial for encoding spatial information from the whole range of sensory inputs within a common external reference frame.

Here we have described a picture of experience-dependent development of body perception in human infancy. However, it is important to note that this development continues beyond infancy into childhood and likely beyond. For instance, visual cues appear to play a more important role in haptic and bodily perception in children than in adults (Gori, Del Viva, Sandini, & Burr, 2008; Gori, Sandini, Martinoli, & Burr, 2010; Cowie, Makin, & Bremner, 2013; Nardini, Begus, & Mareschal, 2013; Cowie, Sterling, & Bremner, 2016; Nava, Bolognini, & Turati, 2017; Cowie, McKenna, Bremner, & Aspell, 2018; Gottwald et al., 2021). For example, the weighting of visual relative to proprioceptive hand position cues is greater than adults' up to 9 years of age (Cowie, Makin & Bremner, 2013), and develops to an adult-like level between 10 to 13 years of age (Cowie, Sterling, & Bremner, 2016).

6. Conclusions

The evidence indicates that some rudimentary competences of body perception emerge innately in human infants (e.g., Filippetti et al., 2012). However, a number of critical abilities in body perception (e.g., referring a tactile sensation from skin-based coordinates to external spatial coordinates), develop according to more extended developmental trajectories across infancy and beyond. Several studies have now also demonstrated that young infants perceive their bodies in very different ways from the way adults do. Before five months of age, bodily perception appears to be based in skin/anatomical coordinates rather than external (visual) space. Infants obtain the ability to perceive the relationships between their bodies and external space in the second half year of their life. It seems likely that visual experience plays an essential role in this development process, but further research is needed to explore both the intrinsic and experiential factors that scaffold the development of a sense of our own bodies, to provide a clearer picture of the development of multisensory body representations, and to investigate how visual experience particularly contributes to the development of multisensory bodily perception.

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