The development of body representations: an associative learning account

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Abstract

Representing one's own body is of fundamental importance to interact with our environment, yet little is known about how body representations develop. One account suggests that the ability to represent one's own body is present from birth and supports infants' ability to detect similarities between their own and others' bodies. However, in recent years evidence has been accumulating for alternative accounts that emphasise the role of multisensory experience obtained through acting and interacting with our own body in the development of body representations. Here we review this evidence, and propose an integrative account that suggests that through experience, infants form multisensory associations that facilitate the development of body representations. This associative account provides a coherent explanation for previous developmental findings, and generates novel hypotheses for future research.

Keywords: body representations, associative learning, multisensory experience, infancy, development

1. Introduction

Our very first sensory experiences are inherently linked to our own body. Foetuses perform isolated limb movements from as early as the fifteenth gestational week (1), and when they do, this generates both proprioceptive and tactile feedback, for example when they touch their face or the uterine wall. From birth, infants' bodies provide the main tool for interacting with the external environment, and thus the development of infants' bodily abilities is fundamentally linked with their ability to interact with, and learn from the world (2). How infants represent this ever-present part of their existence is a fascinating question that has remained largely unanswered. This may be due to the fact that body representation is a multifaceted concept that has been defined in many different ways across the literature. For example, while for some, body representations relate to high-level concepts such as bodily self-awareness (e.g. (3)), for others these representations are more low-level and relate to the multisensory representations of the spatial disposition of our various body parts (e.g. (4)). In the current paper we focus on the development of body representations in infancy defined as the ability to integrate multisensory (visual, proprioceptive, and tactile) bodily information into coherent representations of one's own body.

The past two decades have seen an increasing interest in the study of body representations in adulthood using perceptual illusions such as the 'rubber hand' and 'enfacement' illusion (e.g. (5, 6)). These studies have shown that visual, tactile, postural, and anatomical information all contribute to body representations in adults. More recently, research has suggested that the ability to bind together such multisensory signals lies at the core of a gradual development of body representations from infancy onwards (7-9). However, the exact mechanism through which these multisensory signals become integrated into coherent body representations remains unknown. One theory proposes that infants are able to combine information from multiple senses from birth (e.g. (10)). According to this view, infants are born with a supramodal representational system that is not restricted to modality-specific information and that allows them to process sensory representations of their own and others' bodies in a common framework (11). This account has mainly focussed on how these supramodal representations allow infants to detect similarities between their own felt bodily acts and the perceived bodily acts of others to support neonatal imitation (a controversial claim, see (12) and (13, 14) for recent debate). Based on the same supramodal representational system one would also expect infants to show evidence of very early emerging multisensory body representations. To date, however, this topic remains poorly investigated. Although infants indeed seem able to represent unimodal bodily signals (15, 16) and to detect intersensory body-related contingency from very early in life (7, 9), in recent years, evidence for views that emphasise the role of experience in the development of multisensory body representations has started to accumulate. For example, recent studies have shown a protracted developmental trajectory in infants' abilities to integrate visual-tactile information presented to the limbs (17), to localise tactile stimulation on their body (18, 19), and to distinguish typical from distorted body shapes (20, 21). These findings appear inconsistent with the idea that body representations are present from birth.

Expanding on existing associative learning accounts of visuo-motor integration (22) and visual-tactile integration (23), here we propose that through daily multisensory experience infants form associations between visual, tactile, and proprioceptive signals that lead to gradually emerging multisensory representations of their own body. This account suggests that the kind of learning that leads to more coherent body representations occurs when there is correlated (i.e. contiguous and contingent) excitation of the sensory neurons that represent a certain body part. For example, when an infant sees her own hand touching an object, the correlated excitation of the visual, tactile, and proprioceptive sensory neurons increases the strength of the connections between them, so that subsequent excitation of one of these types of sensory neurons, i.e. when the infant's hand is touched by an external object, leads to co-activation of the others. Thus, through correlated multisensory experience, *uni*sensory body representations become *multi*sensory body representations, which allow infants to represent multisensory bodily events in relation to each other. The learning that supports the formation of these multisensory body representations mainly occurs when infants observe themselves while they touch their body or external objects.

The development of body representations

Our bodies undergo several periods of significant change over the course of our lifespan, for example when we grow in infancy, childhood, and adolescence, and as we gain or lose weight, become pregnant, or age. Here we argue that our associative account of body representation development offers a plausible explanation for how we update representations of our bodies as we develop and change, opening up new avenues for future research. We start by reviewing studies with adult and child participants that demonstrate that body representations are malleable and can be influenced by incoming multisensory signals. Hereafter we discuss what is known about the development of body representations in infancy, and provide evidence for our account by drawing on studies investigating the role of experience in this process. Throughout we provide suggestions for future research that would more directly test this associative hypothesis of body representation development.

2. Multisensory body representations in adulthood

2.1. Evidence from bodily illusions

Research on the mechanisms underlying body representations in adulthood has focused on the role of multisensory integration in defining the perception of one's body. Through experimentally induced manipulations of multisensory inputs, these studies have shown that body representations are highly malleable (for a review see (6)). A well-known example of the plasticity of the representations of our body comes from the 'rubber hand illusion' (RHI; (24)). In this illusion, watching a rubber hand being stroked in synchrony with the real hidden hand causes a change in body ownership, whereby the rubber hand is experienced as part of the own body and the real hand is felt to be closer to the rubber hand (for reviews see (2, 6)). The RHI is not limited to the visual-tactile domain, and can also be elicited by synchronous tactile-proprioceptive (25) and visual-motor experience (26). This illusion provides an indirect demonstration of how correlated multisensory experience during our typical day-to-day interactions likely plays a critical role in the perception of our own body. Indeed, changes in perceptual body representations as a result of the RHI are only significant when information from proprioceptive, visual, and tactile sensory channels is coherent (i.e. spatially and temporally integrated (27, 28)). Instead, the illusion is diminished when the multisensory information provided is incongruent, either because it is temporally asynchronous (24), or because the postural and anatomical positions are disrupted, leading to a spatial mismatch between the rubber hand and the real hand (29).

While correlated visual, tactile, and proprioceptive information is necessary for maintaining a stable representation of one's own hand, it is not sufficient for the RHI to take place. Top-down constraints, such as visual resemblance to the real hand, are also relevant for the illusion to occur (29, 30), suggesting that perceptual body representations arise from an interactive process whereby the immediate sensory signals are compared with stored representations of the body (5). Based on our hypothesis that representations of the body develop gradually through multisensory experience, one would expect that early in development correlated multisensory signals are likely to have a bigger impact on bodily illusions than top-down representations (i.e. expectations about the visual percept that should be associated with certain tactile and proprioceptive input). Indeed, recent research seems to support this proposal. For example, 6-to-8-year-old children are as likely to embody a rubber hand that is significantly larger than their own hand, as they are to embody a rubber hand that is equal in size (31). Similarly, multisensory processing of bodily stimuli shows a protracted development that is dependent upon the substantial physical changes that the body undergoes from infancy to late childhood (32-36). Overall, this evidence suggests that children's body representations are more plastic, presumably because they have had less time to gain substantial multisensory experience with their bodies to establish strong expectations about how proprioceptive, visual, and tactile representations typically co-occur.

Perceptual illusions similar to the RHI have also been demonstrated for other body-parts, such as the face (37, 38), and full body (39). For example, in the enfacement illusion, synchronous visual-tactile stimulation of the participant's face and another person's face induces a change in self-identification. Thus even our own face, which is arguably the most distinguishable component of our personal identity, is susceptible to illusions induced by temporal and spatial sensory correspondences. Together, these studies suggest that our body representations are not solely derived from stored internal representations, or determined by information from one particular sensory domain, but that they are instead flexibly updated based on the available multisensory information.

2.2. Evidence from tactile localisation studies

The ability to combine incoming afferent information with a pre-existing body representation becomes critical when we need to determine the location of a specific body part. Adults rely on statistical information about the sensory input they receive to act on the environment, and therefore they estimate their body configuration, e.g. limb position, based on the high prior probability that limbs usually occupy particular locations with respect to the body. When limbs are not in their usual position, for example when the arms are crossed, the spatial correspondences between external stimuli (e.g. visual information) and the proprioceptive information (limb posture) need to be remapped. Consequently, when asked to localise touch on their hands, adults are less accurate when their hands are crossed than when they are uncrossed. This “crossed-hands deficit” (40) suggests that the extensive correlated tactile, proprioceptive, and visual experience we obtain with our typical body configuration (i.e. with the left hand in our left visual field and the right hand in the right visual field) promotes the emergence of multisensory associations that help localise touch when our hands are in their normal position, but that results in a conflict when our hands are crossed. In line with our account, studies on tactile remapping show that tactile processing and localisation on the body indeed appear to be influenced by multisensory experience. For example, Azañón et al. (41) demonstrated that repeated visual, proprioceptive, and tactile experience in a crossed posture can improve tactile localisation and diminish the crossed-hand deficit (41). Furthermore, prolonged experience with unfamiliar postures leads to a reduction of the deficit in localising touch across such postures (42-44), suggesting that, over time, multisensory experience can produce long-lasting changes in body representations.

The role of experience in coding multisensory spatial information of proprioceptive-tactile stimuli is also apparent when comparing performance across regions of peripersonal space that differ in the amount of visual representation accumulated over time. For example, when an accurate visual representation of the body is lacking (i.e. the space behind our backs, which we rarely get to see), individuals show better performance in a tactile temporal resolution task, compared to when the same task is performed in the frontal space of the body (44). These results are in line with our account as they demonstrate that, in the absence of opportunities to form associations between seeing and feeling touch on one's hands in this posture (e.g. when hands are behind the back), the interference normally seen in the unfamiliar posture is less pronounced. This raises the intriguing question of how changes in body representations occur in the context of similar slow learning experiences such as the ones accumulated across development.

3. The development of body representations

One of the key processes in the development of infants' first rudimentary body representations is their ability to detect contingencies between multisensory information (45). For example, preferential looking studies have shown that infants are able to match the proprioceptive information generated by their own performed arm and leg movements to those observed on a video display from at least 5 months of age (46, 47). At this age, infants also start to demonstrate the ability to localise vibrotactile stimulation on their limbs, successfully combining tactile and proprioceptive information (48). From at least 3 months of age infants respond differently when they observe a specular image of their own face compared to that of another infant (49), suggesting that they are able to detect the contingency between the visual, motor, and proprioceptive information generated by their own actions. Even newborn infants show a differential looking time response to visual displays of an infant face being stroked synchronously or asynchronously to the tactile stimulation they are receiving themselves (9). These early competencies are thought to rely on infants' abilities to match sensory stimulation in one modality (e.g. tactile or proprioceptive) to stimulation in another modality (e.g. visual). Detecting similar intersensory contingencies during every day exploratory behaviours is thought to play an important role in the development of infants' ability to identify their body as belonging to themselves, and as separate from the environment (50), and may facilitate the formation of multisensory body representations from early on.

Despite infants' early competency in detecting contingencies between multisensory signals, it appears that more advanced body representations, which include expectations about the typical configuration and proportions of human bodies, develop much later in infancy. Indeed, habituation studies have demonstrated that infants only start to differentiate between typical and scrambled adult body configurations from about 15 months of age when these are presented as pictures (21), and from 9 months when real-live human models or mannequins are used (20). Nine-month-olds also appear to have an understanding of the typical proportions of adult human bodies, while 5-month-olds do not (51). Additionally, structural encoding of body configuration seems to emerge around 14 months of age when infants start to show a differential neural signature of body processing when they observe upright versus inverted bodies (52). However, there are also preferential looking studies (53) and an ERP study (54) that suggest that infants are sensitive to the overall organisation of body parts from as early as 3.5 months of age. At this age, infants can also discriminate between appropriately and inappropriately proportioned bodies after first being familiarised to the disproportional bodies (53). Together, these studies suggest that infants have expectations about the first-order structure of bodies from relatively early in life, but that these expectations may be fragile and dependent on how closely the stimuli resemble the bodies infants observe in daily life, and on whether they can directly compare the typical and atypical stimuli. These previous studies all used adult human bodies, but it is unknown whether infants' representations of their *own* bodies follow a similar developmental trajectory. As we explain below, our account would predict that the visual, motor, and proprioceptive experience that infants obtain while they observe their own full body would be critical for the development of infants' ability to form expectations about their own body's configuration and proportions.

4. The role of multisensory experience in the development of body representations

Our associative account suggests that situations in which infants receive contiguous and contingent multisensory input are critical for the development of multisensory body representations. The great majority of these experiences comes from infants' own actions (but also see Box 1). We propose that the order in which modalities become integrated into multisensory representations is dictated by the available modalities at different points in development. For example, while in utero proprioception and touch are likely to be dominant, after birth, proprioceptive-tactile representations will become associated with visual representations (see Figure 1). The earliest evidence for the idea that infants' own experiences play a key role in the development of body representations comes from studies that suggest that foetuses use tactile and proprioceptive information to learn to differentiate between their own body and the external uterine environment, including other bodies. For example, Castiello et al. (55) used ultrasound to observe and compare touch movements of twins at 14 and 18 weeks of gestation towards the uterine wall, themselves, and the other twin. They found that while movements towards the uterine wall did not change over time, the proportion of self-directed movements decreased with time, and movements directed toward the twin were instead greater at 18 than 14 weeks of gestation. This study suggests that infants already start to use correlated proprioceptive-tactile information to learn about their own bodies while they are still in the womb. Further evidence for the role of multisensory experience in the development of body representations can be separated into studies investigating representations of the limbs, the face, and the full body.

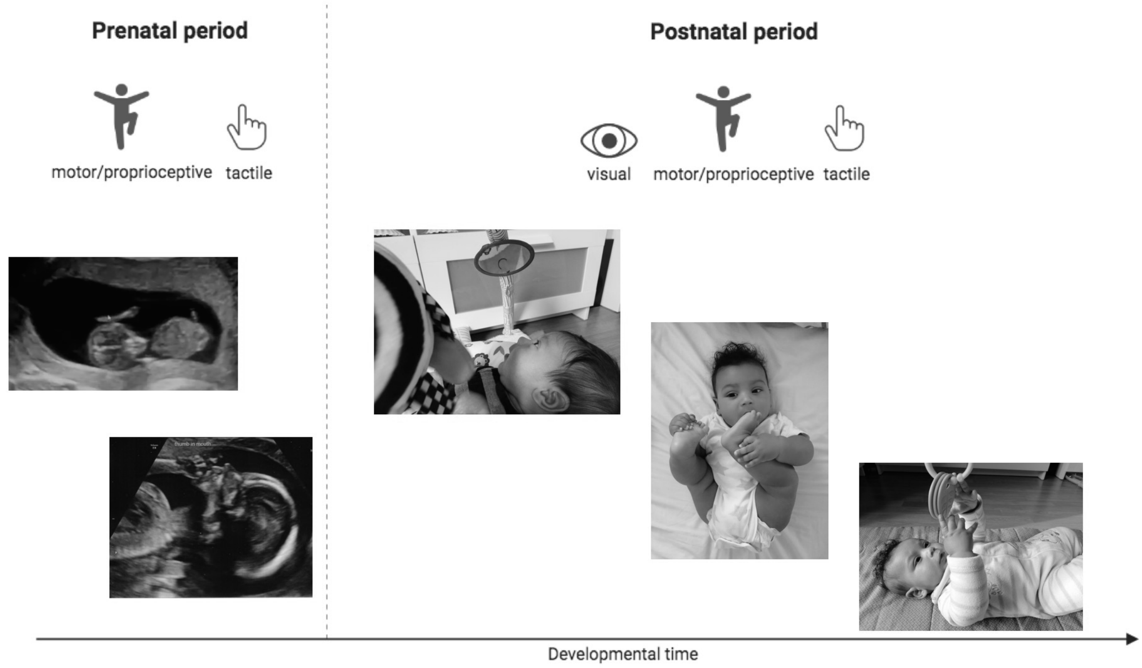

Figure 1. Sources of multisensory bodily information during prenatal and postnatal development. We propose that through daily multisensory experience infants form associations between visual, tactile, and proprioceptive signals that lead to gradually emerging representations of their own body.

4.1. Limbs

When infants start to reach for objects around 4 months of age, not only the visual and motor representation of that action, but also its tactile consequences are activated together. Through the process of associative learning, this repeated experience of seeing and feeling one's body being touched would be expected to result in a link between visual and tactile representations (22, 23). Given that infants do not spontaneously reach across the body midline until they are about 6 to 8 months old (56), young infants would typically see their left hand touching objects in their left visual field, and their right hand in their right visual field. It has been suggested that this consistent early experience promotes the emergence of representations about the most plausible locations of touch (i.e. spatial priors) and prototypical proprioceptive body postures (i.e. canonical posture) (57). Findings from Bremner and colleagues (17, 58, 59) offer a developmental perspective on how infants' experience with reaching with their hands and feet plays a role in the development of the representation of body parts across postures. In the first 6 months of life, infants tend to respond to a vibrotactile sensation presented to one of their hands by moving the hand located on the side of the body where the stimulated hand would typically be, regardless of their posture (crossed or uncrossed hands) (58). It is only in the second half of the first year of life, when infants have accumulated more experience with their limbs in a variety of postures, that the mechanism of postural remapping emerges (58). This finding is consistent with our hypothesis that the correlated visual, proprioceptive, and tactile experience infants obtain while reaching across the midline from about 6.5 months of age supports the integration of the multisensory spatial signals and, as a result, enables infants to make accurate manual responses to the stimulated hand across postures. A similar pattern of results has been found when vibrotactile stimulation was applied to the infants' feet in crossed and uncrossed legs posture (17). In this case, six-month-olds, but not four-month-olds, showed a tactile localisation deficit with their feet crossed, indicating that while the four-month-olds relied on purely anatomical coding of touch, the six-month-olds attempted to integrate the visual-tactile information to the body (17). The authors conclude that because the influence of external spatial coordinates on tactile localization emerges between four and six months of age, this process is likely to be dependent on experience. Between 4 and 6 months of age infants increasingly start to reach for objects with their hands and their feet (60, 61). At these initial stages - when infants do not reach across the midline yet - the proprioceptive, tactile, and visual information coming from their limbs typically is congruent, with the left limbs making contact with objects in the infant's left visual field, and the right limbs in the right visual field. Placing the limbs in an unfamiliar crossed position during tactile stimulation may therefore result in a conflict between the previously associated proprioceptive and visual representation of the limbs, and the current representation of the limbs resulting in the observed 'crossed-limb' deficit.

Converging evidence for the idea that experience with crossing the midline is important comes from an EEG study in which a neural signature of visual-tactile integration across limb posture was observed in 10-month-olds, but not 6-month-olds (62). Posture also modulated somatosensory processing in a group of 8-month-olds who were proficient at reaching across the midline, but not in a group of infants with matched age and motor ability but who did not reach across the midline yet (62). Altogether, this shows how early sensory experience promotes the emergence of representations about the most plausible locations of touch on a canonical limb posture, and how further experience is necessary for the infant to be able to update the postural coordinates and integrate multisensory spatial signals.

Although these studies suggest that experience plays a role in the development of visual-tactile integration, by relying on natural variability in motor skills they do not allow us to rule out alternative explanations such as general maturational processes affecting both visual-tactile integration and the ability to cross the midline. More direct evidence for the role of experience in multisensory integration comes from studies with individuals who had dense bilateral cataracts early in development (63, 64). For example, a participant whose vision was restored by 2 years of age did not show a crossed-hands deficit in a tactile localisation task, suggesting he relied on anatomical rather than visual-external coding of touch (64). However, individuals whose vision was restored by 5 months of age did show a typical crossed-hands deficit (63). These studies suggest that there is a sensitive period between 5 months and 2 years of age during which visual experience is necessary for the development of crossmodal links between touch and vision. In the first 2 years of life, infants spend an increasing amount of time reaching for, touching, and exploring objects with their hands. This experience provides infants with a multitude of opportunities for forming multisensory associations that are fundamental for developing body representations.

4.2. Face

While infants have ample opportunities to form multisensory associations for limbs via self-observation, there are fewer such opportunities for body parts that are visually opaque, such as the face. Without access to a mirror, infants may obtain contiguous and contingent multisensory information when they explore their face with their hands while performing orofacial gestures such as opening their mouth. Infants spend a significant amount of time touching their own face, both pre- and postnatally (65, 66). For example, between 24 and 36 weeks of gestation, foetuses increasingly touch the sensitive parts of their face (the mouth region and the lower part of the face) more than the relatively less sensitive areas of the face (65). The 'double-touch' foetuses experience when they touch their own face provides a unique cue that specifies their face as being separate from the environment and from others. Indeed, when newborn infants touch their own face, they do not demonstrate the same rooting response as when an external object contacts their face (67), suggesting that prenatal multisensory experience contributes to early self/other distinction. Additionally, foetuses perform anticipatory mouth movements when they approach their face with their hand from as early as 24 weeks of gestational age (65). Together with the observation of foetal thumb sucking, which can be seen as early as 10 to 15 weeks of gestation (1, 68), the evidence of coordinated movements between hands and mouths observed in utero suggests that prenatal multisensory experience supports the integration of tactile and proprioceptive information and may play a fundamental role in the early development of body representations.

However, to integrate proprioceptive-tactile experiences with the visual representation of one's own face, infants would need to be able to see themselves in a mirror. There is evidence that infants show a great deal of self-exploration when they are placed in front of a mirror, observing their own movements and reaching for the part of the body reflected in the mirror (69). However, given that most infants will only obtain experience with observing themselves in a mirror when their caregiver places them in front of one, or when a mirror is attached to a toy or their play pen, it may be unsurprising that it takes a relatively long time before infants show evidence of mirror self-recognition between 18 and 24 months of age (69, 70). If it indeed is the case that the formation of associations between visual, proprioceptive, and tactile experiences aids the development of body representations, one would predict that it should be possible to speed up mirror self-recognition by giving infants additional mirror exposure. Studies with rhesus monkeys have provided evidence for this idea by showing that visual-somatosensory (71) and visual-proprioceptive (72) training induces self-directed behaviours in front of a mirror, similar to those observed in the classic rouge task. In the study by Chang et al. (71) monkeys were placed in front of a mirror and trained to touch an irritant laser light that was presented on their own face. After several weeks of training, the monkeys had formed an association between seeing a light spot in the mirror and touching the corresponding area of the face, which allowed them to touch the mark even in the absence of somatosensation. These findings suggest that the formation of multisensory associations supports the development of mirror-induced self-directed behaviours, and have implications for our understanding of what mirror self-recognition as measured by the mark test reflects. There has been lively debate about this in last three decades, with some researchers suggesting that touching the mark reflects the development of self-awareness (70, 73) while others have favoured lower-level interpretations (74, 75). The finding that mark-directed touch can be trained through multisensory experience in non-human primates suggests that it is unlikely that this behaviour always reflects true self-awareness. Instead the development of multisensory associations may constitute a prerequisite process for the ability to identify the face as belonging to oneself. Future studies will need to develop experimental methodologies that will allow us to investigate whether similar training effects can be found in human infants.

4.3. Body

Like our face, our full body is perceptually opaque as we cannot see the visual gestalt of our entire body unless we stand in front of a full-length reflective surface. As a result, we may expect not only infants' representations of their own face, but also those of their own full body to be relatively slow to develop. However, thus far the majority of studies investigating full body representations in infancy have used stimuli of adult bodies (e.g.(20, 21)), and as far as we are aware, no studies have investigated infants' representations of their own full body shape. We hypothesise that simultaneous multisensory experience across different parts of the body influences infants' representations of their own full body configuration.

There is some preliminary evidence that infants' ability to represent the various *parts* of their body may indeed depend on the amount of multisensory experience they have acquired with these body parts. For example, a tactile-localization study in which vibrating stimuli were applied to different points on the head and arms of 7- to 21-month-old infants, showed that the ability to reach to tactile stimuli on the body becomes established in the second half of the first year of life and is refined further during the second year (19). Interestingly, and in line with our account, this study revealed that infants are able to localize targets near the mouth and on the hand at a younger age, compared to targets near the ear or on the forehead, or on other areas of the arm. This developmental trajectory may reflect the amount of multisensory experience with specific body parts the infant acquires with age, from the early prenatal stages onwards (76). Infants are known to spend a significant amount of time contacting their mouth with their hands from as early as the 24^{th} week of gestation (65, 66) and likely obtain significantly less correlated multisensory experience for the ear or forehead. We propose that infants' representations of their own full body are similarly influenced by the amount of full body multisensory experience. For example, as infants start to locomote, there are increased opportunities for them to use their whole body in a coordinated fashion (e.g. crawling, walking) and thus for integrating proprioceptive, tactile and visual experiences (for similar discussion see (52, 77)). Supporting evidence comes from Slaughter et al. (21) who showed that walking 12-month-olds discriminated typical from scrambled body configurations, compared to non-walking 12-month-olds (but see also (78)). Given that full body actions are perceptually opaque, one would expect that mirror exposure while performing such actions would be critical for the development of representations of one's own full body. Future research will need to examine whether multisensory experience obtained while performing whole body actions such as crawling or walking, indeed influences when infants start to represent their own full body. For example, this could be achieved by adapting paradigms that elicit full-body illusions (39, 79) for use with infant populations to investigate the role of multisensory experience and mirror exposure.

Box 1: Social interactions

While our review focuses on infants driving multisensory learning through actions and interactions with their own bodies, social interactions likely also play an important role in the development of multisensory body representations (80, 81). Infants receive multisensory proprioceptive and tactile experience during infant massage, and visual-tactile experience when they receive social touch (see Figure 2). These types of interactions are characterised by the use of ‘affective touch’ - the slow caress-like touch that specifically targets the CT fibres (82). Besides playing an important role in bonding, these experiences of affective touch also allow infants to form associations between visual, tactile, and proprioceptive bodily representations. Indeed, a recent study (83) found that 5-month-old infants showed a preference for body-related visual-tactile synchrony when they received slow velocity CT-optimal ‘affective’ touch, but not when they receive faster velocity non-affective touch. Although the relationship between this preference and the infants’ previous experience with receiving affective touch was not investigated, these findings suggest that slow, caress-like touch, may facilitate the development of multisensory body representations in infancy.

Figure 2. Examples of the kinds of multisensory proprioceptive, visual, and tactile experience infants receive from social touch.

5. Concluding remarks

To summarise, we propose that from the prenatal stages onwards, the correlated multisensory experience infants obtain when they act and interact with their body helps them form representations of their own body. Whether it is through touching the uterine wall, reaching for objects, crawling across the floor, or exploring their face with their hands, the multisensory associations formed through these experiences help the infant update the relative positions of their body parts and enhance the accuracy of their body representations. Adult research is largely consistent with this account; studies using bodily illusions and modifications of the standard posture of the body have shown how multisensory experience can change existing body representations. However, the fact that body representations can be changed by multisensory experience in adults, does not necessarily mean that they also develop through multisensory experience in infancy. Although there is preliminary evidence to suggest that multisensory experience plays an important role in the development of body representations in infancy (e.g. (7, 48)), there is a need for longitudinal and training studies in which this experience is systematically manipulated. These studies could shed light on how much, or what kind of sensory experience (e.g. visual, motor, tactile) is crucial for infants to integrate multisensory information to form more coherent body representations. For instance, we predict that if infants were to be trained to cross the midline to reach for objects, the correlated visual, tactile, and proprioceptive information they would obtain during this experience would improve their ability to localise touch across arm postures.

Further support for our account comes from neural evidence demonstrating the recruitment of key multisensory cortical areas when infants and adults process body-related stimuli (e.g. (7, 84)). Given the posterior parietal cortex' hypothesised role in integrating multisensory bodily signals (84-86), future research could use functional near-infrared spectroscopy (fNIRS) to measure activation over this area while infants obtain correlated multisensory experience. We would expect that the amount of activation over the posterior parietal cortex may predict the extent to which infants' body representations are influenced by the multisensory experience they receive during a training study.

Our account also has implications for developmental disorders in which either the sensory input, or the ability to integrate multisensory signals may differ. For example, a recent longitudinal study that investigated midline crossing behaviours showed that at 10 months of age (but not at 5 and 14 months), infants at risk of ASD or ADHD produced fewer manual actions that involved their hand crossing the body midline into the contralateral side of space compared to low risk infants (87). This reduced level of midline crossing may play a role in the recently demonstrated delay in the ability to represent touch across body postures in children with ASD (88, 89). Individuals with ASD also demonstrate hypo- and/or hypersensitivity to individual sensory channels (90) and show disrupted multisensory integration processes (91). These differences in processing and integrating multisensory signals may impact on the development of body representations. For example, it has been shown that children with ASD are less sensitive to the rubber hand illusion (92, 93) and evidence suggests that these children might require prolonged exposure to multisensory synchronous stimuli for a change in body ownership to take place (92). This opens up avenues for future studies investigating the effectiveness of multisensory training on the development of body representations in this clinical group.

In recent years, evidence has been accumulating for the idea that body representations are not only important for processing bodily events involving our own body but also those of others (e.g. (94)). For example, from early in infancy, somatosensory representations are activated both when our own body is touched, and when we observe touch on others' bodies (15, 95), and representations of our own body and those of our interaction partners are closely intertwined (96). This self-other bodily overlap is an expected consequence of our body representations developing through associative learning. For instance, if an infant tends to look at their hand while it is being touched, the correlated visual-tactile experience results in a link between the two sensory representations, causing the tactile representation to become activated in response to the observation of a visual event that is physically similar, e.g. someone else's hand being touched (23, 97). Given that processes of self-other overlap are thought to play an important role in social cognitive abilities such as empathy (98), future research that investigates the developmental origins of body representations will have wider implications for understanding how infants start to make sense of the social world.

Building on empirical research conducted with infants, adults, and clinical populations, we have argued that body representations not only support our actions and interactions with the world, but are also formed by them. They are a consequence of the rich multisensory experiences we obtain with our own bodies from the prenatal stages onwards. The key challenge for future research will be to determine exactly how much, and what kind of multisensory experience infants need to form more coherent body representations.

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