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Opinion Articles

A Brief Overview of The Development of Body Representations Across Infancy, Childhood and Adulthood

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For centuries, philosophers have pondered over how bodies are represented as unitary entities and contemporary research is beginning to elucidate the answer. This paper will argue that different aspects of body representation develop at different rates across infancy and childhood, with body representation maturing to adult-like states by early adolescence. Firstly, the role of somatosensory cues will be outlined, before highlighting the influence of multisensory temporal and spatial congruity in body representation. A discussion of the early development of proprioceptive mechanisms will follow, before outlining the influence of peripersonal space in body representation. Finally, the role of top-down knowledge on body representation will be examined, clarifying the role of featural information in face representation.

Body representation (BR) refers to an individual's awareness and perception of their body. Both adults and infants exploit somatosensory cues in BR. For example, adults and 5-year-olds perceive that the distance between two points of tactile stimulation (TS) is larger in areas with greater tactile sensitivity (Le Cornu Knight et al., 2017). Further, 4-month-olds, but not 3-month-olds, exhibit contralateral neurological activity to the location of TS (Rigato et al., 2017; Somogyi et al., 2018). These findings suggest that both infants and adults utilise a topological

representation of the body (Gillmeister et al., 2017), indicating that adults and infants exploit somatosensory cues in BR.

However, somatotopic BR appears to be modulated by limb localisation in adults. Evidence for this comes from the crossed-hands deficit (CHD), referring to the phenomenon that crossing one's hands impairs judgments regarding the temporal order of TS to both hands (Shore et al., 2002). This suggests that the limbs are automatically localised in the region of space with which they usually reside; consequently, reversing the locations of the hands impairs the localisation of TS. Indeed, children also automatically localise their limbs in external space. For example, 4-year-olds depict analogous CHDs to adults (Begum Ali et al., 2014) and similar deficits are present in 6-month-olds, but not 4-month-olds, when crossing their feet (Bremner et al., 2008). However, impairment in 6-month-olds ameliorates with visual input, suggesting that 6-month-olds expect somatosensory stimulation to be localised in the ipsilateral region of space, but that visual information supersedes these expectancies until early childhood (Pagel et al., 2009). Such expectancies may be dependent on early visual experience, as congenitally blind individuals who regain sight at 2 years fail to demonstrate a CHD (Ley et al., 2013; Roder et al., 2004). Therefore, both adults and infants utilise somatosensory cues in BR, with the localisation of somatosensory stimulation in exogenous space developing in the first 2 years of life.

Despite the role of somatotopy, adults utilise the temporal correspondence between sensory events to inform BR. The rubber hand illusion (RHI) demonstrates this phenomenon and entails eliciting simultaneous TS to the participant's occluded hand and a rubber hand (RH). Synchronous TS between their hand and the RH manifests embodiment, resulting in declarative ownership over the RH (Botvinick & Cohen, 1998). Adults also exhibit a shift in the perceived location of their index finger towards the RH after synchronous, but not asynchronous, TS; this implicit measure of embodiment is termed proprioceptive drift (PD). These findings elucidate the precedence of visual cues in reconciling contradictory visual and proprioceptive information into the perception of a unitary event (Chen et al., 2018), as exploiting proprioceptive cues would ameliorate the illusion.

Temporal contiguity between multisensory events also informs BR in young children. For example, the RHI induces illusory ownership in 4-year-olds and manifests greater PD during synchronous TS in 6-year-olds (Cowie et al., 2013). However, children aged 4-9 years exhibit greater PD, irrespective of synchrony, and reach adult-like levels by 11 years of age (Cowie et al., 2016); this highlights the precedence of visual cues during childhood, as sight of the RH can induce embodiment. However, congenitally blind, but not late blind, patients fail to exhibit

illusory ownership during a somatosensory variant of the RHI (Nava et al., 2014). These findings suggest that early visual experience is necessary for the pre-eminence of visual stimulation over proprioceptive cues (Petkova et al., 2012).

Indeed, the differential developmental trajectories of visual-tactile and visual-proprioceptive mechanisms, as assessed through illusory ownership and PD, respectively, suggests that these processes develop separately (Cowie et al., 2016). Such mechanisms are rarely correlated (Nava et al., 2014) and the extended development of visual-proprioceptive mechanisms has been suggested to reflect the advantage of proprioceptive malleability during growth (Gori et al., 2008). For example, children exhibit greater proprioceptive errors in navigating their hands through narrow apertures than adults, implying proprioceptive malleability during childhood (De Haan et al., 2018; Hirtz & Starosta, 2002). Therefore, temporal contiguity between visual-tactile and visual-proprioceptive cues informs BR in an analogous manner to adults by 4 and 6 years of age, respectively, with visual-proprioceptive mechanisms continuing to develop into late childhood.

The role of temporal contiguity extends to full-body representation in both children and adults. For example, the full body illusion (FBI) entails viewing one's body through a head mounted display. Synchronous, but not asynchronous, TS applied to the posterior portion of one's own body induces illusory body ownership and PD in adults (Lenggenhager et al., 2007); PD reflects the localisation of one's body to be anterior to one's true location. Self-identification with the virtual body emerges by 6 years of age, reaching analogous magnitudes to adults at 11 years of age (Cowie et al., 2018). However, PD is not present until after 11 years of age, indicating that visual-proprioceptive mechanisms exhibit a latent development. This may reflect reduced peripersonal space (PPS) in children, referring to the proximal external space surrounding the body. Indeed, it has been suggested that objects must be within PPS to be embodied and that diminished PD during childhood reflects the relatively greater distance of the virtual body from the child's PPS (Bremner et al., 2014). Thus, temporal contiguity between multisensory stimuli entails a crucial role in adult BR and such mechanisms emerge by 6 years of age, developing throughout childhood.

Despite the protracted development of tactile-proprioceptive mechanisms, research indicates that proprioception influences infantile BR. For example, 3-month-olds display goal-oriented reaching behaviour towards visually occluded objects (Clifton et al., 1993) and fetuses demonstrate coordinated hand movements towards the mouth (Butterworth & Hopkins, 1988). These findings suggest that rudimentary proprioceptive mechanisms inform motor movements,

and potentially BR, from birth. Additionally, infants also exploit tactile-proprioceptive correspondences in BR. For example, 7-month-olds preferentially look towards visual displays of legs receiving synchronous TS (Zmyj et al., 2011) and preferentially attend to legs with motor movements temporally contingent upon their own actions, compared to delayed motor movements (Schmuckler & Fairhall, 2001). However, preferential looking does not necessitate embodiment and one cannot assume that temporal congruence informs infantile BR in an analogous manner in adults (Bremner et al., 2012). Further, embodiment requires localisation of the stimulus in PPS; as visual displays are in extrapersonal space, preferential looking may not reflect embodiment (Bremner et al., 2014). Despite this, synchronous TS in a visual-proprioceptive task modulates temporal lobe activity, an area implicated in BR, in 5-month-olds in an analogous manner to adults, advocating the role of visual-proprioceptive correspondences in infantile BR (Filippetti et al., 2014; Leube et al., 2003). This suggests that rudimentary proprioception is available from birth and that visual-proprioceptive mechanisms inform BR by 5 months of age. However, subsequent research is required to clarify the role of visual-proprioceptive correspondences in infantile BR.

Spatial congruity between visual and proprioceptive stimulation is also crucial in BR and develops during early infancy. For example, adults report greater embodiment over virtual reality avatars when the avatar's movements are spatially contingent upon their own actions, as compared to spatially incongruent (Spanlang et al., 2014). Indeed, 5-month-olds preferentially attend to visual displays in which the directionality of their leg movements are reversed, suggesting that infants are also sensitive to the spatial congruity of visual-proprioceptive events (Bahrick & Watson, 1985). Preference for spatial incongruence has also been demonstrated in 3-month-olds (Rochat & Morgan, 1995), with evidence of additional motor activity during the incongruent condition. The authors postulated that preference for visual-proprioceptive spatial discrepancies may reflect exploration of novel relations between motor movements and visual feedback; this may consequently aid infantile BR (Bahrick, 2013). Indeed, preference for congruence develops by 9 months of age and may reflect embodiment over the stimulus, compared to preferential exploration of novelty (Hiraki, 2006). Thus, spatial congruity between visual and proprioceptive stimulation informs BR across the lifespan and may aid the construction of one's BR in the first 9 months of life.

Furthermore, the temporal and spatial disparity between cues that are integrated as unitary events declines during childhood. The temporal binding window (TBW) refers to the extent to which discrepant multisensory cues are perceived as unitary events (Wallace et al., 2004). Indeed,

the TBW extends to the spatial domain and narrows from childhood to adulthood. For example, 8-year-olds perceive visual displays to be contingent upon their own actions at greater delays than adults (Jaime et al., 2014) and, when shown virtual hands, 5-year-olds report analogous locations between the virtual and real hand at greater spatial discrepancies than adults (Greenfield et al., 2017). Moreover, performance improved on both tasks across childhood, reaching adult-like levels by 11 years of age. Associative learning and prediction error mechanisms may underpin such phenomena (Myles, 2021a, 2021b; Myles & Merlo, 2022b). These findings suggest that perceptions of temporal and spatial congruity reach maturity by early adolescence, with children integrating more discrepant cues into unitary sensory events than adults.

In addition to multisensory mechanisms, top-down 'knowledge' also influences BR. Reductions in structural (Tsakiris & Haggard, 2010) and textural (Haans et al., 2008) similarity between the RH and true hand result in declinations of illusory ownership during the RHI, suggesting that top-down knowledge mediates the influence of multisensory congruence on embodiment. Top-down knowledge also informs infantile BR, with evidence that 10-month-olds preferentially look at rubber legs, compared to wooden blocks, during synchronous TS (Zmyj et al., 2011). Three-month-olds also preferentially attend to intact, compared to scrambled, bodies (Zieber et al., 2015) and exhibit modulated event-related potentials in response to intact body stimuli (Gliga & Dehaene-Lambertz, 2005). These findings suggest that infants also possess knowledge regarding normal body configurations.

Despite the early development of top-down mechanisms, body size representation is immature during infancy. For example, 17-month-olds often fail to account for body size and make errors such as attempting to navigate through impassable apertures (Franchak & Adolph, 2012). Such errors decline from 18 months to 26 months of age (Brownell et al., 2007), suggesting that experiential use of one's body informs body size representation. This continues to develop across childhood and, by 6 years of age, children exhibit greater implicit and explicit embodiment of RHs with congruent postures during synchronous TS (Gottwald et al., 2018). Indeed, adults are highly sensitive to discontinuities between visual and proprioceptive postural information, as minor deviations in the orientation of the RH from the real hand extensively diminishes illusory ownership (Costantini & Haggard, 2007). Thus, both adults and infants utilise top-down knowledge in BR and such mechanisms mature across infancy and childhood. As previously alluded to, PPS is another top-down mechanism influencing BR from infancy. For example, the RHI does not occur in adults when the hand is largely spatially discrepant

from the body (Lloyd, 2007). Whilst sparse, there is some evidence that infants represent PPS in a similar manner to adults. For example, 8-month-olds utilise postural changes to extend their reach towards a goal object (McKenzie et al., 1993) and estimations of whether an object is within one's reach become adult-like by 5 years of age (Gabbard et al., 2007). Adults exhibit modifications of PPS when using tools, such that the hand's PPS undergoes a transient augmentation (Farnè & Làdavas, 2000). Specifically, the representation of space around the hands of participants was increased subsequent to tool use. Seven-year-olds also demonstrate analogous reach estimations to adults when considering the extent to which a tool will increase their reach (Caçola & Gabbard, 2012). Therefore, evidence suggests that PPS representations manifest by 8 months of age and mature during early childhood, however further research is required regarding the developmental trajectory of PPS.

Contemporary literature suggests that the role of multisensory cues in embodiment varies between body parts. 'Enfacement' refers to the manifestation of illusory ownership over a face during synchronous, but not asynchronous, TS (Sforza et al., 2010). Participants also demonstrate implicit enfacement, stating that pictures of their face entail integrated features of the stimulus-face, and exhibit impaired recognition of their face, suggesting that enfacement extends the categorical representation of one's face (Tajadura-Jimenez et al., 2012). However, explicit reports of enfacement entail reductions in negative ratings of ownership and often fall below affirmative scores (Beck et al., 2015). This suggests that face representation (FR) is only modestly malleable through multisensory stimulation.

Moreover, recent evidence indicates analogous enfacement in infants. For example, neonates preferentially observe faces with temporally and spatially congruent, as compared to incongruent, TS (Filippetti et al., 2013) and 5-month-olds exhibit modulated temporoparietal junction activity in response to TS (Filippetti et al., 2014), an area implicated in self-identification (Apps et al., 2013). However, such studies often delay visual feedback in the asynchronous condition; asynchronous stimulation is consequently predictive of TS, potentially resulting in partial enfacement. Removal of such confounds in studies utilising adult populations results in greater embodiment during synchronous, compared to asynchronous, TS (Bufalari et al., 2014), suggesting that estimations of enfacement in infants may be modest. Despite this, FR matures in early infancy and multisensory cues are ostensibly less influential in the representation of faces than other body parts in adulthood.

Indeed, FR is highly dependent on knowledge regarding featural information. For example, the 'rouge test' assesses self-recognition and involves orienting one's behaviour towards a blemish

on one's face (Bertenthal & Fischer, 1978). Despite a 3-minute delay in visual-feedback, 4-year-olds reach for the blemish (Povinelli et al., 1996), suggesting that recognition is independent of multisensory integration. Indeed, 5-month-olds preferentially look towards a static image of a peer's face, compared to their own, demonstrating knowledge of their facial appearance (Legerstee et al., 1998). Infants often pass the rouge test by 18 months of age (Nielson et al., 2003), however those that fail preferentially look towards their own face during synchronous TS (Filippetti & Tsakiris, 2018). The authors speculated that the infants were utilising multisensory congruency to construct a feature-based representation of their face (Miyazaki & Hiraki, 2006). Indeed, multisensory mechanisms may 'update' feature representation in adulthood, due to incremental changes in appearance (Porciello et al., 2018). Thus, whilst multisensory integration may aid the construction of one's FR during infancy and update featural representations in adulthood, FR is predominantly feature-based.

In conclusion, despite the availability of somatotopic mechanisms during early infancy, multisensory mechanisms appear to inform BR from early childhood and continue to mature into late childhood. Visual-proprioceptive mechanisms entail a protracted developmental trajectory, however rudimentary proprioceptive abilities are available from birth and may be utilised in BR. Indeed, the temporal and spatial binding window declines across childhood, reaching adult-like states by early adolescence. However, top-down knowledge regarding form, texture and PPS may mediate the influence of multisensory cues on BR, with FR more heavily dependent on featural information than multisensory information. Thus, BR consists of multiple mechanisms that develop at varying rates across infancy and childhood, reaching adult-like states by adolescence. Future research should continue to examine the development of BR and also related clinical pathology (Frisone et al., 2021; Merlo et al., 2022; Myles & Merlo, 2021), as such difficulties can have drastic ramifications on both physical and mental health (Gugliandolo et al., 2020; Myles & Merlo, 2022a; Myles et al., 2020; Myles et al., 2021).

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any potential conflict of interest.

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