Body representation in infants: Categorical boundaries of body parts as assessed by somatosensory mismatch negativity

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ABSTRACT

There is growing interest in developing and using novel measures to assess how the body is represented in human infancy. Various lines of evidence with adults and older children show that tactile perception is modulated by a high-level representation of the body. For instance, the distance between two points of tactile stimulation is perceived as being greater when these points cross a joint boundary than when they are within a body part, suggesting that the representation of the body is structured with joints acting as categorical boundaries between body parts. Investigating the developmental origins of this categorical effect has been constrained by infants’ inability to verbally report on the properties of tactile stimulation. Here we made novel use of an infant brain measure, the somatosensory mismatch negativity (sMMN), to explore categorical aspects of tactile body processing in infants aged 6–7 months. Amplitude of the sMMN elicited by tactile stimuli across the wrist boundary was significantly greater than for stimuli of equal distance that were within the boundary, suggesting a categorical effect in body processing in infants. We suggest that an early-appearing, structured representation of the body into ‘parts’ may play a role in mapping correspondences between self and other.

1. Introduction

Within developmental science, increasing attention is being paid to the ways in which the body is perceived by infants and young children. One line of work has examined children and used verbal labelling of body parts (Brownell et al., 2010), while another using visual stimuli has investigated infants’ visual perception of the human body configuration (White et al., 2018; Jibrani et al., 2019). Other work has focused on infants’ perceptions of their own body, as assessed through infant behavioral responses to tactile stimulation (Somogyi et al., 2018; Leed et al., 2019) and the examination of spontaneous self-touching (DiMercurio et al., 2018). Addition knowledge about infant body perception derives from research on: (i) visual-tactile and visual-proprioceptive contingency, which has contributed to our understanding of infants’ perception of their bodies in context of self-motion and object exploration (Bahrick and Watson, 1985; Rochat and Morgan, 1995; Schmuckler, 1996), (ii) infant imitation, which bears on infants’ perception of their own bodies in relation to those of other people (Meltzoff and Marshall, 2018; Meltzoff and Moore, 1997), and (iii) the role of multisensory integration in the development of body awareness (Filippetti et al., 2015a; Filippetti et al., 2015b; Zmyj et al., 2011). Alongside these lines of behavioral research, novel applications of neuroscience methods are sparking new insights into the development of infant body representations (for a review, see Marshall and Meltzoff, 2015). In particular, the examination of cortical responses elicited to tactile stimulation is providing useful information on neural aspects of body representations in infancy (Meltzoff et al., 2018, 2019).

Electroencephalographic (EEG) and magnetoencephalographic (MEG) methods have proven particularly useful for examining infant cortical responses to tactile stimulation. One line of work in this area has shown somatotopic response patterns to stimulation of infants’ hands, feet, and lips (Meltzoff et al., 2018, 2019; Saby et al., 2015). Infant EEG work has also shown that the cortical response to touch on the infant’s body can be influenced by factors such as vision of other’s hands (Drew et al., 2018) and posture (Rigato et al., 2013). These influences are consistent with the notion that lower level representations such as neural body maps in somatosensory cortex interact with higher-level representations of the body (Tamé et al., 2019).

Theoretical work has posited that the processing of touch is influenced by a stored representation of the size and shape of one’s own body, or what has been termed “body model” (Longo et al., 2010). Various lines of evidence suggest that such a higher-level representation...
of the body influences the perception of tactile stimulation (Tame et al., 2019). One prominent methodology for studying these influences involves participants reporting on the distance between two points of tactile stimulation on the body surface. In adults, the perceived distance between equally spaced points of tactile stimulation is greater when these two points are separated by the wrist joint, compared to when the two points are located either on the hand or on the forearm (de Vignemont et al., 2009). Importantly, this finding cannot be explained by differences in tactile receptor density between the hand and arm (Le Cornu Knight et al., 2017). Instead, it suggests that a topological configuration of the body into segmented parts structures tactile distance perception, with joints acting as particularly important landmarks. While the tactile receptor surface (i.e., the skin) forms a continuous sheet, joints segment the body and in this respect, may serve as categorical boundaries.

Developmental work on topological aspects of own-body perception is quite sparse, in part because of methodological constraints. Using a tactile distance perception task, Le Cornu Knight et al. (2017) showed that a categorical effect around the wrist boundary is present in children aged 5–7 years of age. As noted by Brenner and Spence (2017), the preverbal developmental origins of this categorical effect are of particular interest. However, the ability to examine categorical body representations in infants is constrained by the difficulty of conducting behavioral assessments of tactile distance judgement with very young participants. Le Cornu Knight et al. (2017) noted that pilot work showed that meaningful responses on such tasks could not be obtained from children younger than 5 years.

In the current study, we made novel use of infant EEG responses to tactile stimulation as a way of investigating categorical aspects of tactile perception without requiring comprehension of linguistic task instructions or behavioral responses to tactile stimulation. To accomplish this, we employed the mismatch negativity (MMN), which has successfully been used to probe categorical aspects of body perception in adults (Shen et al., 2018a), but to date has not been applied to similar questions in infants.

The MMN is a component in the event-related potential (ERP) that is associated with deviance processing. The MMN has been applied to the study of perceptual discrimination in various sensory modalities across a wide range of ages including both adults and infants (for reviews, see Garrido et al., 2009; Nätänen et al., 2007; Nätänen et al., 2005). The MMN has been particularly useful for studying infant populations because it is elicited without requiring participants to overtly respond or attend to the stimuli presented (Nätänen et al., 2001). Much of the extant work on the MMN in infancy has been in the auditory modality, with studies in this area informing the study of speech and language development in both typical (e.g., Conboy and Kuhl, 2011; Shafer et al., 2012) and atypical (Friedrich et al., 2009; Rinker et al., 2007) populations. The MMN has also been employed to compare aspects of speech perception between monolingual and bilingual infants (Garcia-Sierra et al., 2011, 2016; Shafer et al., 2012).

One important characteristic of the MMN is that its amplitude increases as the perceived salience of the discrepancy between standard and deviant stimuli increases (Chandrakaran et al., 2009; Nätänen and Alho, 1997). This has made the MMN particularly useful in the study of categorical aspects of perception. Indeed, much of the MMN work with infants in the auditory modality has been in the context of categorical perception of speech sounds. In adults, the MMN has proven useful not only for examining categorical effects in the auditory modality (e.g., Dehaene-Lambertz, 1997; Shen and Frisvold, 2019; Xi et al., 2010) but also in the visual (Mo et al., 2011) and somatosensory (Shen et al., 2018a) modalities. These studies all reported an enhanced MMN response to cross-category deviants compared to within-category deviants with equal physical differences.

Of particular relevance to the current study is MMN work that has been carried out with tactile stimuli. Here we build on the studies of Shen and colleagues that used the somatosensory mismatch negativity (sMMN) to study body part categories in adults (Shen et al., 2018a) and to examine aspects of body representation in infants (Shen et al., 2018b). In a study of adults, Shen et al. (2018a) evaluated the sMMN response to tactile distance variance within and across body parts around the wrist joint, specifically the hand and the forearm. The contrast involving tactile stimulation across the wrist boundary (stimulation of the hand and the distal forearm) elicited a significantly larger sMMN than the contrast of two tactile stimuli within the forearm (stimulation of the distal forearm and the proximal forearm), even though the distances were identical in physical space. This led the authors to suggest that neural measures can be used to tap the way that adults organize the body into segments corresponding to “body parts” such as the “hand” versus “arm.”

A recent study took this line of work a step further by providing evidence that tactile stimulation of different parts of the body can elicit a sMMN response in infants aged 6 and 7 months of age (Shen et al., 2018b). In this study, the sMMN was present around 100–150 ms after tactile stimulus onset, and showed greater amplitude for contrasts of bodily locations that are further apart on the homuncular strip in primary somatosensory cortex (SI) than for locations with cortical representations that are closer together in SI. The infant sMMN was followed by a late discriminative negativity (LDN) response around 250–400 ms. The LDN, also known as the late negative mismatch response (“late nMMR”; Conboy and Kuhl, 2011; Friedrich et al., 2009), is commonly observed following the initial MMN response in infants, and has been suggested to reflect higher-order processing of novelty without conscious processing of stimulus change (Ceponiené et al., 2004; Friedrich et al., 2009).

Here we tested whether the infant sMMN exhibits categorical boundary effects to tactile stimulation within and across different body parts, as has been shown in adults. Given that the only other study of the sMMN is with 6- to 7-month-olds (Shen et al., 2018b), we chose to study the same age range. This choice also follows from recent studies that have reported distinct EEG (Saby et al., 2015) and MEG (Melzoff et al., 2018) responses elicited by tactile stimulation of different body parts in 7-month-old infants. Other relevant factors include that infants at this age have extensive reaching and grasping experience that may serve to accentuate the functional categorization of the hand.

The study consisted of two complementary protocols designed to examine the degree to which infant tactile spatial perception is influenced by categorical effects and metric distance. The categorical effects protocol involved presenting two pairs of tactile oddball contrasts with equal physical distances, either across the wrist joint or within the forearm. The metric distance protocol employed the same locations of tactile stimulation but in a different combination (see below) to address the additional question of whether sMMN amplitude was sensitive to increasing tactile distance between points of stimulation within a body part (the forearm). In both protocols we used the “identity MMN” method of analysis that controls for any differences in the physical properties of the two stimuli in a given contrast (Mötönen et al., 2013; Pulvermüller et al., 2006). In this approach, the MMN response is derived from a comparison of responses to the same stimuli presented as infrequent deviants in an oddball block and as control stimuli presented in a separate block. Given that the prior sMMN work with infants (Shen et al., 2018b) showed the presence of the LDN after the infant sMMN, the current study also included an examination of this late response to tactile novelty.

2. Methods

2.1. Participants

Thirty-three infants aged 6–7 months participated in the study (range: 6 months and 0 days to 7 months and 31 days; 18 males). Written consent was obtained from parents at the beginning of each visit. All participating infants were born within three weeks of their due date and
had not experienced serious developmental delays or illness. Infants who were on long-term medication or who had two left-handed parents were excluded from study participation. Data from two infants were excluded from further analyses due to excessive movement (n = 1) or problems with EEG signal acquisition (n = 1), which precluded the recording of a minimum number (40) of artifact-free trials for each deviant and control stimulus. The final sample used in the statistical analyses comprised 31 infants (mean age = 29.4 weeks, SD = 2.3 weeks).

### 2.2. Stimuli

Tactile stimuli were delivered using an inflatable membrane (10 mm diameter) mounted in a plastic casing. The membrane was inflated by a short burst of compressed air delivered via flexible polyurethane tubing (3 m length, 3.2 mm outer diameter). The compressed air delivery was controlled by STIM stimulus presentation software in combination with a pneumatic stimulator unit (both from James Long Company, Caroga Lake, NY) and an adjustable regulator that restricted the airflow to 60 psi. The pneumatic stimulator and regulator were located in an adjacent room to the participant. To generate each tactile stimulus, the STIM software delivered a TTL trigger (10 ms duration) that served to open and close a solenoid in the pneumatic stimulator. Expansion of the membrane started 15 ms after trigger onset and peaked 20 ms later (i.e., 35 ms after trigger onset). The total duration of membrane movement was around 100 ms. This stimulation method has been successfully used in previous EEG and MEG studies of infants (Shen et al., 2017; Meltzoff et al., 2018; Shen et al., 2018a). The analyses were referenced to the onset of membrane expansion, which was set as time zero.

### 2.3. Design and procedure

Three tactile stimulators were attached to the top of the infant’s right hand and forearm with medical tape. Placement of the stimulators was based on the distance between the center of the hand and the back of the proximal forearm, with the distal forearm membrane placed directly between these points. As shown in Fig. 1, the distance between each membrane was physically matched within each participant such that all three stimulators were equally spaced. For any given participant, this spacing ranged between 3 and 5 cm, depending upon the length of their forearm.

Five blocks of tactile stimuli were presented to each participant. These five blocks comprised two oddball blocks with standard and deviant stimuli and three control blocks of stimulation that involved stimulation of only one body part (hand, distal forearm, or proximal forearm). The interstimulus interval in all blocks was 600 ms. One of the oddball blocks was designed to test for a categorical effect across the wrist boundary (referred to here as the categorical comparison protocol). In this block, the distal forearm was designated as the standard, with 80% of the tactile stimuli (800 trials) being delivered to this location. The hand and proximal forearm were designated as the locations of across-category and within-category deviants respectively, with each of these locations receiving 10% of the tactile stimuli in the oddball block (100 trials to each location). The stimuli were presented in a pseudorandom order, with deviant stimuli being separated by at least two standard stimuli. The other oddball block was designed to test the effect of tactile distance on the sMMN. This protocol involved the same tactile stimuli and locations as the categorical comparison, but with the hand (rather than the distal forearm) as the standard. For the tactile distance comparison, the hand was designated as the standard (800 trials), while stimuli to the distal forearm (100 trials) and proximal forearm (100 trials) were designated as the deviants. Deviants presented to the proximal forearm had a greater physical tactile distance from the location of standard stimulation (the hand) than deviant presented to the distal forearm (Fig. 1).

The three control blocks consisted of 1 min of stimulation to only the hand, the distal forearm and the proximal forearm, respectively. Each of these blocks comprised 100 trials to the individual location. These blocks served to establish a control waveform for each body part, which allowed the use of the identity MMN method to control for any physical variance between standard and deviant stimuli. This method involves comparing the ERP elicited to one stimulus presented as a control to the ERP elicited when the same stimulus is presented as the deviant (Möttönen et al., 2013; Pulvermüller et al., 2006).

The duration of the entire recording was 25 min. During presentation of the tactile stimuli, infants were seated on their caregiver’s lap while an experimenter held a series of spinning light-up toys to distract the infant and minimize movement. When infants lost interest in the spinning toys, other toys and some videos were employed to keep them calm and to minimize movement artifact. Both the caregiver and the experimenter controlling the distracting toys were blind to the exact stimulus arrangement and the differences between blocks.

### 2.4. Data acquisition

EEG signals were acquired from 32 electrodes secured in a stretch cap (ANT Neuro, Germany) according to the International 10–20 format. Each electrode site was filled with a small amount of conductive gel. The EEG signals were collected referenced to Cz with an AFz ground, and were re-referenced offline to the average of the left and right mastoids.
prior to analysis. Scalp impedances were kept under 25 kΩ. All EEG signals were amplified by isolatedly isolated, high input impedance (>1 GΩ) bioamplifiers from SA Instrumentation (San Diego, CA) and were digitized using a 16-bit A/D converter (±2.5 V input range) at a sampling rate of 512 Hz using Snap-Master data acquisition software (HEM Data Corp., Southfield, MI). Hardware filter settings were 0.1 Hz (high-pass) and 100 Hz (low-pass) with a 12 dB/octave rolloff; bioamplifier gain was 4000.

2.5 Data analysis

2.5.1 Pre-processing of EEG data

Processing and initial analysis of the EEG signals were performed using the EEGLAB 13.5.4b toolbox (Delorme and Makeig, 2004) implemented in MATLAB. The EEG data were first low-pass filtered as 30 Hz. Epochs of 600 ms duration were extracted from the continuous EEG data, with each epoch extending from −100 ms to 500 ms relative to the stimulus onset. Visual inspection of the EEG signal was used to reject epochs containing other movement artifacts. The mean number of artifact-free trials for each control and deviant conditions was 63 (SD = 8). A one-way ANOVA showed no significant difference between locations in the number of usable trials across all control and deviant conditions (p < 0.427). To prepare the data for ERP analysis, artifact-free epochs were averaged and baseline corrected relative to a 100 ms pre-stimulus baseline.

2.5.2 ERP waveforms and statistical analysis

Based on previous studies of somatosensory evoked potentials and sMMN responses in adults and infants (e.g., Sambo et al., 2012; Saby et al., 2015; Wang et al., 2008; Shen et al., 2017, 2018b), analyses focused on 6 electrodes over left and right frontal (left: F3; right: F4), fronto-central (left: FC1; right: FC2), and central regions (left: C3; right: C4). For computation of the sMMN, the method of adaptive mean fronto-central (left: FC1; right: FC2), and central regions (left: C3; right: C4). For computation of the sMMN, the method of adaptive mean

3. Results

Figs. 2 and 3 show the grand average ERP waveforms and the topography of the sMMN and LDN responses. Visual inspection of the ERP waveforms showed that, compared with control stimuli, deviant stimuli evoked a negative deflection around 100–150 ms for deviant stimuli (the sMMN), followed by a larger negative response around 300 ms (the LDN).

3.1 sMMN

For the categorical effect comparison (between hand and proximal arm stimulation), there was a significant main effect of Stimulus Site, F(1, 33) = 4.425, p = 0.043, η² = 0.093, with significantly larger sMMN response evoked by hand stimulation (across-category deviant) (mean = −5.1 μV, SD = 4.46) than by proximal arm stimulation (within-category deviant) (mean = −3.4 μV, SD = 4.08). Additionally, there was a significant main effect of Region, F(2, 66) = 3.352, p = 0.041, η² = 0.007. Post-hoc analyses using pairwise t-tests with FDR correction showed greater sMMN amplitude at frontal (t(135) = 2.288, p = 0.023) and fronto-central sites (t(135) = 2.116, p = 0.036) than central sites. The results also revealed a significant interaction between Hemisphere and Region, F(2, 66) = 8.203, p < 0.001, η² = 0.099. A post-hoc analysis was conducted separately for each region. A significant effect of hemisphere was found at the central region only, F(1, 33) = 18.38, p < 0.001, η² = 0.07, with greater sMMN amplitude over the right hemisphere.

For the tactile distance comparison (between distal and proximal arm stimulation), there was no significant main effect of Stimulus Site, F(1, 33) = 1.853, p = 0.183, η² = 0.009. Similar to the categorical comparison, there was a significant interaction between Hemisphere and Region, F(2, 66) = 4.431, p = 0.016, η² = 0.005. A post-hoc analysis revealed that there was a significant main effect of Hemisphere at the central region only, F(1,33) = 7.171, p = 0.009, η² = 0.015, with greater sMMN amplitude over the right hemisphere (Fig. 4).

3.2 sMMN latency

For the categorical comparison, the ANOVA showed a main effect of Hemisphere, F(1, 33) = 7.638, p = 0.009, η² = 0.011, with shorter sMMN latency on the left hemisphere (mean = 97.97 ms, SD = 30.93 ms) than the right hemisphere (mean = 104.4 ms, SD = 31.64 ms). There was no other main effect or interactions.

For the tactile distance comparison, there was a significant main effect of Hemisphere F(1, 33) = 11.613, p = 0.002, η² = 0.025, with shorter latency on the left hemisphere (mean = 108.53 ms, SD = 33.07 ms) than the right hemisphere (mean = 118.88 ms, SD = 32.58 ms).

3.3 LDN

The ANOVA on LDN amplitude for the categorical comparison showed a significant main effect of Stimulus Site, F(1, 33) = 5.435, p = 0.026, η² = 0.021, with greater LDN response evoked by hand (across-category) (mean = 5.41 μV, SD = 4.96) stimuli than by proximal arm (within-category) stimulation (mean = −3.89 μV, SD = 5.56). There was also a significant interaction between Hemisphere and Stimulus Site, F(1, 33) = 5.368, p = 0.027, η² = 0.008. A post-hoc analysis revealed that LDN amplitude was greater for hand stimuli than for proximal arm stimuli on the left hemisphere, F(1, 33) = 7.919, p = 0.008, η² = 0.055, but not on the right hemisphere, F(1, 33) = 0.899, p = 0.349, η² = 0.003.

For the protocol testing the tactile distance comparison, there was no significant main effect of Stimulus Site, F(1, 33) = 0.16, p = 0.691, η² = 0.001. There was also no significant main effect of Hemisphere, Region, or interactions between any of the factors (Fig. 4).

4. Discussion

It is well established in both neuroscientific and behavioral-cognitive research that people do not always perceive equally spaced physical distances between stimuli as equal. Rather, it is common for there to be categorical boundaries and groupings such that within-category distances are underestimated and across-category distances are
exaggerated. This has been well established in audition, especially in the case of speech perception, but also has been demonstrated in tactile perception of the body, in which tactile distances within the boundary of one body part are perceived as closer together than these same distances presented across a body-part boundary. This latter phenomenon has been observed in adults and children using behavioral tactile distance estimation tasks across the wrist joint boundary (de Vignemont et al., 2009; Le Cornu Knight et al., 2014, 2016). A recent EEG study in adults provided neurophysiological evidence of this tactile categorical effect by showing that tactile stimuli presented across the wrist boundary (i.e., on the hand and on the distal forearm) elicited greater sMMN responses than equally spaced tactile stimuli presented only within the forearm (Shen et al., 2018a).

The sMMN results from the current study of 6- and 7-month-olds are the first demonstration of a categorical effect in body perception in infants. The contrast involving tactile stimulation across the hand-forearm boundary (i.e., hand/distal forearm) elicited significantly larger sMMN (occurring 80–150 ms after tactile stimulation onset) and LDN (at 250–400 ms) amplitude.
250–450 ms) responses than the contrast of two tactile stimuli within the forearm (i.e., distal forearm/proximal forearm). Yet, tactile stimulation of two sites within the forearm (embedded among standard stimuli of hand stimulation) did not differ from each other in mismatch responses, providing further support for a categorical effect on sMMN amplitude across the wrist boundary.

The results of the current study showed infant sMMN responses in a comparable time window (80–150 ms) and topographic distribution (over frontal and fronto-central areas) as reported in the adult study of Shen et al. (2018a) and the infant study by Shen et al. (2018b). The current results also show a late discriminative negativity (LDN) around 250–450 ms, which is consistent with findings by Shen et al. (2018b) and previous auditory MMN work with infants (e.g., Conboy and Kuhl, 2011; Friedrich et al., 2009; Garcia-Sierra et al., 2016). The infant LDN...
has been suggested to reflect a higher-order, later stage of novelty detection compared with the MMN. The current findings showed that the categorical effects observed in the current study was statistically significant, indicating that the body representation of the current results, but also to expand knowledge on somatosensory change processes and body representations in infants.

At a broader theoretical level, the results of the current study are relevant to the suggestion that the registration of self-other correspondences at the level of body parts may play a role in early social learning processes, for example in imitation (Marshall and Meltzoff, 2014; Meltzoff and Marshall, 2018). Infants develop awareness of their own body in space and demonstrate multisensory integration of body perception at a very young age (Zmyj et al., 2011; Filippetti et al., 2015b), which contributes to the capacity to learn from others. Meltzoff and Moore (1997) proposed that body parts are organized in an explicit and automatic manner. Future work using larger sample sizes and other bodily locations is needed, not only to replicate the current results, but also to expand knowledge on somatosensory change processes and body representations in infants.

In summary, the current findings show that early stages of somatosensory processing are modulated by the categorical segmentation of the body in infants, suggesting a structured representation of the body. Future work investigating how interactions between top-down and bottom-up factors come to shape body representations across infancy and beyond.

Declaration of Competing Interest

The reported study does not involve any conflict of interest.

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