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The somatosensory mismatch negativity as a window into body representations in infancy

Guannan Shen[a,*], Staci M. Weiss[a], Andrew N. Meltzoff[b], Peter J. Marshall[a]

[a] Department of Psychology, Temple University, 1701 N. 13th Street, Philadelphia, PA 19122, USA
[b] Institute for Learning & Brain Sciences, University of Washington, Seattle, WA, USA

ABSTRACT

How the body is represented in the developing brain is a topic of growing interest. The current study takes a novel approach to investigating neural body representations in infants by recording somatosensory mismatch negativity (sMMN) responses elicited by tactile stimulation of different body locations. Recent research in adults has suggested that sMMN amplitude may be influenced by the relative distance between representations of the stimulated body parts in somatosensory cortex. The current study uses a similar paradigm to explore whether the sMMN can be elicited in infants, and to test whether the infant sMMN response is sensitive to the somatotopic organization of somatosensory cortex. Participants were healthy infants ($n = 31$) aged 6 and 7 months. The protocol leveraged a discontinuity in cortical somatotopic organization, whereby the representations of the neck and the face are separated by representations of the arms, the hands and the shoulder. In a double-deviant oddball protocol, stimulation of the hand (100 trials, 10% probability) and neck (100 trials, 10% probability) was interspersed among repeated stimulation of the face (800 trials, 80% probability). Waveforms showed evidence of an infant sMMN response that was significantly larger for the face/neck contrast than for the face/hand contrast. These results suggest that, for certain combinations of body parts, early pre-attentive tactile discrimination in infants may be influenced by distance between the corresponding cortical representations. The results provide the first evidence that the sMMN can be elicited in infants, and pave the way for further applications of the sMMN in studying body representations in preverbal infants.

1. Introduction

The mismatch negativity (MMN), an event-related potential (ERP) component occurring between 100 and 200 ms after the onset of sensory stimulus deviance, is an automatic change-detection response commonly elicited using oddball paradigms in which infrequent deviants are embedded in repeated frequent standard stimuli (see Näätänen et al., 2005, 2007 for review). Because the elicitation of the MMN does not depend on explicit instructions to allocate attention or to respond behaviorally, it has been particularly useful in developmental studies. In the auditory domain, the MMN has been widely employed in the study of speech and language development in both typical (e.g., Conboy and Kuhl, 2011; Shafer et al., 2012) and atypical (e.g., Rinker et al., 2007; Friedrich et al., 2009) populations. It has also been used to examine sensitivities to different speech signals in monolingual and bilingual infants (Garcia-Sierra et al., 2011, 2016; Shafer et al., 2012). Although MMN responses have been observed in other sensory modalities in adults (visual: Mo et al., 2011; somatosensory: Shen et al., 2018a), much less is known about mismatch responses outside of the auditory modality, and related developmental studies are very sparse.

In the tactile domain, the somatosensory MMN (sMMN) can be elicited in adults by deviance in various stimulus properties such as duration (Akatsuka et al., 2005; Butler et al., 2011; Spackman et al., 2010), vibrotactile frequency (Spackman et al., 2010), and spatial location (Shen et al., 2018b; Akatsuka et al., 2007; Naeije et al., 2016; Naeije et al., 2018; Restuccia et al., 2009). To our knowledge, there has been no prior published work on somatosensory mismatch responses in infants. In the current study, our initial aim was to test whether the sMMN could be elicited to the stimulation of different body parts in 6- to 7-month-old infants. Since research on the developmental trajectory and maturation of mismatch responses in infancy has primarily involved auditory stimuli, the literature on the infant auditory MMN response provides the most relevant background for the current study.

In the auditory modality, mismatch responses in infants show some interesting differences from those of adults, with both negative mismatch responses (nMMR) and positive mismatch responses (pMMR) being reported in infants (e.g., Conboy and Kuhl, 2011; Friedrich et al., 2009; Kushnerenko et al., 2002; Partanen et al., 2013). Although the physiological mechanisms underlying the different polarities of these infant responses are yet to be elucidated, it has been suggested that the positive mismatch response, typically elicited between 200 and 400 ms, is a less mature response (Garcia-Sierra et al., 2016; Friedrich et al., 2009), since the extent of this positivity diminishes with age (Cheng et al., 2015; Morr et al., 2002). In general, mismatch responses are primarily positive in infants younger than 4 months of age; most infants then begin to show negative MMN responses to salient stimulus

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[*] Corresponding author.
E-mail address: guannan.shen@temple.edu (G. Shen).

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contrasts between 4 and 6 months of age (Cheng et al., 2015; Partanen et al., 2013; Choudhury and Benasich, 2011; Näätänen et al., 2012).

Aside from age or neural maturity, another factor modulating the polarity of mismatch responses in infants is stimulus characteristics. Contrasts that are more difficult to discriminate (e.g., non-native phonetic units or contrasts with small deviance levels) tend to elicit a positive response, while contrasts that were easier to discriminate elicited more adult-like negative responses in 5- to 6-month-old infants (Cheng et al., 2015; Friedrich et al., 2009). It has been suggested that a negative-going mismatch response reflects a more advanced mapping from acoustic input to phonetic representation, whereas a positive response may indicate less efficient acoustic processing (Ferjan Ramírez et al., 2017; Garcia-Sierra et al., 2016; Shafer et al., 2011). From a clinical perspective, a developmentally delayed shift from a positive response to a negative adult-like mismatch response has been associated with a heightened risk of language impairment (Friedrich et al., 2009; Friedrich et al., 2004; Guttorm et al., 2005).

In addition to the early mismatch responses, auditory oddball paradigms with infants often elicit a late discriminative negativity (LDN) (Bishop et al., 2010, 2011; Cheour et al., 2001; Rinker et al., 2007; Zachau et al., 2005), which is sometimes also referred to as a “late nMMR” (Conboy and Kuhl, 2011; Friedrich et al., 2009; Shafer et al., 2011; Garcia-Sierra et al., 2016). The LDN is commonly observed between 250 and 450 ms, following the initial mismatch response. Although the amplitude of the LDN is largest in infants and children, in adults it has been observed in response to changes in complex auditory stimuli (Cheour et al., 2001; Zachau et al., 2005). Less is understood about the LDN than about infant mismatch responses. It has been suggested that this late discriminative component reflects higher-order processing of novelty but without explicit, conscious processing of stimulus change (Čeponienė et al., 2004; Friedirch et al., 2009). Other studies have interpreted the LDN in infancy as the precursor of an adult-like MMN (Garcia-Sierra et al., 2016; Shafer et al., 2011).

Inspired by the successful application of the auditory MMN in the study of speech and language development in infancy, combined with the lack of developmental research on the MMN in other sensory modalities, the goal of the current study was to explore somatosensory mismatch responses in infants aged 6 to 7 months. As well as testing for the existence of a somatosensory MMN in infants, we were interested in exploring the potential for infant sMMN responses to inform the study of how the body is represented in the developing brain. Recent research in this area has included a focus on somatotopic representations of the body in the infant brain (Marshall and Meltzoff, 2015) as studied using measures derived from the electroencephalogram (EEG) such as the somatosensory evoked potential (SEP; Meltzoff et al., 2018a; Saby et al., 2015) and the sensorimotor mu rhythm (Marshall and Meltzoff, 2015). We aimed to further this line of work by adapting a recent study of the adult sMMN which found that the somatotopic organization of body part representations in primary somatosensory cortex (SI) appears to influence the amplitude of the sMMN elicited by spatial tactile contrasts (Shen et al., 2018a).

The current study of young infants employed a task protocol similar to that used by Shen et al. (2018a) with adults. This protocol leverages a discontinuity in the cortical representation of body parts in SI, specifically between the representations of the hand, the face, and the neck. In primary somatosensory cortex, the hands and the face are represented adjacent to each other, while the cortical representation of the face and the neck are further apart, despite being closer to each other on the 3-D body surface. In Shen et al. (2018a), two oddball contrasts were employed by delivering frequent tactile stimuli to the face (standard stimulus) and infrequent stimuli to either the hand (deviant 1) or the neck (deviant 2). The main finding of this adult study was that the amplitude of the sMMN response was greater for the contrast between face and neck stimulation than for the contrast between face and hand stimulation. A further finding was that the later P300 response showed the opposite pattern, which suggests that sMMN responses are influenced by the ordering and separation of body part representations in SI, while later ERP responses to tactile novelty may be more influenced by separation of the stimulated body parts on the 3-D body surface itself.

In the current infant study, we employed a similar protocol to Shen et al. (2018a) by employing the same two contrasts (face/neck and face/hand) used in that adult work. Our working assumption was that the ordering of body parts on the tactile homunculus in SI would be similar in 6- and 7-month-olds as in adults. If the infant sMMN is indeed sensitive to the distance between the representations of body parts in SI, we predicted that the sMMN elicited by the face/neck contrast would have greater amplitude than the sMMN response elicited by the face/hand contrast.

2. Methods

2.1. Participants

Thirty-three infants aged 6 or 7 months participated in the study (range: 6 months and 0 days to 7 months and 31 days). Infants were recruited using birth records and commercially available mailing lists. All participating infants were born within three weeks of their due date and had not experienced serious developmental delays or illness. Infants taking 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 of artifact-free trials for each deviant and control stimulus (40 trials). The final sample used in the statistical analyses comprised 31 infants (mean age = 30 weeks, 6 days, SD = 2.72 weeks; 16 male; 16 African-American, 7 Caucasian, 2 Hispanic, 6 other/multi-race).

2.2. Stimuli

Tactile stimuli were delivered using an inflatable membrane mounted in a plastic casing (10 mm external diameter; MEG International Services). A similar device for producing tactile stimulation has been used in prior EEG and MEG studies (Meltzoff et al., 2018b; Saby et al., 2015; Shen et al., 2017). Each 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) and an adjustable regulator that restricted air flow to 60 psi. For each tactile stimulus, a trigger generated by the stimulus presentation software opened a solenoid in the pneumatic stimulator for 10 ms, with expansion of the membrane beginning 15 ms after trigger onset and peaking 20 ms later (i.e., 35 ms after trigger onset). The total duration of membrane expansion and contraction was around 100 ms. The pneumatic stimulator unit was located in an separate room to minimize audible solenoid operation in the EEG collection room.

2.3. Procedure

Infants were fitted with an EEG cap while seated on their caregiver's lap. Three tactile stimulators were attached to the infant's body, one on the midpoint of the dorsal surface of the right hand, one on the right side of the neck below the ear, and one on the right side of the face, on the cheek. The stimulators were attached using double-sided adhesive electrode collars secured with medical tape. Throughout the presentation of the tactile stimuli, an experimenter displayed a spinning, light-up toy. When infants lost interest in the toy, other toys and cartoon videos were employed to keep them calm and to minimize movement artifact. Up to 2000 trials of tactile stimulation were delivered, with the entire protocol lasting up to 18 min (not including cap placement). The

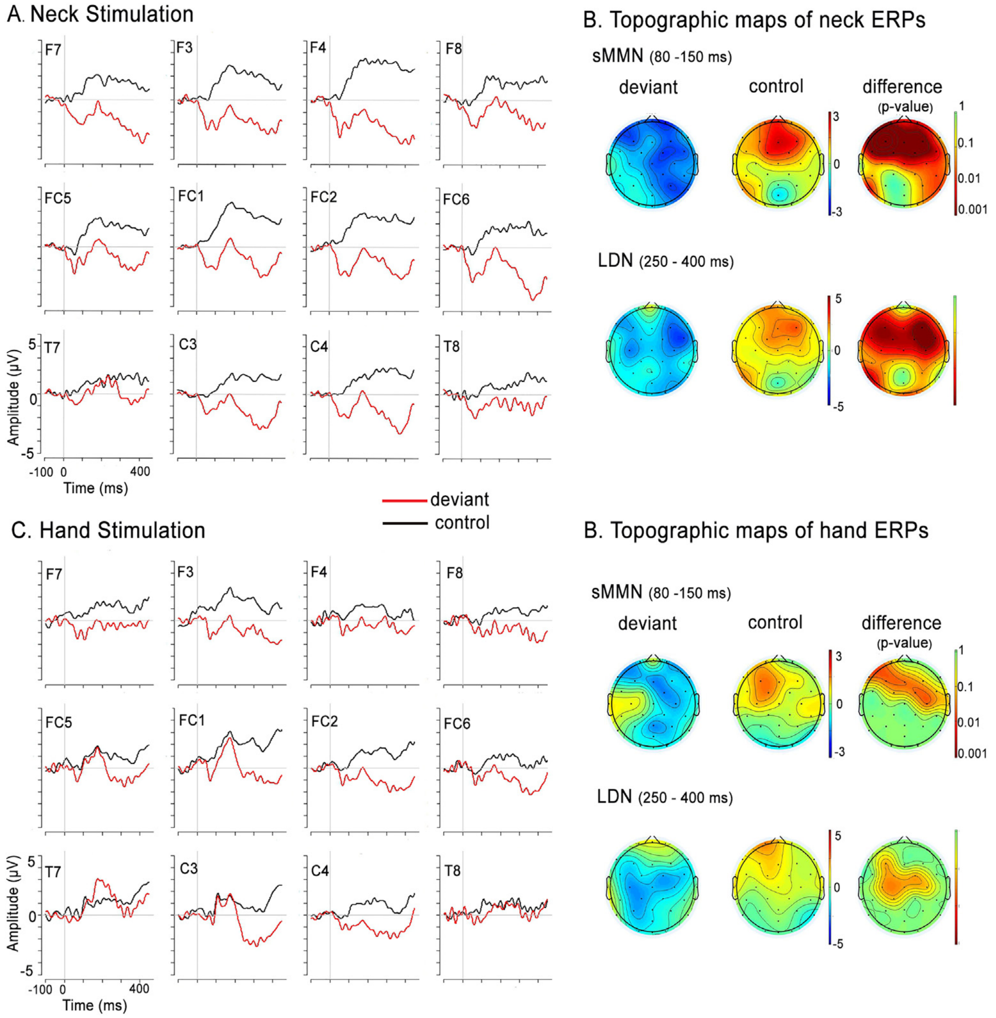

Fig. 1. Grand average ERP waveforms at frontal, fronto-central and central electrodes elicited to hand (A) and neck (C) stimulation when presented as frequent controls (black) and deviants (red) embedded in repeated standard stimulation of the face. (B) and (D) show topographic plots of mean ERP amplitudes for the sMMN (80–150 ms) and LDN (250–400 ms) responses for deviants (left) and controls (middle). The topoplots on the right indicate the significance level of the differences between deviants and controls (pair-wise *t*-test with FDR correction). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

actual duration of the protocol depended on infants' tolerance for the protocol: if the infant became overly fussy, data collection was stopped.

Infants were presented with 1000 trials of tactile stimulation in the first block (oddball block), with face stimulation designated as the standard stimulus and hand and neck stimulation designated as deviant stimuli. During this 10-min block, 80% of the tactile stimuli (800 trials) were delivered to the face, with the hand and neck each receiving 10% of the tactile stimuli (100 trials to hand and 100 trials to neck). The stimuli were presented in a pseudorandom order, with deviant stimuli being separated by at least two standard stimuli. To establish control ERP waveforms for each deviant (see Section 2.5.2), the second block consisted of 1 min of stimulation to the neck (100 trials), and the third block consisted of 1 min of stimulation to the participant's hand (100 trials). Blocks one to three (1 oddball block, and 2 control blocks) were the main part of the study that every participant had to complete. An additional three blocks were designed with the same stimuli but with half of the trials numbers as the first three blocks, in case the infants could tolerate more trials. The fourth experimental block consisted of 500 stimuli in total, with 400 stimuli presented to the face, and 100 stimuli being presented to the neck and hand locations (50 to the neck and 50 to the hand). This block lasted approximately 5 min. The fifth and sixth blocks consisted of 50 trials of tactile stimulation delivered only the hand and neck, to provide additional trials for the control waveforms. Throughout the entire protocol, the inter-stimulus interval was 600 ms.

2.4. EEG recording

EEG was recorded from 32 electrode sites using a Lycra stretch cap (ANT Neuro, Germany) with electrodes positioned according to the International 10–20 system. The signals were collected referenced to Cz with an AFz ground, and were re-referenced offline to the average of the left and right mastoids. Scalp impedances were kept under 40 kΩ. EEG and EOG signals were amplified by optically isolated, high input impedance (> 1 GΩ) bio amplifiers 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 roll-off. Bioamplifier gain was 4000 for the EEG channels.

2.5. Data analysis

2.5.1. Preprocessing 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. Epochs of 600 ms duration were extracted from the continuous EEG data, with each epoch extending from −100 ms to 500 ms relative to tactile stimulus onset at time zero. Independent component analysis (ICA) was employed to identify and remove eye movement artifacts (Hoffmann and Falkenstein, 2008). Visual inspection of the EEG signal was used to reject epochs containing other movement artifacts. The mean number of artifact-free trials for each deviant and control stimulus was 77 ($SD = 15$). A one-way analysis of variance (ANOVA) showed that there was no significant difference in the number of usable trials across all standard and deviant conditions ($p = 0.296$). To prepare the data for ERP analysis, artifact-free epochs were low-pass filtered at 30 Hz using linear finite impulse response (FIR) filtering before being averaged and baseline corrected relative to a 100 ms pre-stimulus baseline.

2.5.2. ERP waveforms and statistical analysis

To control for physical differences between the standard and deviant stimuli, the "identity MMN" method of analysis was used, which 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). Fig. 1 shows the grand average ERP waveforms for hand and neck stimulation presented as deviant and control stimuli. Visual inspection of the waveforms shows that compared to control stimuli, deviant stimuli evoked a larger negative-going deflection around 80 to 150 ms (sMMN), as well as a later negative component around 300 ms (LDN).

Fig. 1 also shows topographic maps of sMMN and LDN amplitudes, with differences between deviants and control stimuli being apparent over frontal and fronto-central electrode sites. Based on this pattern, and consistent with other studies of somatosensory evoked potentials (e.g., Sambo et al., 2012; Saby et al., 2015; Wang et al., 2008; Shen et al., 2017), analyses focused on 12 electrodes over left and right frontal (left: F3, F7; right: F4, F6), fronto-central (left: FC5, FC1; right: FC2, FC6), and temporo-central regions (left: T7, C3; right: C4, T6). Statistical analyses employed analysis of variance (ANOVA) with Greenhouse-Geisser correction. Generalized eta-squared measures of effect size (η^2) are reported. Pair-wise *t*-tests with FDR correction were used for post hoc analyses.

For computation of the sMMN, the most negative peak in the deviant-minus-control difference wave between 60 and 180 ms was identified for each participant. This window was selected based on visual inspection of the waveforms as well as on the sMMN peak latency for neck and hand stimulation (Table 1). The difference wave amplitude was then averaged across a 20 ms time window extending 10 ms before and 10 ms after the negative peak. Three-way repeated measure ANOVAs were conducted with factors *Stimulus Site* (hand/neck), *Hemisphere* (left/right), and *Region* (frontal/fronto-central/temporo-central).

Further analyses examined the late discriminative negativity. To compare LDN amplitude between hand and neck stimulation, LDN amplitude was calculated for each participant by averaging the amplitude of the deviant-minus-control waveform in a 100 ms window surrounding the most negative value between 200 and 450 ms. Mean LDN amplitude was subjected to a three-way repeated measures ANOVA using factors *Stimulus Site* (hand/neck), *Hemisphere* (left/midline/right), and *Region* (frontal/fronto-central/temporo-central).

3. Results

Figs. 1 and 2 show the grand average ERP waveforms and the topography of the sMMN and LDN responses. Fig. 3 shows bar plots of the mean peak amplitudes of the responses to the control and deviant stimuli within the time windows of the sMMN and LDN. Mean peak amplitudes and latencies for each condition are summarized in Table 1.

3.1. MMN

For the comparison of sMMN amplitude between hand and neck stimulation, there was a significant main effect of *Stimulus Site* (F (1, 30) = 4.786, $p = 0.037$, $\eta^2 = 0.04$), with significantly larger sMMN responses evoked by neck stimulation than by hand stimulation. There was also a significant main effect of *Region* (F (2, 60) = 9.747, $p < 0.001$, $\eta^2 = 0.021$), with sMMN amplitude being significantly larger at frontal electrodes than the other analyzed regions (frontal > fronto-central, $p = 0.0185$; fronto-central > temporo-central, $p = 0.019$).

3.2. LDN

The ANOVA for LDN amplitude showed a significant main effect of *Region* (F (2, 60) = 7.455, $p = 0.001$, $\eta^2 = 0.015$). Post hoc analyses showed that LDN amplitude was largest over frontal and fronto-central electrodes (frontal > temporo-central; $p = 0.007$; fronto-central > temporo-central, $p < 0.001$; fronto-central > frontal, $p = 0.705$). There was also a significant interaction between *Hemisphere* and *Stimulus Site* (F (1, 30) = 4.176, $p = 0.048$, $\eta^2 = 0.005$). To explore the interaction, individual ANOVAs were conducted for each hemisphere separately. For the right hemisphere, there was a significant main effect of *Stimulus Site* (F (1, 30) = 4.961, $p = 0.034$, $\eta^2 = 0.054$), with greater LDN amplitude evoked by neck stimulation than by hand stimulation. For the left hemisphere, the difference between neck and hand stimulation was not significant (F (1, 30) = 1.653, $p = 0.208$, $\eta^2 = 0.014$).

4. Discussion

The current study provides the first evidence that the somatosensory MMN can be elicited in infants with a broadly similar time window and morphology as observed in adults (Shen et al., 2018a; Naeije et al., 2016, 2017). Previous studies have reported sMMN responses using tactile oddball contrasts in adults (e.g., Butler et al., 2011; Akatsuka et al., 2005; Naeije et al., 2016) and children aged 6 to 11 years (Restuccia et al., 2009). The adult-like sMMN responses in infants aged 6 to 7 months of age observed in this study are in line with findings in the auditory domain, where infant mismatch responses shift from positive to negative polarity around 3 to 6 months of age, and resemble the adult MMN after 6 months (Cheng et al., 2015).

Building on prior work in adults (Shen et al., 2018a), the use of the oddball contrasts of face/hand and face/neck was designed to investigate the effect of cortical body representations on sMMN responses in infancy. Importantly, the use of the identity MMN method allowed the isolation of responses to spatial deviance by essentially controlling for any differences between stimulation sites in the evoked response to tactile stimulation. In the study of Shen et al., (2018a) with adults, the contrast of lip/neck elicited greater sMMN responses than the contrast

Table 1

Adaptive mean amplitude (deviant-minus-control) and peak latency of sMMN and LDN at the left central (C3), fronto-central (FC1), and frontal (F3) electrodes.

Electrode		sMMN		LDN	
		Amplitude (μV)	Latency (ms)	Amplitude (μV)	Latency (ms)
C3	Neck	−4.1 (SD = 3.39)	116.68 (SD = 42.73)	−6.03 (SD = 5.83)	332.85 (SD = 74.61)
	Hand	−3.18 (SD = 4.04)	118.89 (SD = 39)	−5.55 (SD = 5.29)	336.69 (SD = 80.57)
FC1	Neck	−5.64 (SD = 3.75)	132.25 (SD = 38.59)	−6.6 (SD = 5.34)	322.08(SD =80.09)
	Hand	−3.83 (SD = 4.62)	112.46 (SD = 42.92)	−6.01 (SD = 5.86)	343.06(SD = 90.7)
F3	Neck	−6.09 (SD = 2.93)	128.84 (SD = 39.45)	−6.59 (SD = 4.92)	321.51 (SD = 86.11)
	Hand	−5.08 (SD = 4.67)	121.41 (SD = 44.21)	−5.36 (SD = 5.05)	341.29 (SD = 85.83)

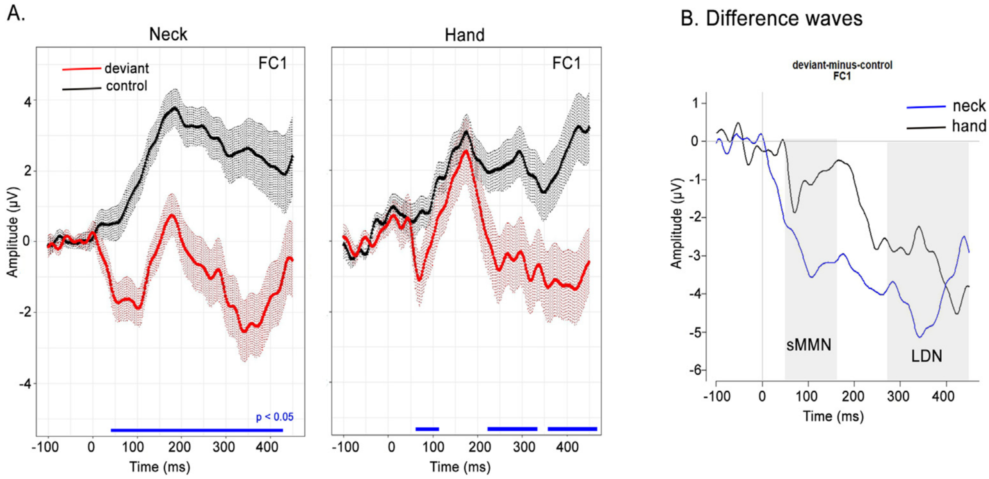

Fig. 2. (A) Grand average ERP waveform at electrode FC1. The shadow shows standard errors across participants at each time point. The blue horizontal bars in the bottom indicate time periods when amplitudes of deviant and control are significantly different from each other ($p < 0.05$, pair-wise *t*-test with FDR correction). (B). Deviant-minus-control difference waves at FC1 for neck (blue) and hand (black) stimulation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of lip/hand. One explanation for this finding is that sMMN amplitude elicited by stimulation of two different body parts is more influenced by the degree of separation of the cortical representations of these body parts in SI than by the degree of separation on the 3-D body surface. More specifically, the representations of the lip and neck are further apart in SI than the representations of the lip and the hand, yet the inverse is true when considering the distances between these body parts on the 3-D body surface.

The present results with infants showed a similar pattern to the adult findings of Shen et al. (2018a), with the face/neck contrast eliciting significantly larger sMMN (at 80–150 ms) and LDN (at 250–400 ms) responses than the face/hand contrast. This result suggests that, as in adults, cortical somatotopy may exert a stronger influence on infant sMMN and LDN responses than does the degree of physical separation of stimulated sites on the body surface. Likely because the main generators of the sMMN are located in primary somatosensory cortex (Downar et al., 2000; Butler et al., 2011; Akatsuka et al., 2007), the somatotopic organization of SI appears to have a downstream influence on sMMN responses elicited by stimulation of different body parts, in both adults and infants. This finding suggesting an effect of SI organization on neural measures of early tactile discrimination could be further clarified by using different combinations of body parts that vary in cortical distances.

Future studies using improved spatial resolution, such as high-density EEG or MEG, can further elucidate the influence of cortical somatotopic organization on neural activities across MMN generators in somatosensory cortex and in higher-order memory updating systems in frontal cortex (Garrido et al., 2009). The current results highlight the modulatory effect of cortical representations of body parts on tactile processing, echoing a previous report where SI organization influenced tactile perception in a task involving visual-tactile interaction in adults (Serino et al., 2009). The putative influence of somatotopy on infant sMMN responses also fits with prior findings showing that infants of the age tested here exhibit somatotopic patterns of evoked responses to tactile stimulation (Saby et al., 2015; Meltzoff et al., 2018b).

In the adult sMMN study of Shen et al. (2018a), the deviant stimuli also elicited a prominent later positive component (novelty P300) that likely reflects attentional orienting to novelty as well as memory updating (Polich, 2007; Huang et al., 2005). This component peaked around 250–300 ms after stimulus onset, following the earlier sMMN

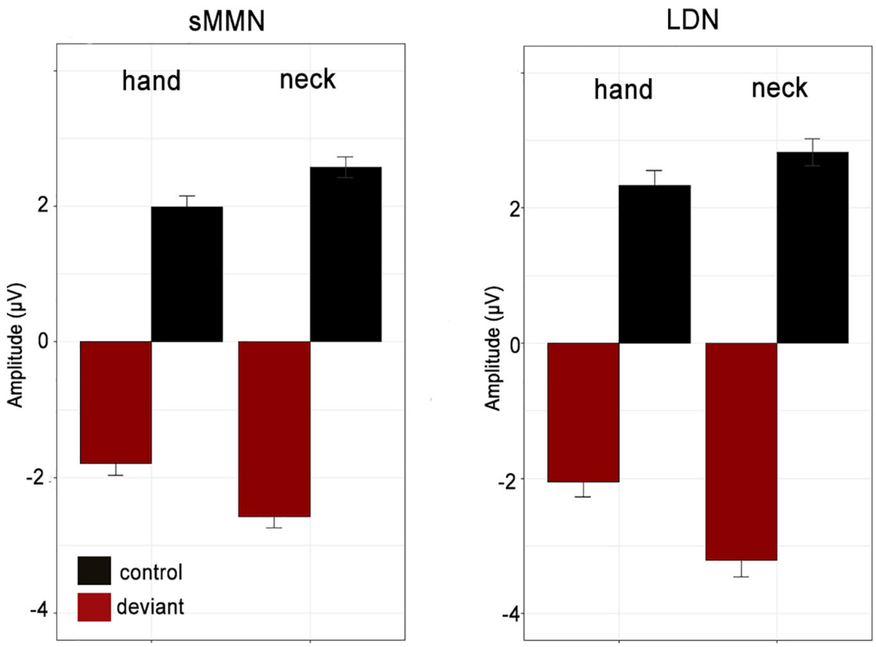

Fig. 3. Mean ERP amplitude in the sMMN (right) and LDN (left) time window for each control (black) and deviant (red), averaged across all 12 fronto-central electrodes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses. In contrast, in the current infant study, the deviant stimuli did not elicit a positive-going component but instead elicited a late discriminative negativity (LDN) between 300 and 400 ms. This difference is likely associated with two factors, maturational constraints and stimulus salience. First, the processes associated with novelty detection and attention switching in oddball tasks may differ between adults and infants (Nelson and Collins, 1991). The morphology of the P300 response, as well as the activity of the fronto-parietal attention networks and working memory system underlying it, undergo major changes from childhood to adulthood (Dinteren et al., 2014; Polich et al., 1990). In terms of stimulus salience, since elicitation of the P300 may require explicit awareness of stimulus deviance, this component may only appear in infants when the level of stimulus deviance is very high (Shafer et al., 2011; Marshall et al., 2009).

The factors noted above may also explain the lack of a novelty P300 in the current sMMN study and in studies of the auditory MMN in infants (e.g., Conboy and Kuhl, 2011; Garcia-Sierra et al., 2016; Friedrich et al., 2009). In these studies, the infant MMN responses are typically followed by the LDN (also sometimes referred to as the late nMMR), which has been proposed to reflect a late stage of automatic, pre-attentive processing of stimulus change (Čeponienė et al., 2004; Friedrich et al., 2009). Since both the P300 and LDN are both elicited by oddball paradigms, and are observed in similar time windows, further investigations are needed to systematically examine the modulatory effect of developmental maturation and stimulus salience on these two components in order to shed light on the specific development of novelty detection mechanisms in infancy.

In the study of Shen et al. (2018a), the amplitude of the P300 in adults was significantly greater for the lip/hand contrast than for the lip/neck contrast, suggesting that external, anatomical distance on the 3-D body influences this attention-orienting component to a larger extent than the distance between cortical representations of body parts in SI. This finding is consistent with the fact that P300 amplitude is particularly sensitive to the degree of salience of stimulus contrasts (Polich, 2007) and is also in line with a dissociation between the MMN and P300 found in previous adult studies (Horváth et al., 2008). In contrast, the current results with infants did not reveal a later component that was sensitive to distances on the 3-D body surface. One speculative suggestion is that for infants at this age, the contrast between stimulation of the pairs of body parts in our protocol was not salient enough to trigger explicit attentional orienting mechanisms. There may be related changes as a function of age in the perceptual and cognitive representation of the body (i.e., the developing body schema) that may contribute to the differences observed between adults and infants.

In further interpreting their findings, Shen et al. (2018a) suggested that the sMMN and P300 responses reflect two stages of somatosensory processing, with an early bottom-up stage of novelty processing that occurs with reference to cortical somatotopy being followed by a shift toward processing of tactile stimulation relative to a frame of reference involving the location of body parts in external space (e.g., Azañón and Soto-Faraco, 2008; Engel et al., 2013). A speculative interpretation of the results from the current study of infants is that, while early, bottom-up, somatotopic stage of tactile processing (indexed by sMMN responses) are apparent in infants at 6–7 months, later stages of processing that involve a shift in the frame of reference may be still be developing at this age in conjunction with changes in experience (e.g., reaching) and the body schema. The ability to map body locations relative to external and peripersonal space and to contrast touches of different body parts requires the integration of information about touch with postural information and often with vision (Bremner et al., 2008). Further empirical studies using both behavioral and neural measures are needed to elucidate the early developmental trajectories of these multimodal aspects of body representations.

One common issue when studying sensorimotor development in infants is the high level of individual differences at this stage of development. Even over the two-month age range of infants seen in the current study, there might be significant individual differences in the development of motor and perceptual abilities. Future studies could focus on infants with a narrower age range, or follow the same infants over time, in order to form a more complete picture of somatosensory mismatch responses in infants.

In conclusion, the current findings provide the first evidence that somatosensory mismatch responses can be elicited in infants using tactile stimulation of different locations on the body. The somatotopic pattern of the infant sMMN response, which is similar to findings from adults (Shen et al., 2018a), suggests that the sMMN in infants may be sensitive to the degree of separation between neural representations of different body parts on SI. As such, studying the infant sMMN response can shed light on the early development of neural body maps in infants, a line of research that is ripe for further study (Marshall and Meltzoff, 2015). These findings open up possibilities for further related work investigating neural aspects of typical and atypical sensorimotor development, including examinations of plasticity in body map representations and the categorical perception of body parts. One technology that may be of particular use in this respect is MEG, the use of which can shed new light on fine-grained spatial and temporal aspects of how tactile stimulation is processed in the infant brain (Meltzoff et al., 2018b). Further investigations of somatosensory mismatch responses in infancy also have the potential to inform applied research on the integrity of early somatosensory processing (Chen et al., 2014; Näätänen, 2009).

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