Neuropsychology of Human Body Parts: Exploring Categorical Boundaries of Tactile Perception Using Somatosensory Mismatch Responses

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Abstract

■ The focus of the current study is on a particular aspect of tactile perception: categorical segmentation on the body surface into discrete body parts. The MMN has been shown to be sensitive to categorical boundaries and language experience in the auditory modality. Here we recorded the somatosensory MMN (sMMN) using two tactile oddball protocols and compared sMMN amplitudes elicited by within- and across-boundary oddball pairs. Both protocols employed the identity MMN method that controls for responsivity at each body location. In the first protocol, we investigated the categorical segmentation of tactile space at the wrist by presenting pairs of tactile oddball stimuli across equal spatial distances, either across the wrist or within the forearm. Amplitude of the sMMN elicited by stimuli presented across the wrist boundary was significantly greater than for stimuli presented within the forearm, suggesting a categorical effect at an early stage of somatosensory processing. The second protocol was designed to investigate the generality of this MMN effect, and involved three digits on one hand. Amplitude of the sMMN elicited by a contrast of the third digit and the thumb was significantly larger than a contrast between the third and fifth digits, suggesting a functional boundary effect that may derive from the way that objects are typically grasped. These findings demonstrate that the sMMN is a useful index of processing of somatosensory spatial discrimination that can be used to study body part categories. ■

INTRODUCTION

The organization of a physically continuous range of stimuli into discrete categories is a fundamental component of human cognition. One prominent example of categorization that has been extensively studied is the phenomenon of categorical perception. For example, evidence for category boundary effects is apparent in the domains of speech perception (Harnad, 1987; Liberman, Harris, Hoffman, & Griffith, 1957) and color recognition (Franklin et al., 2008; Roberson, Davidoff, Davies, & Shapiro, 2005) using both behavioral measurements and neurophysiological indices. Behavioral studies using classical stimulus discrimination and identification tasks show that stimulus variance across a categorical boundary is more easily discriminated than within-category variance across a stimulus continuum (e.g., Shen & Froud, 2016; Werker & Tees, 2005; Francis, Ciocca, & Ng, 2003). In neuroimaging studies, a nonlinear, discontinuous representation of auditory and visual stimuli has been found to occur in early stages of sensory processing (e.g., Bidelman, Hutka, & Moreno, 2013; Mo, Xu, Kay, & Tan, 2011; Liebenthal et al., 2010). A great deal of related research has added to the foundational notion that, due to the categorical nature of perception, similar degrees of physical deviance between pairs of stimuli do not always elicit similar differences in behavioral or neural responses (Shen & Froud, 2018; Kazanina, Phillips, & Idsardi, 2006; Kasai et al., 2001; Sharma & Dorman, 1999; Winkler et al., 1999; Dehaene-Lambertz, 1997).

A classic case of the perceptual nonlinearities associated with categorical perception was first reported in the domain of speech perception (Liberman et al., 1957). As originally described, it involved establishing both an "identification" and a "discrimination" function for a series of stimuli separated by equal physical steps. The peak in the discrimination function occurred at the boundary between the two categories. The term categorical perception is now commonly applied to a broader set of cases beyond the domain of speech. In many tests of infants and adults, only the discrimination of pairs of stimuli equally distant along a stimulus continuum is tested. In the current experiment, we adopt this latter approach and test for enhanced discrimination for across-category compared with within-category stimuli in the tactile domain.

Although categorical perception in the auditory modality has been studied intensively, this phenomenon is less well understood in the somatosensory domain. A few studies have used behavioral measures to examine the categorical perception of body parts in relation to spatial

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tactile perception (Knight, Cowie, & Bremner, 2017; Knight, Longo, & Bremner, 2014; de Vignemont, Majid, Jola, & Haggard, 2009). Similar to auditory and visual perception, tactile distance perception has been found to be nonlinear (Miller, Longo, & Saygin, 2014), even though the tactile receptor surface (i.e., the skin) forms a continuous sheet (de Vignemont et al., 2009). A focus of recent work in this area has been on body part boundaries that are established by the joints (e.g., the wrist joint). Although as a continuous sheet, the skin surface does not have natural boundaries, the joints act as specific landmarks for segmenting the body (de Vignemont, Tsakiris, & Haggard, 2006; Bermúdez, 1998).

The notion of joints as marking category boundaries is supported by findings that tactile stimuli presented at either side of the wrist joint (i.e., one stimulus on the hand and one on the wrist) are perceived as further apart than pairs of stimuli presented within the forearm or within the hand, even when the physical distances between stimulation points are identical (Knight et al., 2014, 2017; de Vignemont et al., 2009). It has been argued that this enhanced tactile spatial acuity across body part boundaries is due to a categorical segmentation effect and is not a result of increased acuity and density of innervation of primary afferent fibers at the wrist and hand skin surface (Knight et al., 2014; Gibson & Craig, 2005).

The categorical and nonlinear perception of distance across joints reflects a part-based representation of body structure (Knight et al., 2017; Longo & Haggard, 2010), with touch being automatically referenced to this topologically structured body representation (Mancini, Longo, Iannetti, & Haggard, 2011; de Vignemont, Ehrsson, & Haggard, 2005). This representation of body parts is present in childhood and may be sharpened by the functional roles of body parts through action learning (de Vignemont et al., 2006; Berthier, Clifton, McCall, & Robin, 1999) as well as by the acquisition of language for labeling distinct separate parts of the body (Enfield, Majid, & Van Staden, 2006).

Complementing the influence of anatomical joint bound- aries, categorization effects in tactile perception may also arise from differences in the functional usage of body parts. How body parts are used in motor acts modulates how they are represented and perceived (Miller et al., 2014; Braun, Schweizer, Elbert, Birbaumer, & Taub, 2000; Hamilton & Pascual-Leone, 1998). However, because functional categories usually overlap with anatomical, joint-based body part categories, the specific relations between the functional use of body parts and the categorical segmentation of tactile perception are unclear. We suggest that tactile stimulation of digits of the hand may provide a useful opportunity to study the effects of functional categories on tactile perception, because digits are anatomically similar but functionally distinct.

One salient functional distinction is between the first digit (the thumb) and the second through fifth digits. The use of the first digit is of special interest to evolutionary biologists, because of the role it plays in tool use. The thumb and the fingers are employed differently during grasping and picking up objects, with the thumb positioned on one side of the object and fingers positioned on the other side (Wing & Fraser, 1983). In the human infant, the thumb–finger opposition grip "precision grip" develops from an earlier imprecise "power grip" in which objects are held between the fingers and the palm (e.g., Butterworth, Verweij, & Hopkins, 1997; Newell, Scully, McDonald, & Baillargeon, 1989). Although the functional distinction between the thumb and the fingers in grasping has been well studied, potential perceptual categorization effects based on this experience have not been investigated. This may be because of the challenges of performing behavioral perceptual assessments such as tactile distance judgments and 2-point discrimination tests on different fingers. However, advances in neuroimaging methods have provided tools to examine sensory–perceptual categorization that can be readily applied to this question.

The MMN is a well-documented aspect of the ERP associated with involuntary deviance processing (Garrido, Kilner, Stephan, & Friston, 2009; Näätänen, Jacobsen, & Winkler, 2005; Pincze, Lakatos, Rajkai, Ulbert, & Karmos, 2001). In the auditory modality, the MMN is commonly elicited over frontocentral sites in response to deviant stimuli embedded in a train of standards (referred to as an "oddball paradigm") and appears around 100–200 msec after change onset. It is thought to reflect the neural activity associated with change detection mechanisms in primary and secondary auditory cortex, and eliciting this component does not require listeners' conscious attention (e.g., Näätänen, 2001). The amplitude of the auditory MMN increases as the perceived salience of the acoustic discrepancy between standard and deviant stimuli increases (Chandrasekaran, Krishnan, & Gandour, 2009; Näätänen & Alho, 1997). This characteristic of the MMN allows it to be used to evaluate the electrophysiological correlates of categorical perception. As shown in a number of studies in both the auditory and visual modalities, larger MMN amplitudes are elicited by across-category deviants compared with within-category deviants. For example, discontinuous MMN responses reflecting adult categorical perception have been reported for phonemes (Kazanina et al., 2006; Kasai et al., 2001; Sharma & Dorman, 1999; Winkler et al., 1999; Dehaene-Lambertz, 1997), Mandarin tones (Xi, Zhang, Shu, Zhang, & Li, 2010), and colors (Mo et al., 2011). These findings suggest that the enhanced MMN response to cross-category deviants compared with within-category deviants with equal physical variance is a reliable indicator of categorical discrimination at a relatively early stage of perceptual processing. One further important observation is that, although the categorical effects indexed by MMN responses occur in the absence of overt attention, other findings suggest that these effects are sensitive to experience. For example, the categorical effect on Mandarin tone perception indexed by MMN responses was only observed in native Mandarin speakers and not in English speakers or adult learners of Mandarin Chinese (Shen & Froud, 2018).

In the tactile domain, the somatosensory MMN (sMMN) can be elicited by deviance in various stimulus properties, such as duration (Butler et al., 2011; Spackman, Towell, & Boyd, 2010; Akatsuka et al., 2005), vibrotactile frequency (Spackman, Boyd, & Towell, 2007), and spatial location (Shen, Smyk, Meltzoff, & Marshall, 2018; Naeije et al., 2016; Restuccia et al., 2009; Akatsuka et al., 2007). Analogous to findings concerning the auditory MMN response, the sMMN is generated in primary somatosensory cortex (Akatsuka et al., 2007; Shinozaki, Yabe, Sutoh, Hiruma, & Kaneko, 1998), with additional generators in secondary somatosensory cortex (Naeije et al., 2016; Butler et al., 2011) and frontal cortex (Kekoni et al., 1997). One study reported that spatially larger deviance evoked greater sMMN, suggesting that sMMN amplitude is modulated by the degree of tactile distance between points of stimulation (Akatsuka et al., 2007). A recent study showed that sMMN amplitude is sensitive to the nature of the cortical body map representation in somatosensory cortex, as indicated by greater amplitude and shorter latency of the sMMN for stimulation of body locations with more separated representations in primary somatosensory cortex (Shen et al., 2018).

The current study investigated the effect of categorical boundaries and functional experience on tactile perception using the sMMN, a tool that can provide a unique window into the early stages of somatosensory processing and the neurophysiological correlates of tactile perception. In addition to the sMMN, the analyses also included an early obligatory somatosensory ERP component, the N80 (Sambo et al., 2012; Schubert et al., 2008), and a later attention orienting component, the P300, which often co-occurs with MMN in oddball paradigms (Lugo et al., 2014; Polich, 2007). The study consisted of two complementary experimental protocols. For the investigation of nonlinearity in body perception, we first leveraged a categorical segmentation of tactile space at the wrist and presented two pairs of tactile oddball stimuli with equal spatial distances, either across the wrist or within the forearm. A second oddball paradigm was based on the functional distinction between the thumb and other digits in goal-directed motor acts, such as picking up and grasping objects. In this second protocol, the amplitude of the sMMN was compared for a contrast involving first versus third digit stimulation (hypothesized to be cross-boundary) and a contrast involving stimulation of the fifth versus third digits (hypothesized to be within category). Because the sMMN response reflects a relatively early stage of tactile processing and because tactile perceptual categorization is thought to involve automatic reference to body part representations (Mancini et al., 2011, de Vignemont et al., 2005), we hypothesized that cross-boundary deviants should elicit greater sMMN responses than within-boundary deviants.

METHODS

Thirty-five undergraduate students received course credit in return for participation. Data from four participants were excluded from the analysis because of participant fatigue ($n = 2$) or insufficient numbers of artifact-free trials (< 50 trials per condition; $n = 2$). The final analyses utilized data from a total of 32 participants (10 men; mean age = 20.47 years, *SD* = 2.01). All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), had normal-to-corrected vision, and reported no history of neurological illness or abnormality. This study was carried out with approval from the institutional review board at Temple University, with informed consent obtained from each individual before participation.

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) 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-msec duration) that served to open and close a solenoid in the pneumatic stimulator. Expansion of the membrane started 15 msec after trigger onset and peaked 20 msec later (i.e., 35 msec after trigger onset). The total duration of membrane movement was around 100 msec. This stimulation method has been successfully used in a number of previous EEG and MEG studies (Meltzoff et al., 2018; Shen et al., 2018; Shen, Saby, Drew, & Marshall, 2017).

During presentation of the tactile stimuli, participants watched a video presented on a CRT monitor (40 cm viewable). Participants were seated approximately 70 cm from the monitor screen. The video consisted of around 30 min of footage of a wildlife documentary presented via DVD. No auditory soundtrack was presented, and subtitles were displayed in English. To mask any subtle sounds associated with delivery of the tactile stimuli, participants wore earplugs during data collection, and ambient white noise was broadcast in the testing room.

Design and Procedure

Six blocks of tactile stimuli were presented across two protocols: hand/forearm stimulation and digit stimulation. There were three blocks within each protocol, and the order of protocol presentation was counterbalanced across participants.

Hand/Arm Stimulation

The first block of the hand/arm protocol consisted of 1000 trials, during which stimulation was delivered every 600 msec to the hand, the distal forearm, or the proximal forearm (see Figure 1A). The inflatable membranes used to deliver tactile stimulation were affixed to the top of the hand and forearm with medical tape. Placement of the membranes 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. The distance between each membrane was kept within 8 and 11 cm, with matched distances used within each participant such that all three membranes were equally spaced. 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 deviants, with each region receiving 10% of the tactile stimuli (100 trials), respectively. The stimuli were presented in a pseudorandom order, with deviant stimuli being separated by at least two standard stimuli. The second and third blocks consisted of 1 min of stimulation to only the hand and the proximal forearm, respectively; each of these blocks contained 100 trials, with a 600-msec ISI. These trials served to establish a control waveform for each body part (see Statistical Analysis section).

Digit Stimulation

The first block of this protocol consisted of 1000 trials, during which stimulation was delivered every 600 msec to the first digit (thumb), the third digit (middle finger), or the fifth digit (little finger) of the hand (Figure 1B). The inflatable membranes used to deliver tactile stimulation were attached to each digit via plastic clips. The third digit was designated as the standard, with 80% of the tactile stimuli (800 trials) being delivered to this digit. The thumb (first digit) and fifth digit were designated as deviants, with 10% of the tactile stimuli (100 trials) being delivered to each. The pattern of tactile stimulus presentation in this protocol was similar to the protocol for hand/arm stimulation (above). The second and third blocks consisted of 1 min of stimulation to only the thumb and the fifth digit, respectively, to establish a control waveform for these digits. The second and third blocks had 100 total trials each and an ISI of 600 msec.

Data Acquisition

EEG signals were acquired from 32 electrodes secured in a stretch cap (ANT Neuro) 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 before analysis. Eye blinks were monitored via EOG electrodes placed above and below the left eye. Scalp impedances were kept under 25 kΩ. All EEG and EOG signals were amplified by optically isolated, high input impedance (>1 GΩ) bioamplifiers from SA Instrumentation (San Diego, CA) and were digitized using a 16-bit A/D converter (±5 V input range) at a sampling rate of 512 Hz using Snap-Master data acquisition

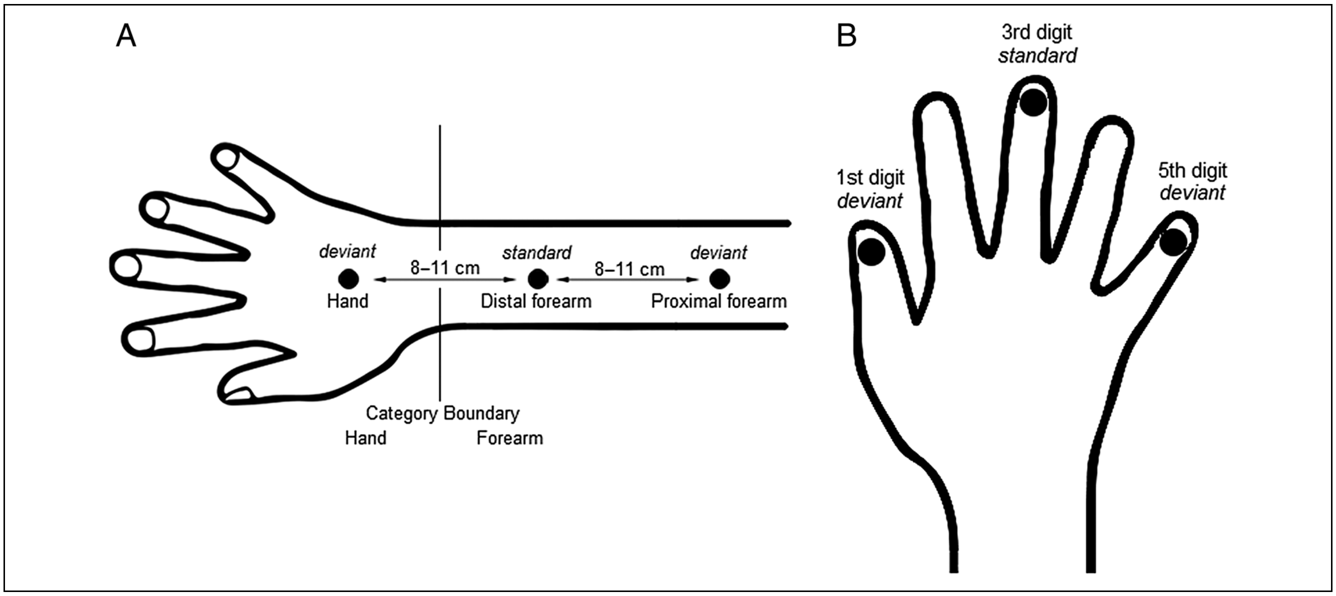

Figure 1. Placement of tactile stimulators for the hand/arm stimulation protocol (A) and digit stimulation protocol (B). Each stimulator is represented by a black dot. The exact distances between each stimulator differed across participants due to differences in arm length. Distances between each stimulator were equalized within each participant.

software (HEM Data Corp.). 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 and 1000 for the EOG channels.

Data Analysis

Preprocessing of EEG Data

Processing and initial analysis of the EEG signals were performed using the EEGLAB 13.5.4b toolbox (Delorme & Makeig, 2004) implemented in MATLAB (The MathWorks). Epochs of 600-msec duration were extracted from the continuous EEG data, with each epoch extending from −100 msec to 500 msec relative to stimulus onset. Independent component analysis was used to identify and remove eye movement artifacts (Hoffmann & Falkenstein, 2008). Visual inspection of the EEG signal was used to reject epochs containing other movement artifacts. The mean number of artifact-free trials per body part location or digit was 86 ($SD = 8$). A one-way ANOVA showed that there was no significant difference between locations in the number of usable trials across all standard and deviant conditions ($p = .572$). To prepare the data for ERP analysis, artifact-free epochs were low-pass filtered at 30 Hz before being averaged and baseline-corrected relative to a 100-msec prestimulus baseline.

Statistical Analysis

As well as the sMMN, the ERP analyses included the N80, a mandatory tactile ERP component, as well as a later P300 component. Because early somatosensory ERP components typically have frontal and central scalp distributions (e.g., Shen et al., 2017; Sambo et al., 2012; Wang, Mouraux, Liang, & Iannetti, 2008), analyses of the N80 and sMMN focused on 12 electrodes over frontal (F7, F3, F4, F8), frontocentral (FC5, FC1, FC2, FC6), and centrotemporal (T7, C3, C4, T8) regions. N80 amplitudes were calculated by averaging the mean amplitude in the 12-msec window, extending 6 msec before and after the most negative peak within the period of 60–100 msec following stimulus onset. To compare N80 amplitude elicited by different deviants and controls, a four-way repeated-measures ANOVA was conducted separately for digit stimulation and arm/hand stimulation with factors Stimulus type (deviant/control), Category type (within-boundary deviants: arm, fifth finger; across-boundary deviants: hand, thumb), Region (frontal/frontocentral/central), and Hemisphere (left/right).

The first step in computing sMMN amplitude was to subtract the ERPs for one stimulus as the control from the ERP when the same stimulus was the deviant (Zheng, Minett, Peng, & Wang, 2012; Xi et al., 2010). The most negative peak in the deviant-minus-control difference wave between 100 and 200 msec (Garrido et al., 2009; Näätänen et al., 2005) was identified at the selected electrodes for each participant. To compute sMMN amplitude, the difference wave amplitude was then averaged over a 20-msec time window, extending 10 msec before and 10 msec after this negative peak. Three-way repeated-measures ANOVAs were conducted separately for digit stimulation and arm/hand stimulation using factors Category type (within-boundary deviants: arm, fifth finger; across-boundary deviants: hand, thumb), Region (frontal/frontocentral/central), and Hemisphere (left/right). Pairwise t tests with false discovery rate (FDR) correction were used in all post hoc comparisons.

The analysis of P300 amplitude followed a similar procedure as for the sMMN. In line with prior work on the P300 scalp distribution (Polich, 2007), three midline electrode sites were selected for statistical analysis: Fz, Cz, and Pz. Mean P300 amplitude was calculated by averaging the amplitude of the deviant-minus-control waveform in a 100-msec window surrounding the most positive value between 180 and 400 msec. Two-way repeated-measures ANOVAs on P300 amplitude were conducted separately for digit stimulation and arm/hand stimulation using factors category type (within-boundary deviants: arm, fifth finger; across-boundary deviants: hand, thumb) and electrode (Fz/Cz/Pz). Pairwise t tests with FDR correction were used in all post hoc comparisons.

RESULTS

Figures 2 and 3 show the grand-averaged waveforms to the deviant and control stimuli at frontal and central sites and the topographic plots for hand/arm stimulation and digit stimulation, respectively. Visual inspection of the ERP waveforms shows that, compared with control stimuli, deviant stimuli evoked a larger early negative component, N80, a more negative-going deflection around 100–150 msec for deviant stimuli (sMMN), followed by a larger positive response around 200–300 msec (P300).

N80

For arm/hand stimulation, the four-way repeated-measures ANOVA, with factors Stimulus type (deviant/control), Category type (within-/across-boundary deviants, arm/hand), Region (frontal/frontocentral/central), and Hemisphere (left/right) revealed a significant main effect of Hemisphere ($F(1, 31) = 6.998, p = .013$; left hemisphere > right hemisphere). There was also a significant main effect of Region ($F(2, 62) = 35.597; p < .001$), with greater N80 responses at frontal and frontocentral regions than centrotemporal regions ($p < .001$). There was no significant main effect of Category type ($F(1, 31) = 2.343, p = .136$). In addition, the results showed a significant interaction between Stimulus type and Category type ($F(1, 31) = 7.013$,

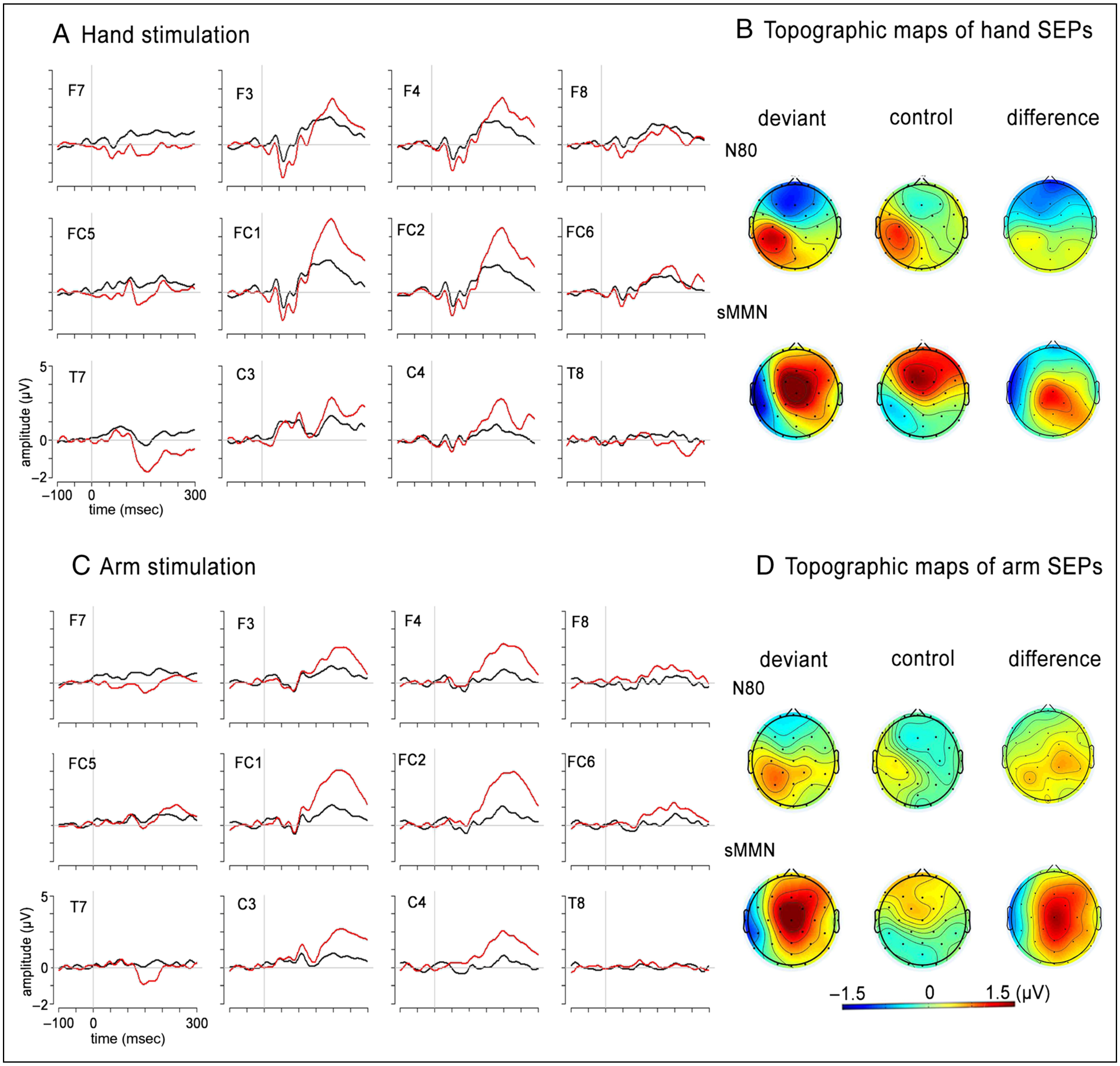

Figure 2. Hand/arm sMMN. (A) Grand-averaged ERP waveforms in response to hand (A) and arm (C) stimulation presented as frequent controls (black) in the control blocks and as infrequent deviants (red) in the oddball block. (B, D) Topographic plots of mean N80 and sMMN amplitude.

p = .013). Two separate three-way ANOVAs were conducted for arm and hand stimulation for post hoc analysis. Results showed a significant main effect of Stimulus type for hand stimulation ($F(1, 31) = 9.875, p = .004$), with greater N80 responses to deviant than control stimuli. No significant main effect of Stimulus type was found for arm stimulation ($F(1, 31) = 0.321, p = .575$).

For digit stimulation, the four-way repeated-measures ANOVA revealed a significant main effect of Stimulus type ($F(1, 31) = 6.017, p = .019$), with greater N80 amplitude for deviant stimuli than for control stimuli. The results also showed a significant main effect of Region ($F(2, 62) = 16{,}441, p < .001$), with greater N80 responses at frontal and frontocentral regions than centrotemporal regions ($p < .001$). In addition, there were two significant three-way interactions between Stimulus type, Category type, and Hemisphere ($F(1, 31) = 8.712, p = .006$), as well as between Stimulus type, Category type, and Region ($F(2, 62) = 4.102, p = .028$). There was no significant main effect of Category type ($F(1, 31) < 0.001, p = .998$). To further examine the significant interactions, two separate three-way ANOVAs were conducted on N80 amplitude for the thumb and fifth digit stimulation. There was a significant main effect of Stimulus type for the thumb

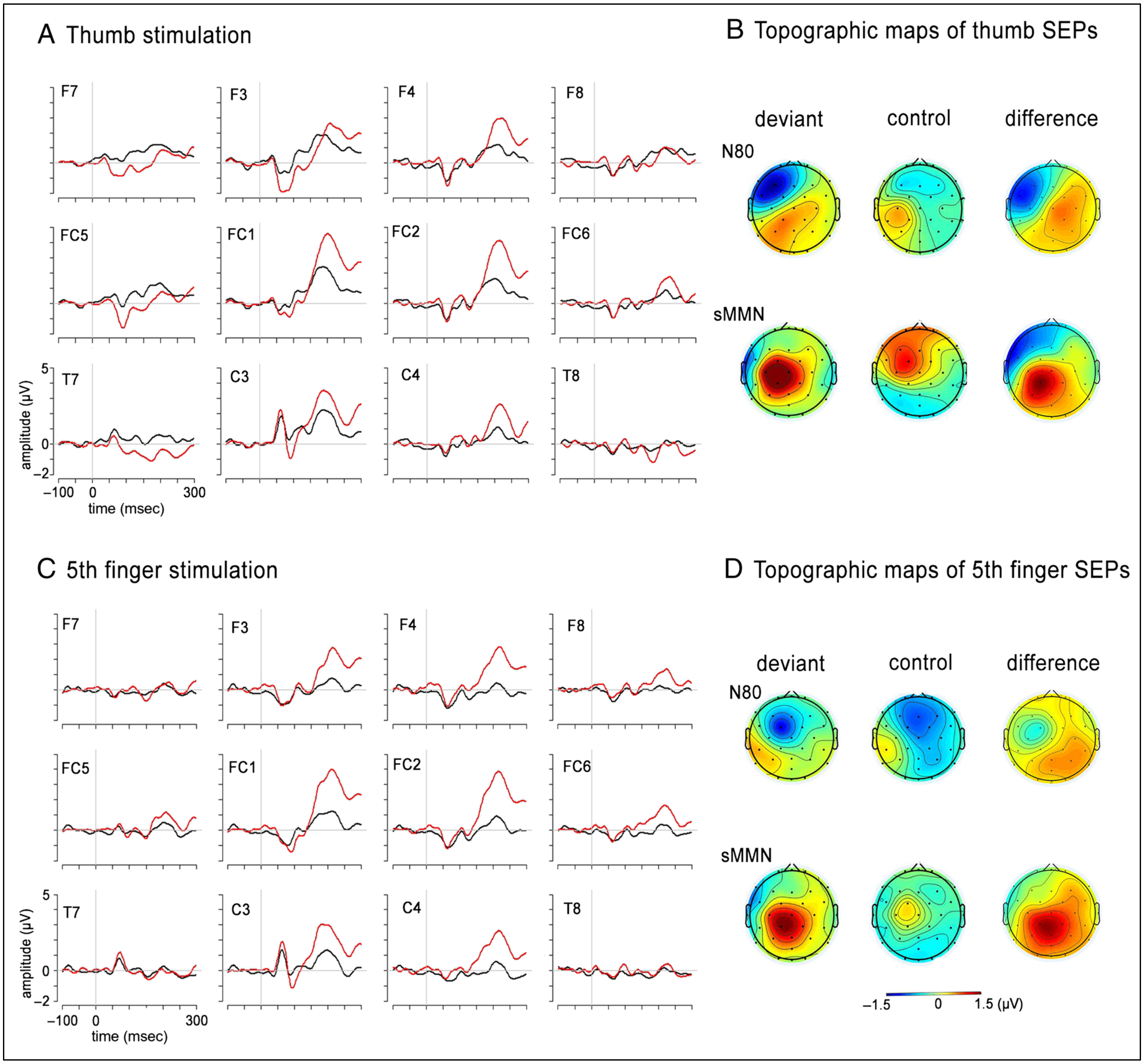

Figure 3. Digit sMMN. Grand-averaged ERP waveforms at frontal and central electrodes elicited to the thumb (A) and fifth digit (C) stimulation when presented as frequent controls (black) and as infrequent deviants (red) embedded in repeated standard stimulation of the third digit. (B, D) Topographic plots of mean ERP amplitudes for the N80 (70–100 msec) and sMMN (130–160 msec) for deviants (left), controls (middle), and the deviant-minus-control difference (right).

stimulation ($F(1, 31) = 7.186$, $p = .012$; deviant > control), but not for the fifth digit stimulation ($F(1, 31) = 0.45$, $p = .507$; Figure 5).

MMN

The ANOVA on sMMN amplitude showed a significant main effect of Category type ($F(1, 31) = 5.427$, $p = .026$), with significantly greater sMMN amplitude for hand than arm stimuli, as well as a significant main effect of Hemisphere ($F(1, 31) = 8.014$, $p = .008$; left > right hemisphere). The ANOVA also revealed a significant main effect of Region ($F(2, 62) = 5.147$, $p = .009$), with greater sMMN responses over frontal electrodes than frontocentral sites ($p = .001$) and centrotemporal sites ($p = .22$). There were no significant interactions between any of the factors.

For digit stimulation, an ANOVA on sMMN amplitude revealed a main effect of Category type ($F(1, 31) = 6.441$, $p = .016$), with significant greater sMMN responses for the thumb than the fifth digit stimulation. In addition, there was a significant main effect of Hemisphere (F(1,

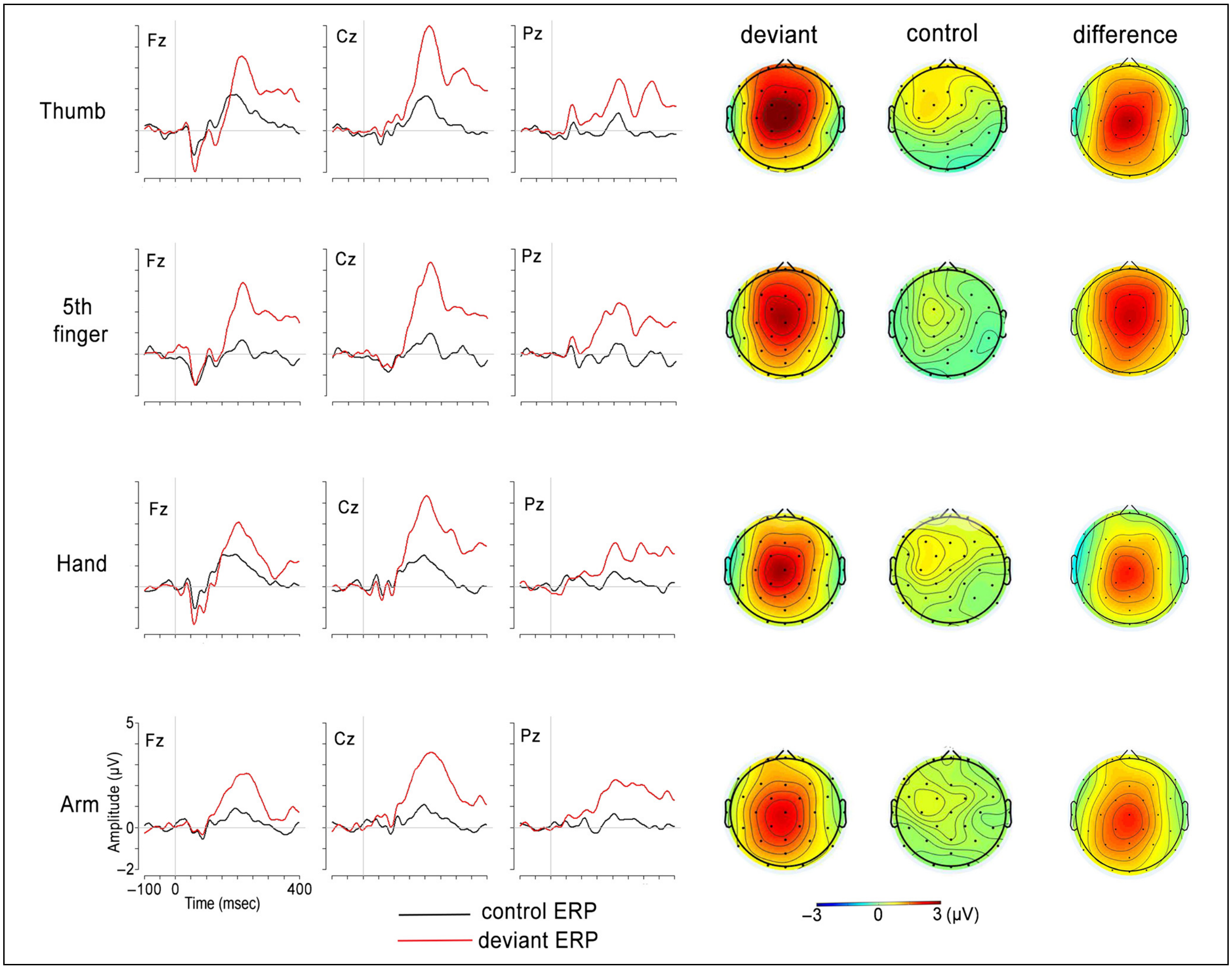

Figure 4. Grand-averaged waveforms showing the P300 component at Fz, Cz, and Pz (left) and topographic plots of mean P300 amplitude (200–300 msec; right).

31) = 12.153, p = .001, left > right hemisphere). There were no significant main effect of Region and no significant interactions between factors.

P300

The P300 waveforms at Fz, Cz, and Pz, along with the topographic maps for each deviant and control stimuli, are shown in Figure 4. The ANOVA on P300 amplitudes elicited by digit stimulation showed a significant main effect of Electrode ($F(2, 62) = 11.182$, $p < .001$). A post hoc t test with FDR correction showed that the P300 response was strongest at Cz (Cz > Pz, Cz > Fz, $p < .001$). There was no significant main effect of Category type ($F(1, 31) = 0.068$, $p = .796$).

Similar results were found for P300 elicited by hand/arm stimuli. There was a significant main effect of Electrode ($F(2, 62) = 11.48$, $p < .001$). Post hoc pairwise t test with FDR correction showed that P300 amplitude was significantly greater at Cz than at Fz ($p < .001$) and Pz ($p < .001$). There was no significant main effect of Category type ($F(1, 31) = 0.399$, $p = .532$; Figure 5).

DISCUSSION

The current results provide novel electrophysiological evidence of categorical discrimination in the tactile modality, in line with findings in the domain of speech perception (e.g., Xi et al., 2010; Minagawa-Kawai, Mori, & Sato, 2005). In our first protocol, the category boundary that was examined was the wrist joint, which separates the hand from the forearm. The contrast involving stimulation across the hand–forearm boundary elicited a significantly larger sMMN response than the contrast involving stimulation within the forearm. Because the physical distance for the two contrasts was equal within each participant and the effect of other differences (e.g., in receptor density) within each tactile contrast was controlled

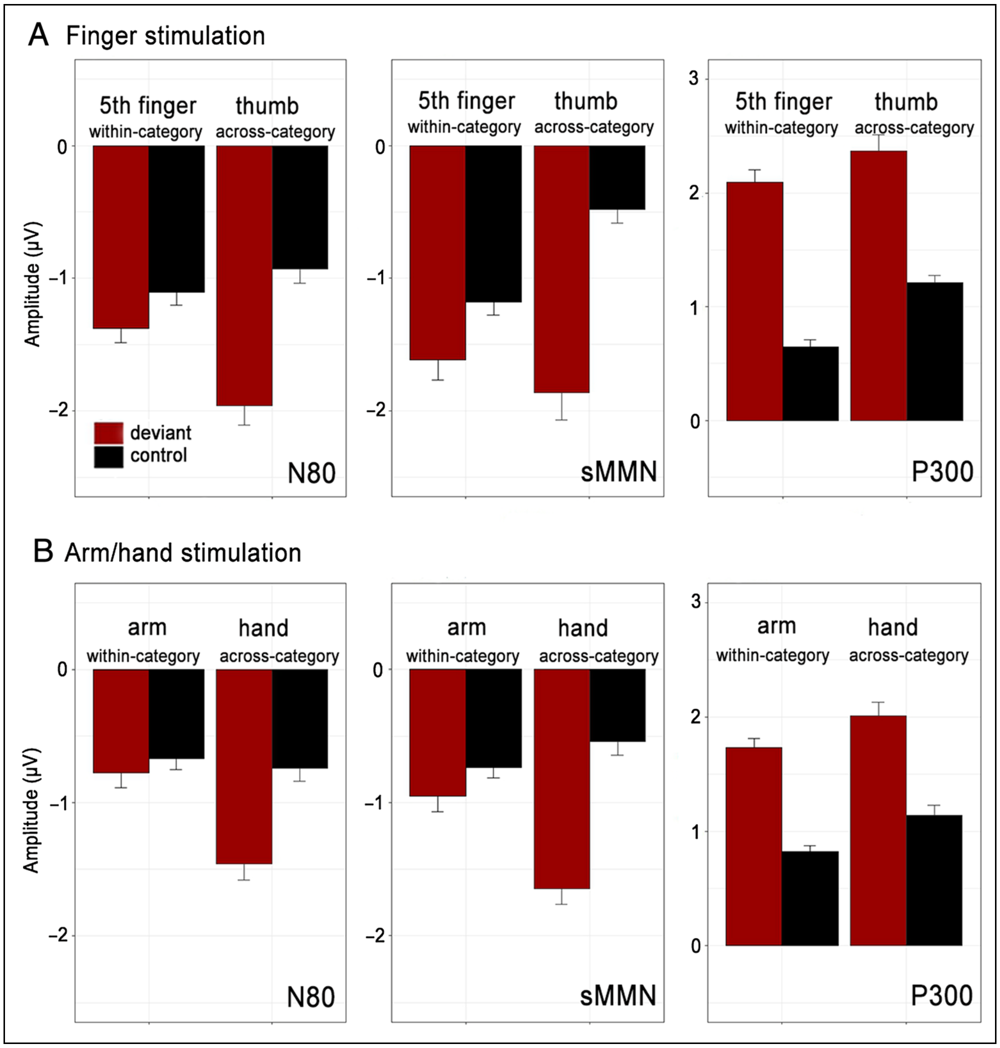

Figure 5. Mean amplitude of N80, sMMN, and P300 by stimulus type (deviant: red; control: black) and category type (within-category: right; across-category: left) for finger stimulation (A) and arm/hand stimulation (B). Error bars represent standard error. The mean amplitude of N80 and sMMN were calculated by averaging across four left frontocentral electrodes (F3, F7, FC1, FC5) where N80 and sMMN responses were greatest. The amplitudes of P300 were averaged across Fz, Cz, and Pz.

by comparing deviant and control ERP evoked by the same tactile stimuli, the findings provide neurophysiological support for categorical segmentation of body parts at early stages of tactile processing.

The current findings are consistent with behavioral studies reporting that pairs of tactile stimuli presented across the wrist boundary were perceived as further apart than stimuli with the same physical distance but presented within the forearm or the hand (Knight et al., 2014, 2017; de Vignemont et al., 2009). The current results add support from electrophysiological recordings for an enhanced discrimination for across-category contrasts compared with within-category contrasts in the tactile domain.

The second protocol addressed a possible experience-related boundary effect arising from the functional categorization of different digits. By contrasting two pairs of digits (third digit vs. thumb, and third vs. fifth digits), this protocol leveraged the functional distinctions between the thumb and the other digits in terms of their involvement in common motor acts (e.g., grasping and picking up objects). Results showed that the sMMN amplitude elicited by the oddball contrast of the third digit and the thumb was significantly larger than for the contrast of the third and fifth digits. This novel finding suggests the possibility that long-term sensorimotor experience can modify tactile perceptual space by enhancing tactile distinctions between body parts that have different functional roles and/or reducing sensitivity to tactile contrasts within a functional category.

One possibility for further investigation is to examine the neuroplasticity of the functional boundary effects in two ways. First, it would be interesting to study special populations such as professional musicians (particularly pianists and violinists) in whom the functional role of each individual finger may be more distinct than in non-musicians. Second, one could take a developmental perspective and study young infants with and without the relevant functional experience. In human infancy, there are large individual differences in the age at which infants acquire fine motor skills and an orderly developmental progression from the exclusive reliance on a "power grip" to a more dexterous "precision grip," which uses the opposable thumb in a new way (e.g., Butterworth et al., 1997; Newell et al., 1989). If functional experience plays a significant role, then individual infants differing in their fine motor skills (and matched in age) will demonstrate significantly different MMN responses in a thumb versus third versus fifth digit protocol, and similarly, longitudinal studies of the same infant over time would be expected to show the neural responses after he or she has acquired functional experience with the precision grip.

The N80—which occurs before the MMN and is generated in primary somatosensory cortex contralateral to the tactile stimulation (Sambo et al., 2012; Schubert et al., 2008)—also appears to show categorical effects. The current results show that across-boundary deviant stimuli evoked significantly larger N80 amplitudes than the corresponding control stimuli, whereas a difference in N80 amplitude between within-category deviants and controls was less apparent. The enhancement of the N80 by deviant tactile stimuli in an oddball paradigm has been observed in other sMMN studies (Strömmer, Tarkka, & Astikainen, 2014; Hötting & Röder, 2009; Akatsuka et al., 2007), although the meaning of this enhancement has not been thoroughly explored. The suggestion in these prior studies was that this early SEP effect reflects obligatory sensory processing that precedes higher-order cognitive processing (Strömmer et al., 2014) and that the N80 enhancement may be due to physical differences in the tactile stimuli between deviant and standard stimuli (Hötting & Röder, 2009). Crucially, the current study employed the identity MMN paradigm that involves comparing the SEP elicited by the same tactile stimuli presented as deviants and as controls (Möttönen, Dutton, & Watkins, 2013), and thus, the N80 enhancement in the current study cannot be explained purely by bottom–up, featural differences in the tactile stimuli.

One potential explanation for the differences in N80 enhancement for across- versus within-boundary contrasts may be that categorical effects on sensory processing start before the higher-order processing that occurs around 100–200 msec poststimulus onset and is typically indexed by MMN responses (e.g., Bidelman et al., 2013; Zheng et al., 2012; Mo et al., 2011; Xi et al., 2010). Recent studies of somatosensory processing have revealed that early processing in primary somatosensory cortex is not only influenced by bottom–up featural variation in sensory stimuli but is also modulated by cognitive factors such as sustained attention (Eimer & Forster, 2003), spatial attention (Schubert et al., 2008), and multisensory congruency (Cardini & Longo, 2016). Consistent with these views, the findings of the current study may indicate that initial stages of somatosensory processing in primary somatosensory cortex, indexed by N80, is already reflective of categorical representations of body parts and sensorimotor functions, echoing recent findings in the auditory domain that emphasize a role of primary sensory cortex in early processing of language-related stimuli (Papanicolaou, Kilintari, Rezaie, Narayana, & Babajani-Feremi, 2017).

In addition to the early N80 and MMN responses, we also observed an enhanced positive component at 200–350 msec elicited by deviant stimuli compared with control stimuli. This component is known as the P300 or P3a and reflects an orienting response to the violation of expected patterns of sensory stimulation (Light, Swerdlow, & Braff, 2007; Polich, 2007). The P300 is commonly elicited in oddball paradigms and often follows the MMN response in the form of an "MMN/P3a complex" (Hermens et al., 2010). In the current study, we found that P300 amplitude was enhanced by all deviants compared with their corresponding control stimuli, but in contrast to the pattern of sMMN responses, the degree of increase in P300 amplitude was similar for cross- and within-boundary deviants. This is in line with other recent studies reporting that changes in MMN amplitude are often dissociated from changes in P300 amplitude in both the auditory (Horváth, Winkler, & Bendixen, 2008) and somatosensory domains (Shen et al., 2017). The current finding may lend support to previous work on somatosensory deviance detection, which suggested that sMMN amplitude is modulated by somatotopic cortical representations of body parts, whereas the P300 response may be more related to tactile processing referenced to the actual 3-D human body in space (Shen et al., 2017). Because P300 responses can be enhanced by attentional deployment and behavioral tasks involving novelty detection (Polich, 2007), future studies could shed light on the differences between the sMMN and P300 by asking participants to attend to the tactile stimuli and to respond to deviant stimuli.

Parallel to perceptual categorization of speech in the auditory modality (e.g., Shen & Froud, 2018; Dehaene-Lambertz, 1997) and color perception in the visual domain (e.g., Mo et al., 2011), our findings suggest that body part categorization can modulate early stages of somatosensory processing, without overt attentional deployment. Further questions for investigation can further address the neural mechanisms of body categorization. For instance, are receptive fields in the primary somatosensory cortex reflective of the cognitive categorization of body perception and related functional segmentations? Or, is this knowledge stored in areas associated with further processing, such as secondary somatosensory cortex. Future studies using high-resolution neuroimaging could shed light on the neural mechanisms of categorical perception in the tactile domain by examining differential activations to across- and within-category deviance in cortical areas that contribute to the sMMN response, specifically SI and SII (Akatsuka et al., 2007), as well as frontal cortex (Garrido et al., 2009).

In conclusion, these novel findings provide evidence that relatively early stages of neural processing of tactile stimulation are influenced by the categorical segmentation of the body into discrete body parts. Perceptual effects related to categorization are apparently ubiquitous in human cognition and have been observed in a number of sensory modalities. Future research on the relations between body part categorization and sensorimotor experience in adults as well as developmental studies examining changes in tactile perception as a function of specific motor experiences (e.g., with grasping and picking up objects) will further illuminate this phenomenon.

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