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Body representations as indexed by oscillatory EEG activities in the context of tactile novelty processing

Guannan Shen[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, USA

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ABSTRACT

Neural oscillatory activities in different frequency bands are known to reflect different cognitive functions. The current study investigates neural oscillations involved in tactile novelty processing, in particular how physically different digits of the hand may be categorized as being more or less similar to one another. Time-frequency analyses were conducted on EEG responses recorded from a somatosensory mismatch protocol involving stimulation of the 1st, 3rd, and 5th digits. The pattern of tactile stimulation leveraged a functional category boundary between the 1st digit (thumb) and the other fingers. This functional category has been hypothesized to derive, in part, from the way that the hand is used to grasp and haptically explore objects. EEG responses to standard stimuli (the 3rd digit, probability of 80%) and two deviant stimuli (1st digit as across-boundary deviant and 5th digit as within-boundary deviant, probability of 10% each) were examined. Analyses of EEG responses examined changes in power as well as phase information. Deviant tactile stimuli evoked significantly greater theta event-related synchronization and greater phase-locking values compared to the corresponding control stimuli. The increase in theta power evoked by the contrast of the 3rd digit and the 1st digit was significantly larger than for the contrast between the 3rd and 5th digits. Desynchronization in the alpha and beta bands was greater for deviant than control stimuli, which may reflect increased local cortical excitation to novel stimuli, modulated by top-down feedback processes as part of a hierarchical novelty detection mechanism. The results are discussed in the context of the growing literature on neural processes involved in the generation and maintenance of body representations.

1. Introduction

The efficient detection of changes in the environment is a basic perceptual ability that has been proposed to stem from hierarchical networks involving feedback from predictions of inputs and feedforward signaling of prediction errors (Friston and Kiebel, 2009; Phillips et al., 2016). Electrophysiological studies using the mismatch negativity (MMN) response, an event-related potential (ERP) elicited using oddball paradigms that employ unexpected auditory deviants embedded in repetitive frequent stimuli, have been particularly useful for understanding novelty detection mechanisms (Garrido et al., 2009; Näätänen, 2000). Studies of the MMN have revealed that perceptual deviance is registered in the ERP signal in a relatively early time window (~150 ms) without requiring participants to actively attend to the deviant stimuli (Näätänen et al., 2005). Auditory MMN studies using source localization techniques and Granger causality models have identified generators of mismatch responses in primary auditory cortex and frontal cortex (Choi et al., 2013; Garrido et al., 2009). Related studies of EEG and MEG responses to stimulus deviance have also examined frontotemporal connectivity (Phillips et al., 2016) and cross-region phase synchronization (MacLean and Ward, 2014; Hsiao et al., 2010). Taken together, these studies have suggested interconnected roles for frontal cortex and local sensory cortex in novelty detection processes.

Recent work has extended the use of the MMN to novelty detection in the tactile modality, and has established that tactile oddball paradigms can reliably elicit somatosensory MMN (sMMN) and novelty-related P3 responses (e.g. Shen et al., 2018a; Butler et al., 2011). Mismatch responses in the somatosensory modality can be elicited by deviance in various stimulus properties, such as duration (Butler et al., 2011), vibrotactile frequency (Spackman et al., 2007), intensity (Zhang et al., 2019), and spatial location (Shen et al., 2018a; Naeije et al., 2016; Restuccia et al., 2009). A recent study reported that the sMMN elicited by spatial tactile deviance is modulated by part-based body

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

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perception and function-based categorical perception (Shen et al., 2018a). This relates to a key finding on the auditory mismatch response to speech stimuli, which is that MMN amplitude is sensitive to categorical boundaries. Previous studies have consistently reported that across-category contrasts elicit greater MMN than within-category phonetic contrasts with a similar degree of physical deviance (e.g., Shen & Froud, 2019; Kasai et al., 2001; Dehaene-Lambertz, 1997).

Converging evidence from recent MMN studies in the auditory modality has suggested that theta oscillations (4–8 Hz) may play a particularly prominent role in the frontotemporal change detection network (Choi et al., 2013; Garrido et al., 2009; Phillips et al., 2016; MacLean and Ward, 2014; Hsiao et al., 2010). Frontal theta oscillations have also been associated with various high-level cognitive processes such as memory encoding and retrieval (Jacobs et al., 2006; Rutishauser et al., 2010), working memory (Raghavachari et al., 2006), and cognitive control (Cavanagh and Frank, 2014; Phillips et al., 2016). The focus of the current study is on the role of theta band oscillations in lower-level novelty and change detection processes (Phillips et al., 2016; Garrido et al., 2015; Zhang et al., 2019). In auditory oddball paradigms, both frontal theta power and theta phase locking values (PLV) across trials within the time window of the MMN response are greater for an unexpected mismatch condition than for a predictable standard condition, during both attentive change detection and passive listening tasks (Fuentemilla et al., 2008; Hsiao et al., 2009; Isler et al., 2012; Ko et al., 2012; Choi et al., 2013; MacLean et al., 2015). In addition, across-region phase coherence in the theta band between temporal and frontal regions is larger following deviant stimuli compared with standard stimuli (Hsiao et al., 2010; Phillips et al., 2016). Recent evidence also suggests an important role for theta oscillations arising from fronto-hippocampal networks in novelty detection (Garrido et al., 2015; Chen et al., 2013; Brockmann et al., 2011).

Most existing studies on theta oscillations in the context of sensory novelty detection have employed auditory or visual mismatch protocols, yet the connections between EEG oscillations and tactile change detection processes are not well understood. A recent study found that the sMMN can be elicited by tactile stimulation to different fingers, and the sMMN amplitude was sensitive to functional boundaries between body parts (Shen et al., 2018a). This study focused on the salient functional distinction between the first digit (the thumb) and the second through fifth digits, which arises from the fact that the thumb and the rest of the fingers are employed differently during grasping and picking up objects. The thumb is positioned on one side of the object and the fingers positioned on the other side (Wing and Fraser, 1983). The amplitude of the sMMN elicited by a contrast of the third digit and the first digit was significantly larger than a contrast between the third and fifth digits, suggesting a functional boundary effect that may derive from the way objects are typically grasped. These findings provide neurophysiological support for function-related categorical segmentation of body parts at early stages of tactile processing. The current study extends this finding by conducting time-frequency analyses on the raw dataset from Shen et al. (2018a), in order to investigate the oscillatory activities associated with tactile novelty detection, with a focus on the relation between theta oscillations and sMMN responses. We are also interested in how electrophysiological investigations of novelty processing in the tactile modality can inform the study of how body representations are generated and maintained. For instance, given the hypothesized role of theta oscillations arising from frontal-hippocampal networks in tactile novelty detection, it is notable that certain tactile responses related to body representation have been found to arise from the parahippocampal gyrus (Bernasconi et al., 2018).

In addition to theta band activity, alpha (8–14 Hz) and beta (15–25 Hz) oscillations may also be involved in tactile novelty processing. Changes in the alpha rhythm are theorized to reflect alterations in cortical inhibition (Jensen and Mazaheri, 2010; Foxe and Snyder, 2011). Alpha is most prominent over visual cortex (Ergenoglu et al., 2004) and sensorimotor areas (in the form of the mu rhythm; Jones et al., 2010; Anderson and Ding, 2011). An increase in alpha amplitude (i.e., an event-related synchronization, ERS) is related to task-related inhibitory activities (e.g., Jensen et al., 2014), while an attenuation of alpha power (event-related desynchronization, ERD) indicates sensorimotor activation and excitation (Della Penna et al., 2004; Anderson and Ding, 2011). Since it reflects local cortical sensory inhibition/excitation, alpha amplitude may be sensitive to the processing of unexpected novel (mismatch) stimuli in relation to expected standard stimuli. Indeed, a recent study on the visual MMN found that alpha ERD was significantly larger for deviant stimuli than for standards (Tugin et al., 2016), suggesting that local sensory excitation indexed by the alpha rhythm is modulated by sensory processing of novel or deviant stimuli. Additionally, although beta rhythm responses have been less studied, beta ERD is often associated with tactile stimulus processing and related modulations of attention (van Ede et al., 2014; Sherman et al., 2016). Given this background, we also therefore evaluated whether beta activity was involved in tactile novelty detection.

Conventionally, somatosensory mismatch responses have been examined by averaging ERP responses across trials, with the resultant sMMN preserving only some of the brain signals that are phase-locked and time-locked to the onset of the stimulus (Makeig et al., 2004). Modulations of oscillatory amplitude and phase consistency across trials can provide further insights, and may serve as complementary measures of brain dynamics and underlying cognitive processes involved in change detection. Phase locking values, ranging from 0 (random phase relations across trials) to 1 (perfect phase locking), are a measure of across-trial phase coherence that describe the extent to which signals exhibit a relatively consistent phase difference at a given time-frequency point. Analysis of phase-locking can estimate alignment and resetting of event-related oscillations across trials – processes that are involved in the generation of different ERP components (Hertrich et al., 2004; Fell et al., 2004; Mazaheri and Picton, 2005; Makeig et al., 2002).

The aim of the current analyses is to examine oscillatory responses in the theta, alpha, and beta bands in the context of tactile novelty detection. Given that theta rhythm activity may reflect memory formation (Jacobs et al., 2006; Rutishauser et al., 2010), and that frontal theta band power and phase coherence have consistently been associated with auditory change detection (Hsiao et al., 2009; Ko et al., 2012; Garrido et al., 2015), we hypothesized that changes in the frontal theta rhythm would be observed during tactile novelty detection tasks. We also expected that the pattern of effects may reflect the functional category boundary between the thumb and the fingers that has been suggested by prior work on the sMMN. Although our focus was on the theta band, we also expected alpha and beta rhythms to be sensitive to the differential processing of unexpected novel stimuli relative to frequent control stimuli. Finally, we also examined the relation of the oscillatory changes to the amplitude of the sMMN and of the P3 component of the ERP response to the standard and deviant stimuli.

2. Method

2.1. Participants

Undergraduate students received course credit in return for participation. Based on previous studies (Shen et al., 2018a, b), a power analysis with a target power of 0.80 and a Type 1 error rate of 0.05 suggested that a sample size of 31 would be adequate to detect the hypothesized effects. 35 participants were recruited for the study. Data from three participants were excluded from analyses due to participant fatigue ($n = 2$) or insufficient numbers of artifact-free trials (less than 50 trials per condition; $n = 1$). Final analyses utilized data from 32 participants (10 males; 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. The study was carried out with approval from the Institutional Review Board at Temple University, with informed consent being obtained from each participant prior to participation.

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), which resulted in a punctate ‘tap’ to the body part being stimulated. 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 avoid auditory correlates of the tactile stimulation. 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. For the purposes of statistical analyses, 0 ms indicated the onset of tactile stimulation. This tactile stimulation method has been successfully used in a number of previous EEG and MEG studies (Shen et al., 2017, 2018b; Meltzoff et al., 2018).

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.

2.3. Procedure

The first block of the protocol consisted of 1000 trials, during which stimulation was delivered every 600 ms to either the 1st digit (thumb), the 3rd digit (middle finger), or the 5th digit (little finger) of the right hand (Fig. 1B). The inflatable membranes used to deliver tactile stimulation were attached to each of these digits via plastic clips. The 3rd digit was designated as the standard, with 80% of the tactile stimuli (800 trials) being delivered to this digit. The 1st digit and 5th digit were designated as deviants, with 10% of the tactile stimuli (100 trials) being delivered to each. The second and third block consisted of 1 min of stimulation to only the 1st and the 5th digit respectively, in order to establish a control waveform for these digits. The second and third blocks had 100 total trials each with an interstimulus interval of 600 ms.

Identity MMN. We employed a particular method – the identity MMN – in order to account for differences between the frequent standard and infrequent deviant stimuli in their physical properties. The identity MMN method involves subtracting the ERP elicited to one stimulus when presented as the control from the ERP elicited with the same stimulus when presented as the deviant (Möttönen et al., 2013; Pulvermüller et al., 2006). The use of the identity MMN has been shown to be an effective control for intrinsic differences in deviant and standard stimuli (Chandrasekaran et al., 2007; Pulvermüller et al., 2006). This method is also particularly useful in the context of the stimulation of different body locations that may differ in tactile sensitivity (Shen et al., 2018a).

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. 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 (± 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 for the EEG channels and 1000 for the EOG channels.

2.5. Data analysis

2.5.1. Pre-processing

Processing and initial analysis of the EEG signals were performed using the EEGLAB 13.5.4 b 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 stimulus onset. Independent component analysis (ICA) was used 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 per body part location or digit was 85 ($SD = 8$, 1st digit: deviant = 85, standard = 86; 5th digit: deviant = 88, standard = 86). A one-way ANOVA showed that there was no significant difference between locations in the number of useable trials across all standard and deviant conditions ($p = 0.572$).

2.5.2. Time-frequency analysis

Time-frequency decompositions of single trial data were conducted using event-related spectral perturbation (ERSP) analysis (Makeig, 1993). ERSP was computed using a Morlet wavelet decomposition over a frequency range of 5–30 Hz, with 100 over-lapping windows starting with a 0.8-cycle wavelet at the lowest frequency. The baseline was defined as the 100 ms pre-stimulus window. Significant ERSP differences between each deviant and its corresponding control were computed by permutation analysis with 2000 randomizations ($p < 0.005$) (Figs. 1 and 2).

Based on previous studies on modulation of oscillations involved in novelty processing (e.g., Hsiao et al., 2009; MacLean & Ward, 2016; Tugin et al., 2016), the regions of interest for analysis were the midline frontal site (Fz) and central electrodes overlying somatosensory areas (C3, C4). In line with this previous literature, the time-frequency plots and topographic maps (Figs. 1 and 2) indicate that theta power differences between deviants and controls were primarily present around Fz, while alpha and beta band modulations were most robust around C3 and C4. The statistical analyses for theta, alpha and beta activity focused on these recording sites.

For theta band (4–8 Hz) analysis, the trial-by-trial ERSP values at electrode Fz across a window of 150–250 ms were averaged for each participant. Phase-locking values (PLV; range from 0 to 1) corresponding to the degree of phase coherence across trials were averaged across the same window (150–250 ms) at electrode Fz. Both ERSP and PLV were then subjected to repeated measures ANOVA with factors Stimulus Type (deviant; control) and Category Type (across-category deviant, 1st digit; within-category deviant, 5th digit). The results presented below employ the Greenhouse-Geisser correction as appropriate.

For alpha (8–14 Hz) and beta (15–30 Hz) band analysis, ERSP values at electrodes C3 and C4 were averaged across the window of 100–400 ms, and were then subjected to ANVOAs with factors Stimulus Type (deviant; control) and Category Type (across category deviant, 1st digit; within-category deviant, 5th finger), Hemisphere (left, right).

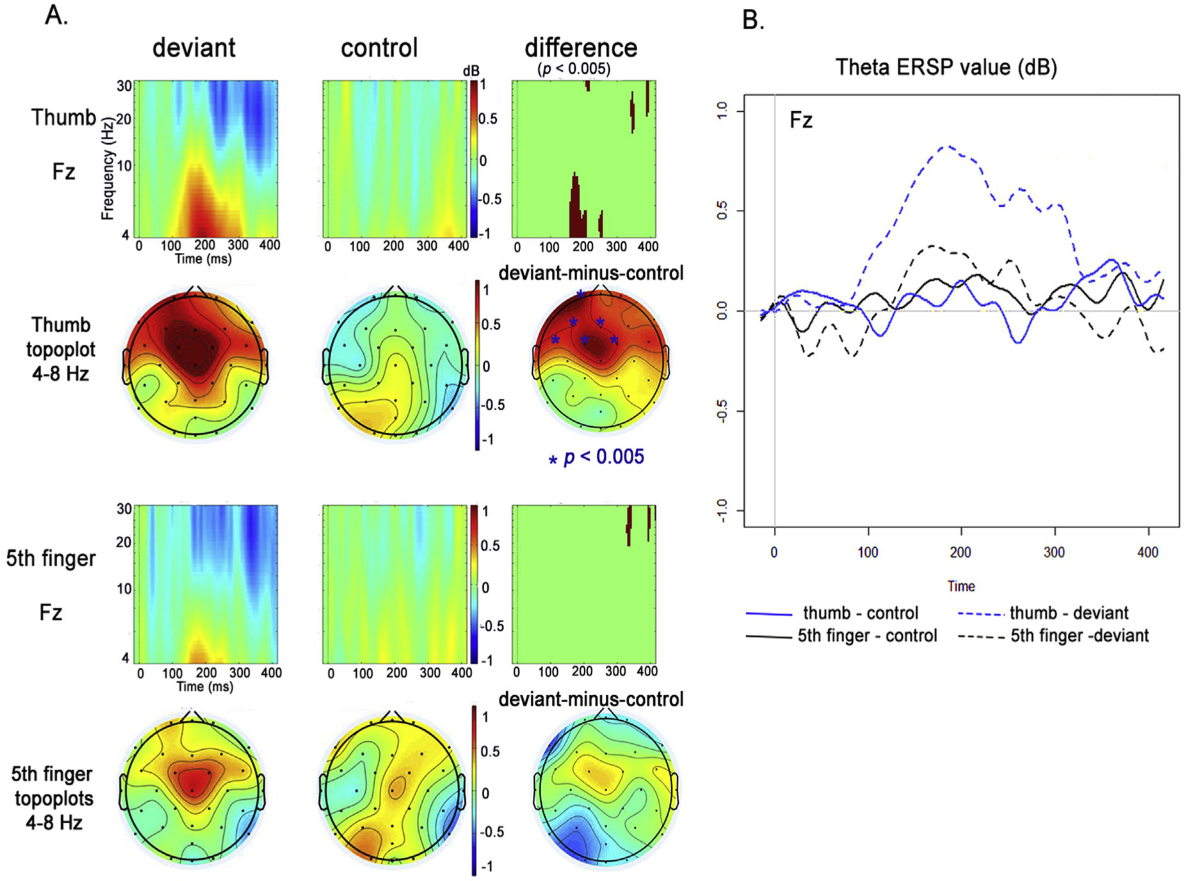

Fig. 1. (A) Time-frequency plots at Fz and topographic plots for theta oscillations (4–8 Hz) averaged across a window of 150–250 ms. Asterisks indicate electrodes at which the deviant and control responses were significantly different from each other. Statistical comparisons between deviant and control employed permutation tests with 2000 randomizations. (B) Theta ERSP waveform at electrode Fz.

2.5.3. *Correlational analyses*

To investigate the relation between novelty-related ERPs and theta oscillations, Pearson correlations between sMMN and P3 amplitude (reported in Shen et al., 2018a) and theta ERSP and PLV were computed. Amplitude of the sMMN was computed by averaging across a 20 ms time window around the most negative peak in the ERP waveform between 100 ms and 200 ms at six left fronto-central electrodes (F7, F3, FC5, FC1, T7, C3). P3 amplitude was calculated by averaging the amplitude in a 100 ms window surrounding the most positive value between 180 and 400 ms at Cz (see Shen et al., 2018b).

3. Results

3.1. *Theta power and phase-locking values*

Fig. 1 shows time-frequency and topographic plots for theta, alpha and beta band activity. Fig. 2 shows the theta phase-locking values for each deviant and control comparison. Visual inspection suggested that deviant stimuli evoked stronger theta synchronization (ERS) and PLV than control stimuli at around 150–250 ms, over frontal and central sites.

The ANOVAs for mean theta ERSP (4–8 Hz) in the time window of 150–250 ms revealed a significant main effect of Stimulus Type (F (1, 27) = 5.104, p = 0.032), with greater theta ERSP for the deviant stimulus than the control stimulus. There was also a significant interaction between Stimulus Type and Category Type (F (2, 27) = 5.082, p = 0.032). For post-hoc analysis, pairwise t-tests were conducted separately for deviants and controls. Stimulation of the 1st digit (thumb) as the deviant stimulus elicited significantly stronger theta synchronization than 5th digit stimulation as the deviant stimulus (p = 0.031), while theta ERS elicited by the two control stimuli were not significantly different (p = 0.621). Additional post-hoc analysis was conducted separately for each category type. For the 1st digit (thumb), the deviant stimulus elicited significantly stronger theta ERS than control stimulus (p = 0.004), whereas the difference between deviant and control was not significant for the 5th digit (p = 0.593).

The analysis on theta PLV focused on the same time window of 150–250 ms. There was a main effect of Stimulus Type (F (1, 31) = 35.029, $p < 0.001$), with significantly greater theta PLV for deviant stimuli than control stimuli. There was no main effect of Category Type or interactions between factors.

3.2. *Alpha and beta event-related desynchronization*

Fig. 3 shows time-frequency plots and topographic plots for alpha and beta band activity. Visual inspection suggests that post-stimulus alpha and beta desynchronization occurred around 150 ms post stimulus onset, and that the extent of alpha and beta ERD was greater for deviants than controls.

The ANOVA on mean alpha ERSP revealed a significant main effect of Stimulus Type (F (1, 31) = 14.639, $p < 0.001$), with significantly greater alpha desynchronization for deviants than controls. There was also a significant main effect of Hemisphere (F (1, 31) = 5.969, p = 0.02), with stronger alpha ERD in the left hemisphere, contralateral to the site of tactile stimulation.

Similarly, the analysis of beta ERSP showed significant main effects of Stimulus Type (F (1, 31) = 21.995, $p < 0.001$; deviant > control), and Hemisphere (F (1, 31) = 11.695, p = 0.002; left > right). There

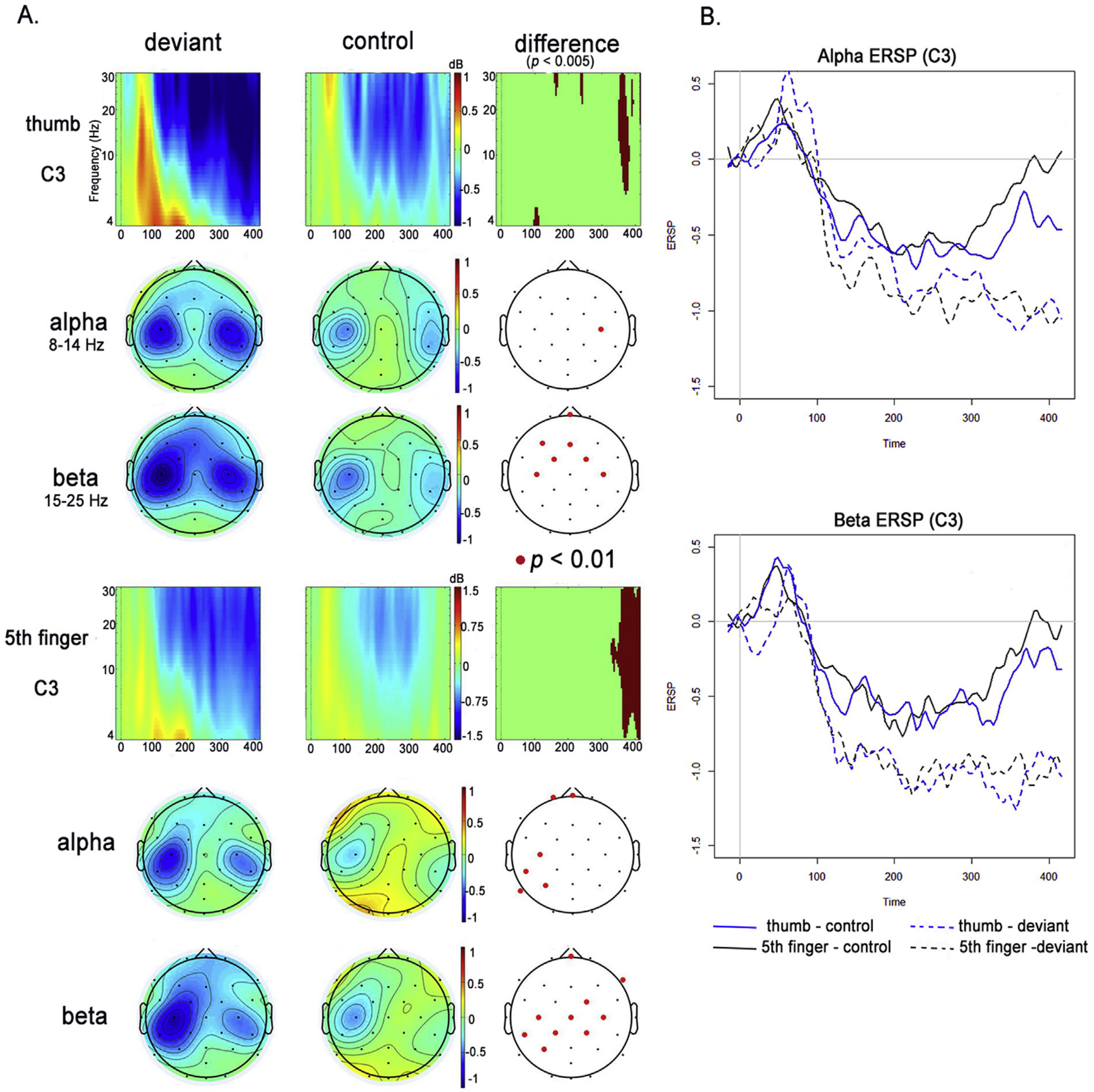

Fig. 2. Alpha (8–14 Hz) and beta (15–25 Hz) ERSP patterns. (A) Time-frequency plots for thumb and 5th finger stimuli at C3, and topographic plots for alpha and beta ERSP averaged across the window of 150–400 ms. Red dots indicate electrodes at which deviant and control responses were significantly different from each other. (B) Alpha (top) and beta (bottom) ERSP waveforms at C3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

were no significant main effects or interactions involving Category Type.

3.3. Correlations between ERPs and theta band modulations

To explore the connection between novelty-related ERPs and theta band activities, four sets of Pearson correlations were computed between ERP amplitude (sMMN and P3) and theta band ERSP and PLV elicited by deviants (Fig. 4). A strong positive correlation was found between P3 amplitude and theta band PLV ($r = 0.78$, $p < 0.001$). P3 amplitude was also significantly correlated with theta band ERSP ($r = 0.59$, $p < 0.001$). For the MMN responses (Fig. 5), the correlations between MMN amplitude with theta band ERS and PLV were both significant ($r = 0.538$, and $r = 0.407$, $p < 0.001$).

4. Discussion

The current study examined EEG oscillatory responses to infrequent (deviant) tactile stimuli to the 1st (thumb) or 5th digit (little finger) in relation to frequent (standard) tactile stimulation of the 3rd digit (middle finger). The focus of the analyses was on oscillations in the theta band, which have been suggested to play an important role in novelty detection and processing in the auditory and visual modalities, as indexed by MMN responses (Chen et al., 2013; Phillips et al., 2016; Hsiao et al., 2009; MacLean and Ward, 2014; Bishop et al., 2010; Tugin et al., 2016). The current study provides novel evidence of specific changes in power and phase alignment of the theta rhythm over frontal areas in the context of tactile deviance detection and novelty processing. Consistent with previous studies of auditory deviance detection, theta power and phase coherence were significantly greater for tactile deviant stimuli than for control stimuli. The convergence of findings

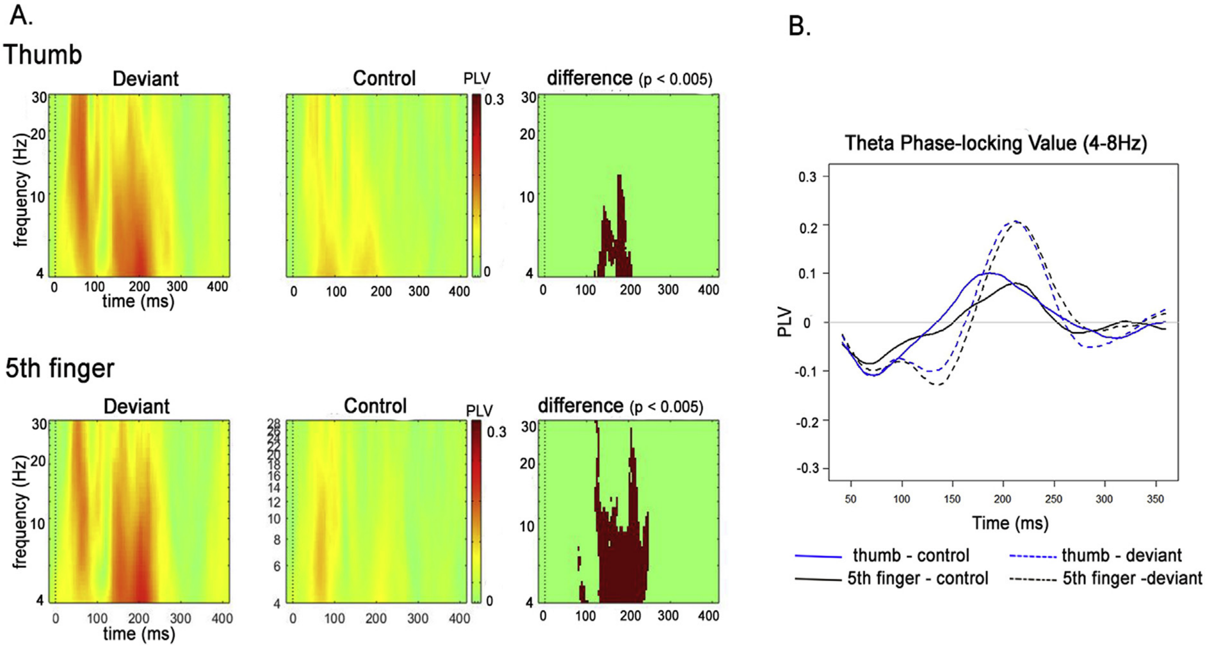

Fig. 3. Theta phase-locking values for thumb and 5th finger stimuli at electrode Fz.

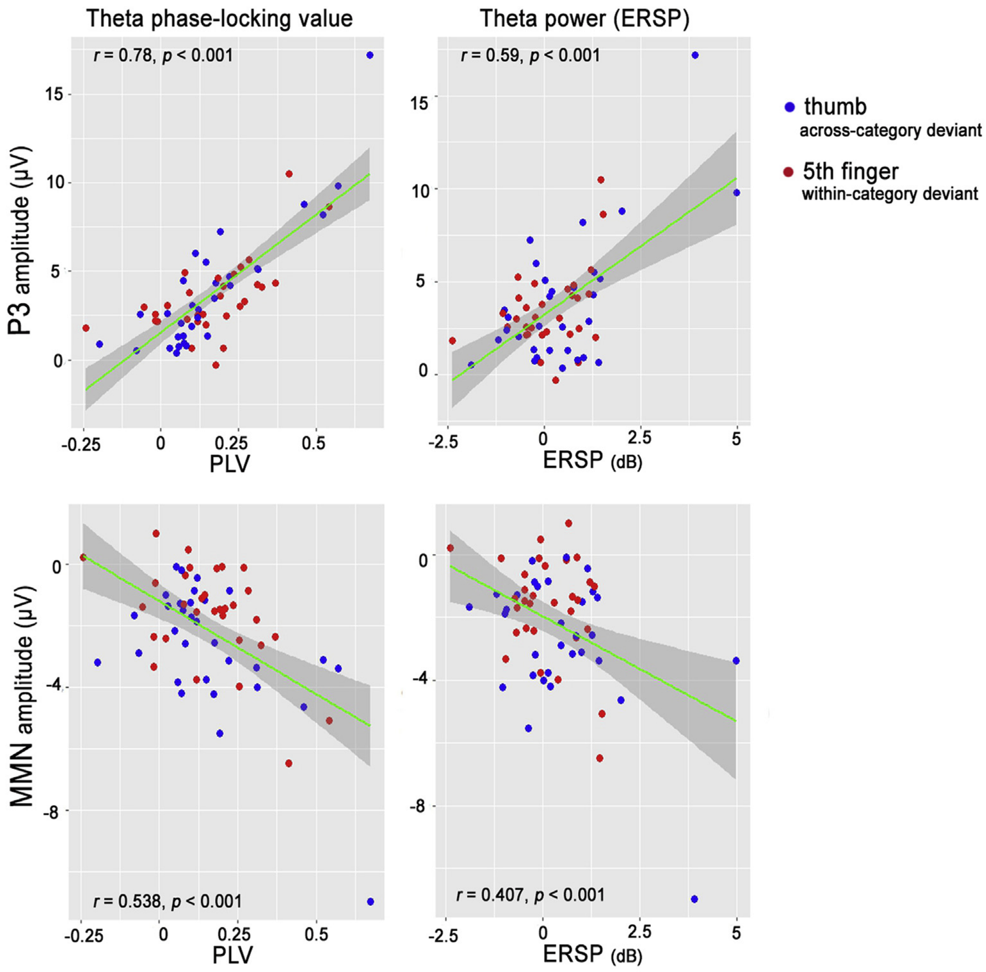

Fig. 4. Correlations between P3 and sMMN amplitudes and theta ERSP/PLV.

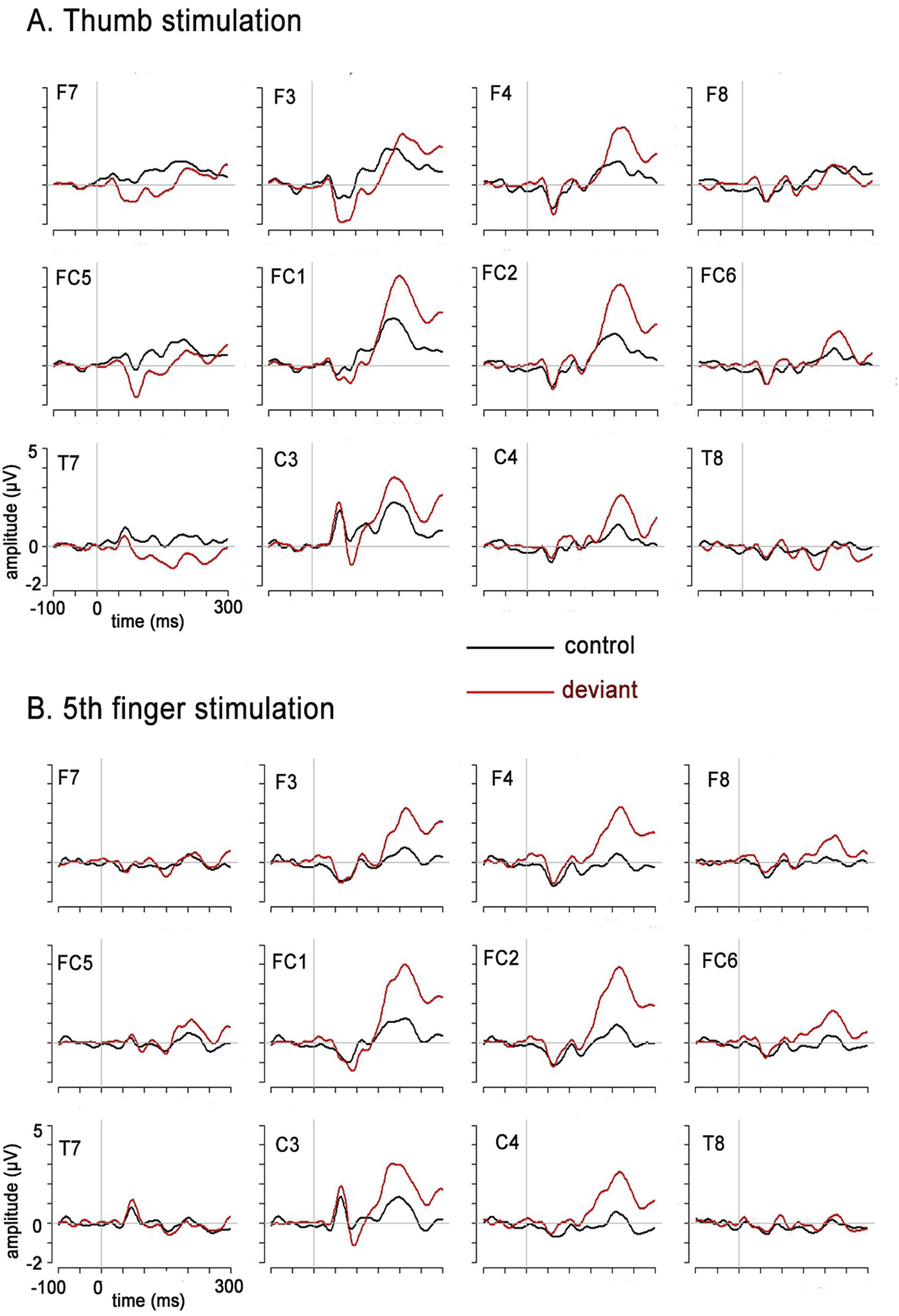

Fig. 5. sMMN waveforms elicited by thumb stimulation (A) and 5th finger stimulation (B) (adapted from Shen et al., 2018a).

across studies of auditory and tactile deviance suggests a potentially important role for theta band activity in novelty detection within different modalities of stimulation.

The theta activity around 200 ms post-stimulus onset may reflect change detection processes in the somatosensory modality, with enhanced phase synchronization and an increase in power following the presentation of deviant stimuli. A role for frontal theta oscillations in sensory novelty detection may be related to the involvement of theta in memory processing. Recent studies using MEG (Garrido et al., 2015) and intracranial EEG recordings (Chen et al., 2013) found that hippocampal theta power was enhanced for a mismatch condition, as compared to predictable control conditions. This suggests that frontal-hippocampal communication in the theta band, which is typically associated with memory formation and error detection (Hyman et al., 2011; Lisman and Grace, 2005), may play a role in pre-attentive sensory change detection. In the context of the current study, this suggestion relates to a potential role for the hippocampal area in bodily self-consciousness and self-location (Guterstam et al., 2015) as well as in multisensory processes related to peripersonal space (Bernasconi et al., 2018). It is possible that the frontal theta oscillations during somatosensory novelty detection in the current study may at least partially stem from hippocampal areas involved in the internal representation of the bodily self.

The current study further revealed that changes in the power of theta oscillations are sensitive to a categorical discrimination in the tactile modality. The double oddball paradigm (third digit vs. thumb, and third vs. fifth digit) was designed to compare brain responses to deviance within and across functional boundaries related to common motor acts (e.g., grasping and picking up objects). The results show that theta power elicited by the contrast of the third digit and the thumb was significantly greater than for the contrast of the third and fifth digits. This finding is consistent with changes in sMMN amplitude reported in a previous study (Shen et al., 2018b), and it further suggests that theta responses associated with sensory novelty detection are sensitive to functional categorical boundaries. In this particular case, the category boundary between the thumb and the fingers is thought to arise from the differential involvement of these digits in the way objects are explored and grasped. A distinctive evolutionary feature of the human hand is that we use our opposable thumb versus the rest of the fingers in typical fine motor control, tool use, and other haptic activity. Whether theta activity is also involved in categorical discrimination in other sensory modalities could be addressed in future investigations.

Another finding regarding theta activity in the mismatch conditions is that theta power and phase coherence were significantly correlated with the amplitude of the sMMN and the P3, which suggests that the sMMN and P3 components of the ERP are influenced by changes in phase alignment and power modulation of theta oscillations (Hsiao et al., 2009, 2010; Fuentemilla et al., 2008). In particular, theta phase-locking values at around 200 ms were highly correlated with P3 amplitude. This finding echoes previous studies that supported a close link between theta activity and P3 responses (Harper et al., 2014; Polich, 2007), and is consistent with the hypothesis that the P3 response can be explained by phase resetting of ongoing theta band activities (Fell et al., 2004; Mazaheri and Picton, 2005).

The increased alpha and beta desynchronization to deviant stimuli can be considered in the light of two different hypotheses about the underlying mechanisms of MMN responses. Stimulus-specific adaptation (SSA; Ulanovsky et al., 2003) refers to selective adaptation of sensory neurons and their and reduced responsivity to highly repetitive stimuli, while retaining their responsiveness to deviant features (Musall et al., 2015). This sensory-perceptual phenomenon has been widely observed in different sensory modalities (auditory: Farley et al., 2010; Girrado et al., 2009; visual: Reches et al., 2010; somatosensory: Musall et al., 2015), and in both humans and non-human primates (De Baene and Vogels, 2009; Miller et al., 1993) through the examination of single-cell responses and local field potentials. SSA has been linked to habituation in single-cell recordings (Gutfreund, 2012) and local sensory depression (Musall et al., 2015). The repetition attenuation effect has also been reported during multisensory interaction (Coll et al., 2015; Simon et al., 2017). Similarly, the increased alpha desynchronization found for deviants compared to control stimuli in the current study could be a result of SSA. However, SSA in single-cell recordings was observed relatively rapidly (30–60 ms) following stimulus onset (Musall et al., 2015; Todorovic and de Lange, 2012), while the alpha ERD occurred later (after 100 ms) in the current study. We suspect that the differences in alpha band responses between deviant and control stimuli observed in this study could potentially be related to top-down feedback from frontal cortex that involves predictive coding mechanisms.

The suggestion of frontal influences on mismatch responses is consistent with the proposal that MMN responses are generated via a hierarchical information processing network, such that top-down predictions are compared with bottom-up input, and prediction error is returned when a mismatch occurs (Rao and Ballard, 1999; Garrido et al., 2009a). This predictive coding hypothesis has gained support from hierarchical Bayesian inference models (Bastos et al., 2012; Friston and Kiebel, 2009; Lee and Mumford, 2003), as well as neuroimaging studies that reported fronto-temporal connections during auditory MMN tasks (e.g., Hsiao et al., 2010; Garrido et al., 2015). Under this hierarchical inference framework, it is likely that the different alpha and theta responses to control and deviant stimuli reflect sensory excitation/suppression modulated by top-down feedback information from frontal cortex. This interpretation is consistent with a recent study on oscillatory activities which found that while gamma band responses may signal feedforward processing, the alpha rhythm is likely associated with top-down feedback from higher-order cortical areas (van Kerkoerle et al., 2014). In the context of the current study, it is notable that top-down predictive signals are thought to be essential for maintaining stable body representations and for the experience of body ownership, in part by mediating perception-action linkages and cross-modal perceptual integration (Seth, 2013; Noel et al., 2018). For instance, work on the rubber hand illusion has found that the perception of body ownership is closely linked to Bayesian causal inferences of multisensory interaction (Samad et al., 2015). The findings from the current study suggest that further study of alpha and theta oscillations may be useful for understanding the neurophysiology of top-down prediction in the context of body representations.

In conclusion, the current study provides novel evidence that oscillatory activities in the theta, alpha and beta bands may play a role in tactile deviance detection processes, consistent with previous findings in the auditory and visual modalities. The theta power increase around 200 ms was also sensitive to a functional category boundary (thumb vs. fingers), while theta phase-locking value was highly correlated with P3 amplitude. Future work can expand on these findings to further explore the utility of EEG oscillations in the study of the development of tactile discrimination and in disorders affecting tactile perception and novelty detection.

CRediT authorship contribution statement

Guannan Shen: Conceptualization, Data curation, Formal analysis, Writing - original draft. **Andrew N. Meltzoff:** Writing - review & editing. **Peter J. Marshall:** Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing.

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