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RESEARCH ARTICLE

Exploring developmental changes in infant anticipation and perceptual processing: EEG responses to tactile stimulation

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Abstract

There is an increasing interest in alpha-range rhythms in the electroencephalogram (EEG) in relation to perceptual and attentional processes. The infant mu rhythm has been extensively studied in the context of linkages between action observation and action production in infancy, but less is known about the mu rhythm in relation to cross-modal processes involving somatosensation. We investigated differences in mu responses to cued vibrotactile stimulation of the hand in two age groups of infants: From 6 to 7 months and 13 to 14 months. We were also interested in anticipatory neural responses in the alpha frequency range prior to tactile stimulation. Tactile stimulation of infants' left or right hand was preceded by an audiovisual cue signaling which hand would be stimulated. In response to the tactile stimulus, infants demonstrated significant mu desynchronization over the central areas contralateral to the hand stimulated, with higher mu peak frequency and greater contralateral mu desynchronization for older infants. Prior to the tactile stimulus, both age groups showed significant bilateral alpha desynchronization over frontocentral sites, which may be indicative of generalized anticipation of an upcoming stimulus.

Guannan Shen and Staci M. Weiss are contributed equally to this manuscript.

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The findings highlight the potential of examining the sensorimotor mu rhythm in the context of infant attentional development.

1 | INTRODUCTION

Advances in developmental cognitive neuroscience are shedding light on diverse aspects of perceptual and cognitive abilities in human infants. The array of available methodologies for infancy researchers includes the electroencephalogram (EEG) and magnetoencephalogram (MEG), both of which have been useful for advancing the understanding of infant capabilities (Meltzoff & Marshall, 2020). One aspect of developmental EEG work has focused on sensorimotor neural oscillations, particularly the mu rhythm, which is maximal over central electrode sites in the alpha frequency range (Marshall et al., 2002).

Studies of the infant mu rhythm have often been carried out in the context of linkages between the action observation and execution (Cuevas et al., 2014; Marshall & Meltzoff, 2011; Southgate et al., 2009), including action imitation (for reviews see Marshall & Meltzoff, 2014; Meltzoff & Marshall, 2018), and the perception of bodily correspondences between self and other in infancy (Saby et al., 2013). The emphasis in the infant mu literature on the connections between action observation and execution is consistent with the notion of the mu rhythm as being tied to sensorimotor experience (Cannon et al., 2016; Cuevas et al., 2014).

Given that the mu rhythm appears to have origins in the somatosensory cortex (Ritter et al., 2009), there is also interest in the connections between the mu rhythm, somatosensation, and the development of maps of the body in the infant's brain (Marshall & Meltzoff, 2015; Meltzoff & Marshall, 2018). Here, we build on this line of work by examining infant mu rhythm responses elicited to tactile stimulation of the hand, with an additional novel focus on potential anticipatory responses of the mu rhythm to upcoming stimulation. We were particularly interested in exploring whether infants can use an informative audiovisual cue to predict the temporal and spatial properties of upcoming tactile stimulation.

1.1 | Neural correlates of somatosensory processing

In adults, tactile stimulation of the hand elicits a desynchronization (decrease in power) of the mu rhythm in the EEG over the contralateral central region (Anderson & Ding, 2011; Haegens et al., 2012; Shen et al., 2017). Contralateral mu desynchronization to tactile stimulation of the hand in adults has also been reported using MEG (Gaetz & Cheyne, 2006; van Ede et al., 2014). In comparison, there is very little work focusing on the infant oscillatory responses following somatosensory stimulation, with developmental studies instead of focusing on event-related potentials (ERPs) elicited to tactile stimulation. These studies have shown that stimulation of the hands, feet, lips, or face of infants elicits spatial patterns of ERP responses across the scalp that are consistent with the homuncular organization of the somatosensory cortex (Meltzoff et al., 2018, 2019; Saby et al., 2015; Shen et al., 2018).

A study of EEG mu rhythm responses to tactile stimulation in infancy by (Drew et al., 2018) reported that tactile stimulation of the right hand of 6-month-olds elicited a desynchronization of the mu rhythm over the left (contralateral) central region, while stimulation of the right foot was associated with a mu response over the midline at the central region. Mu rhythm desynchronization at central midline electrodes to foot stimulation was also evident in a recent study of 10-month olds (Piccardi et al., 2021).

Here, we examine infant mu responses to tactile stimulation of the left and right hand across two age groups (from 6- to 7-month olds and 13- to 14-month olds). We were also interested in whether external cues can enable the infant to register attention to a particular bodily location prior to the delivery of the tactile stimulus. Tactile stimulation was applied separately to the left and right hands, enabling an investigation of spatially and temporally distinct neural modulation for visuotactile mapping, by tracing mu rhythm responses to infant hand stimulation (delivered in peripersonal space) following a reliable, spatially informative visual cue (delivered in extrapersonal space).

1.2 | Neural correlates of anticipation

As well as testing the infant mu rhythm response to stimulation of the left and right hands, a further aim of the current study was to employ EEG methods to explore neural aspects of anticipation in infancy. Specifically, we tested for anticipatory alpha-range EEG responses (including a possible anticipatory mu rhythm response) following audio-visual cues that were designed to signal an impending vibrotactile stimulus that was delivered to infants' left or right hands.

Prior work has suggested that attentional control in the first year of life shifts from more exogenous, reactive processes to reflect increasingly endogenous, proactive processes of selective attention (Colombo, 2002; Johnson, 1990; Posner et al., 2012). Studies of anticipation in the visual modality have used measures such as look duration (Reynolds et al., 2013), visual fixation (Kannass & Oakes, 2008), as well as psychophysiological responses (Richards & Casey, 1991; Xie et al., 2018). There is also evidence that infants deploy anticipatory attention by moving their bodies and orienting their eyes, head, and hands in expectation of changes in their environment (Amso & Johnson, 2006; Reddy et al., 2013; Yu & Smith, 2016). From an individual differences perspective, behavioral measures of anticipation have been associated with self-regulation and attentional orienting abilities between 6 and 8 months of age (Gomes et al., 2000; Rothbart et al., 2011). Xie et al. (2018) reported a shift in infant visual attention that was apparent between 10 and 12 months of age (and not in younger infants), wherein the shift from exogenous, cue-elicited orienting to endogenous, sustained attention is accompanied by attenuation of alpha-range EEG responses. There is also evidence from anticipatory eye movements that suggests a similar transition in anticipatory alpha responses might be evident by 13–14 months of age (Martinez-Alvarez et al., 2017).

Much of the work on anticipatory aspects of infant attention has been carried out solely within the visual modality. Infant behavioral responses to stimuli presented simultaneously across different modalities remain a topic of current interest (Begum Ali et al., 2021; Thomas et al., 2018), although there is less work using temporally separated crossmodal stimulus pairings. Of particular relevance to the current study are the developmental neuroscience findings showing the evidence of anticipatory infant brain responses between temporally separated auditory/visual cues and target stimuli (Kouider et al., 2015; Mento & Valenza, 2016).

Studies in adults and older children have shown that when tactile stimulation of a specific bodily location (typically one of the hands) is preceded by a spatially informative visual or auditory cue, there is an anticipatory desynchronization of the mu rhythm over central electrode sites contralateral to the expected site of stimulation. In adults, the extent of this lateralization is modulated by the side of tactile stimulation both in terms of the location on the body and the location in space (Schubert et al., 2019). In a study of children aged between 6 and 8 years, Weiss et al. (2018) reported a contralateral anticipatory desynchronization of the mu rhythm in the epoch leading up to tactile stimulation of the left or right hand, following a spatially informative visual cue. Notably, the magnitude of the anticipatory mu desynchronization was associated with children's scores on an executive function battery (Weiss et al., 2018). The preverbal origins and development of this anticipatory mu rhythm response have yet to be addressed. In adults, the extent of anticipatory mu attenuation is correlated with properties of the behavioral response to the subsequent tactile stimulus (Anderson & Ding, 2011; Jones et al., 2010; Linkenkaer-Hansen, 2004; Schubert et al., 2009), and is associated with the amplitude of early components of the ERP response to the tactile stimulus (Zhang & Ding, 2010).

Findings in adults and children of anticipatory desynchronization of the mu rhythm ahead of cued tactile stimulation are consistent with broader work suggesting a role for alpha-range oscillations in attentional control (Gomez-Ramirez et al., 2016). In the somatosensory modality, research in this area has focused on the mu rhythm over the central scalp region, while in the visual modality, the alpha rhythm over posterior sites (the "visual alpha rhythm") has been of particular interest. Studies of anticipatory changes in the amplitude of the visual alpha rhythm typically involve a spatially informative central cue preceding a target visual stimulus that appears on the left or right side of a monitor screen. Modulations of visual alpha amplitude have been consistently reported in the interval leading up to the target stimulus. More specifically, desynchronization of the visual alpha rhythm at the occipital electrode contralateral to the expected field of presentation (left/right) occurs alongside an ipsilateral increase in alpha power (Klimesch, 2012; Sadaghiani & Kleinschmidt, 2016; Worden et al., 2000).

The anticipatory alpha attenuation seen over contralateral electrodes for the sensorimotor mu rhythm (in adults and children) and the visual alpha rhythm (in adults) may reflect the release of task-relevant sensory cortical areas from inhibition (Gomez-Ramirez et al., 2016; Klimesch et al., 2007). This release facilitates a subsequent increase in local cortex excitability, which in turn increases the perceptual salience of incoming tactile stimuli (Foxe & Snyder, 2011; Zhang & Ding, 2010). Anticipatory modulation of alpha-range rhythms (e.g., sensorimotor mu/visual alpha) over different scalp regions (central/occipital) has been suggested to reflect modality-specific attentional processes that share this common mechanism (Frey et al., 2015; Schroeder & Lakatos, 2009). Although work in children to investigate anticipatory modulation of alpha-range oscillations is still very sparse, we suggest that related studies are possible in still younger populations, in infants. Such work has the potential to expand our understanding of the ontogenesis of selective attention and its neurobehavioral correlates.

1.3 | Rationale and plan for the current infant study

The current study aimed to advance the understanding of EEG responses prior to and following tactile stimulation of the infant's hand, with a focus on somatosensory mu rhythm across two age groups (6–7 months and 13–14 months). The age range from 6 to 14 months of age is a period of distinct growth in the amplitude of the infant mu rhythm (Marshall et al., 2002), but little is known about the changes in the temporal and spatial properties of the mu response to tactile stimulation (and its magnitude) over this time. Further, as noted above, this age range is also of broader interest in terms of the development of perceptual and attentional abilities, both in terms of anticipatory attention and the capacity to relate stimuli across different modalities.

We employed an age-appropriate somatosensory selective attention paradigm in which EEG was collected during a series of trials involving a spatially informative audiovisual cue presented in extrapersonal space, prior to the delivery of vibrotactile stimulation to the infants' left or right hand. The term "cue" is used here to denote the onset of spatially informative visual and auditory information that was temporally associated with the subsequent tactile stimulation. Given the age range of the participants, no behavioral response to the tactile stimulus was required or measured.

Analyses addressed the three interrelated aims: (i) to examine the development of the somatosensory mu rhythm using an individual differences approach to mu peak identification, (ii) to assess whether the infant mu rhythm response to tactile stimulation of the right and left hand reflects lateralized modulation, as is evident in adults, (iii) to test for anticipatory EEG responses during a cue–target paradigm across modalities (audiovisual cue and tactile target). Planned comparisons tested differences in alpha-range responses over different scalp regions across the two age groups and across the hand stimulated (left/right). We were particularly interested in the possible anticipatory modulation of the EEG signal during the interval between the audiovisual cue and the delivery of the tactile stimulus.

2 | METHOD

2.1 | Participants

This study was carried out with approval from the institutional review board at Temple University, with informed consent obtained from the parent of each infant before participation. Forty-three infants across two age groups were recruited to participate in this cross-sectional study. Eleven infants were excluded from further analyses due to hardware failure ($n = 1$), technical problems with EEG signal acquisition ($n = 3$), or excessive movement (younger = 3; older = 4) that precluded the recording of a minimum number (20) of artifact-free trials for each condition (left-hand stimulated/right-hand stimulated). The EEG data from 32 infants aged from 6 to 7 months ($n = 17$) and 13–14 months ($n = 15$) met the criteria for further analysis. The younger age group comprised of infants from 6 months 0 days to 7 months 31 days (M = 222 days, SD = 13, 7 male, 10 female). Infants in the older age group ranged from 13 months 0 days to 14 months 31 days (M = 419 days, SD = 17, 7 male, 8 female). From this point, we refer to these groups as "younger infants" and "older infants," respectively. All participating infants were reported by parents as being typically developing, and all were born within 15 days of their due date. Infants with two left-handed parents were precluded from study participation.

2.2 | Experimental procedure

Infants initially viewed a 2-minute video to familiarize them with the Elmo and Cookie Monster characters that were part of the spatial cues. Following the EEG cap placement, electrode preparation, and placement of the vibrotactile stimulators and mittens (see below), the infant was seated on the lap of their caregiver, facing an LCD monitor. The parents were seated in a chair positioned 60 cm away from the display (24 in/60 cm viewable). The hands of the infants were not restrained.

At the beginning of each trial, a fixation image of an infant's face was displayed in the center of the monitor screen. After 1000 ms, the fixation image was replaced by a visual cue consisting of an image of a Sesame Street character (Elmo or Cookie Monster) that was presented either on the left or the right side of the screen. The location of the cue on the screen (left or right) was congruent with the hand to which a vibrotactile stimulus was presented 2000 ms after cue onset (left or right hand). The visual cue was displayed for 3000 ms. The association of cue character (Elmo/Cookie Monster) and visual cue lateralization (left/right) was consistent within each participant and was counterbalanced across participants. Simultaneous with the onset of the visual cue, an audio clip of the specific sound made by Elmo or Cookie Monster (700 ms duration) was presented via a loudspeaker placed behind the monitor. A schematic showing the structure of a single trial is shown in Figure 1.

To further increase the salience of the correspondence between the cues and the hand to which the vibrotactile stimulus was presented, infants' hands were fitted with puppet mittens of the Sesame Street characters such that each mitten was on the same hand (left/right) as the side of the matching visual cue. The multimodal combination of cues was designed to promote learning of the associations between the cues and the hand (left/right) to which vibrotactile stimulation was presented.

The full protocol lasted about 22 min, with infants receiving tactile stimulation to the right ($n = 100$) or left ($n = 100$) hand in a randomized order across 200 trials. In preliminary analyses, we found no differences in EEG responses to the various combinations of audiovisual cue stimuli that were employed.

Stimulus presentation was controlled by STIM software from James Long Company. Vibrotactile stimuli were delivered using custom devices placed on infants' left and right palms. Each device consisted of a plastic disc (see Figure 2) containing a 10-mm disc motor (10,000 rpm/166 Hz), with a cable connecting the device to a control box. The discs were attached to the infant's palm with medical tape, with the cable oriented toward the arm (Figure 2). The motor pattern generating the vibrotactile stimulus had a 45-ms rise time, 940 ms of peak movement, and a 15-ms brake time, for a total of 1000 ms of stimulation. The vibrotactile stimulus did not produce a sound that was audible to the infant.

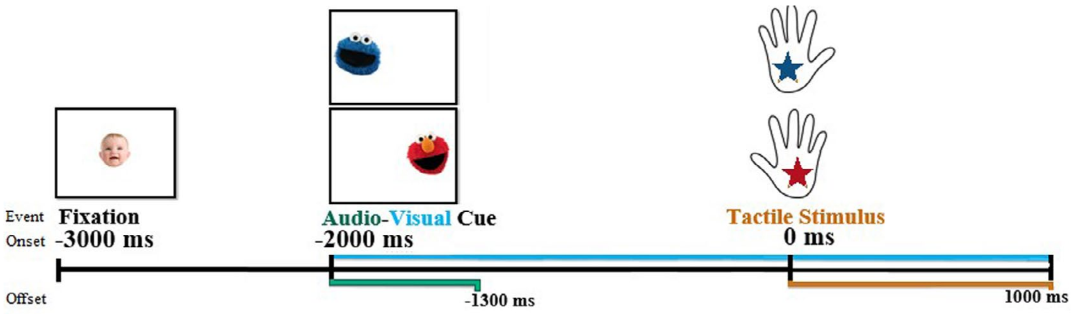


FIGURE 1 Trial structure: A picture of an infant's face (serving as fixation) was first displayed centrally for 1000 ms. The onset of the directional visual cue (Sesame Street character displayed continuously for 3000 ms) was simultaneous with the onset of a 700 ms auditory stimulus consisting of "Elmo" or "Cookie" via open field speakers. The delivery of the vibrotactile stimulus to the left or right hand occurred 2000 ms following the cue onset. The vibrotactile stimulus was delivered continuously for 1000 ms

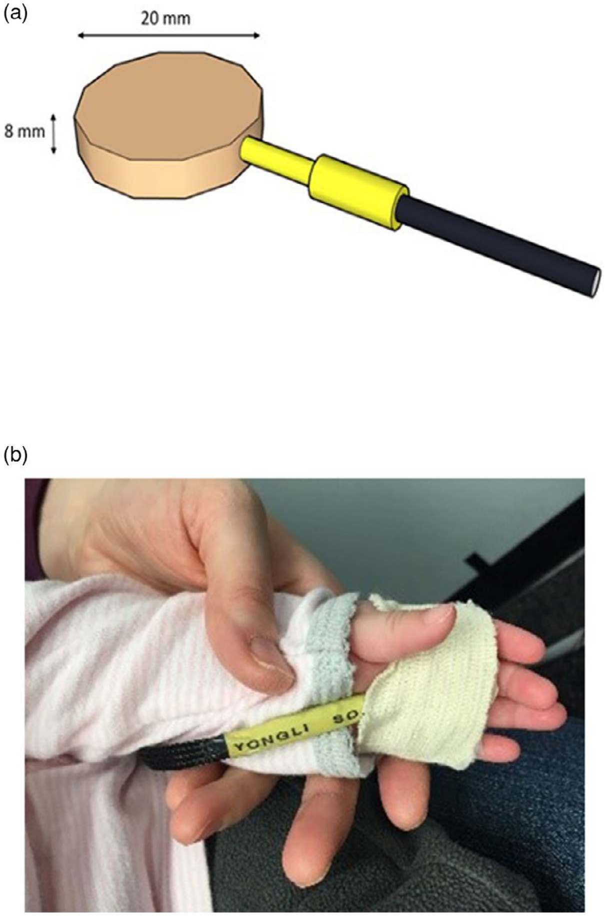


FIGURE 2 Top: Rendering of the vibrotactile device. Bottom: Placement of the device on the hand of an infant participant, after securing with medical tape and a bandage

2.3 | EEG acquisition and analysis

EEG signals were acquired from 32 electrodes secured in a stretch cap (ANT Neuro) and placed according to the International 10–20 format. As a part of cap preparation, each electrode was filled with a small amount of conductive gel. The EEG signals were collected referenced to Cz with an AFz ground and were re-referenced offline to the average of the left and right mastoids prior to analysis. Scalp impedances were kept under 25 kΩ. All EEG signals were amplified by optically isolated, high input impedance (>1 GΩ) bioamplifiers from SA Instrumentation 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.). Bioamplifier gain was 4000 and hardware filter settings were 0.1 Hz (high-pass) and 100 Hz (low-pass) with a 12 dB/octave roll-off.

Processing and initial analysis of the EEG signals were performed using the EEGLAB 13.5.4b toolbox (Delorme & Makeig, 2004) implemented in MATLAB. Epochs of 5000 ms duration were extracted from the continuous EEG data, with each epoch extending from −3000 to 2000 ms relative to vibrotactile stimulus onset. The experimental session was recorded on the video for the purpose of coding infant movement. During recording, a vertical interval time code (VITC) was placed on the video signal that was aligned with EEG collection at the level of one NTSC video frame. Videos were coded offline and trials were rejected if they contained upper limb movements for the entire 5000 ms analysis epoch. Further trials were discarded if they included orienting of the head to the cue or stimulus in the 2000 ms window prior to tactile stimulus presentation. After video coding, older infants had a mean of 52 valid trials per condition (left-hand stimulation or right-hand stimulation), and younger infants had a mean of 63 trials per condition, due to more movement in older infants than younger infants. Visual inspection of the EEG signal was used to reject epochs containing significant muscle artifacts. The mean number of artifact-free trials per condition (left-hand stimulation or right-hand stimulation) was 33.5 for older infants (left: M = 32, SD = 14; right: M = 35, SD = 13) and 33 for younger infants (left: M = 33.5, SD = 14; right: M = 32.9, SD = 15). A one-way ANOVA showed no significant difference in the number of usable trials between conditions ($p = .572$). There was also no difference in usable trial numbers between the two age groups ($p = .965$).

2.4 | Identification of age-specific mu rhythm peak frequency

Prior work has shown that the mean peak frequency of the infant mu rhythm increases from around 6 Hz at 6 months of age, to just above 7 Hz by 12 months (Berchicci et al., 2011; Marshall et al., 2002). To assist with the selection of age-specific mu frequency bands, oscillatory activity in the 4–12 Hz range was compared between two epochs: During the presentation of the fixation stimulus (baseline: −3000 to −2000 ms) and an epoch following vibrotactile stimulation (post-stimulus: 200 to 1200 ms). To capture the maximum mu attenuation evoked by tactile stimuli, analyses focused on the mu response to the right-hand stimulation condition at the left central electrode (C3). Time-frequency analysis was performed using Morlet wavelet decomposition, with 100 overlapping windows starting with a 0.8-cycle wavelet at the lower frequency. Power spectra from the two epochs were compared to quantify the mu rhythm peak frequency for each participant, which was identified as the frequency showing the maximum power difference between the two epochs. The peak frequency was first identified using a routine in R (version 3.5.3) and was then confirmed with a visual inspection of individual power spectrum plots.

2.5 | Mu rhythm responses in relation to vibrotactile stimulation

Based on prior studies of adults and children examining oscillatory mu rhythm responses during anticipation of tactile stimulation (Shen et al., 2017; Weiss et al., 2018), analyses focused on the frontocentral and central scalp regions (i.e., electrodes FC5/FC6 and C3/C4). Initial examination of ERSP responses showed them to be mainly over frontal and central sites (Figure 6), further guiding this focus. Although some infant EEG studies combine results from the frontal and central sites, we kept them separate since we were interested in possible differential effects across these regions. Further, the low-density electrode array in the current study precluded averaging across electrode clusters. Based on prior infant EEG work and the results of the individualized mu peak frequency analysis (above), the mu frequency ranges used were 5–8 Hz for the younger age group and 6–9 Hz for the older age group (Marshall et al., 2002).

To characterize changes in EEG oscillations prior to and following the presentation of the vibrotactile stimulus, 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 overlapping windows starting with a 0.8-cycle wavelet at the lowest frequency. The baseline for the ERSP analyses was defined as a 900-ms window prior to cue presentation, during the presentation of the fixation stimulus (−3000 to −2100 ms). The pre-stimulus analysis window was defined as −1300 to −300 ms and the post-stimulus window was 200–1200 ms.

Trial-by-trial ERSP values at electrodes FC5, FC6, C3, and C4 were averaged for each participant. Repeated-measures ANOVAs were conducted separately for pre-stimulus window and post-stimulus window, with factors age group (younger, older), region (frontocentral, central), hand (left, right), and hemisphere (left: FC5, C3; right: FC6, C4).

3 | RESULTS

3.1 | Age-related change in peak mu rhythm frequency

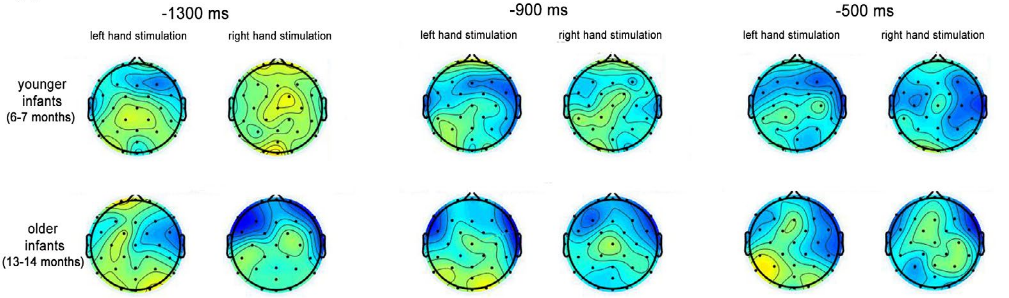
A peak at electrode C3 in the 4–12 Hz range was present in 13 of 17 younger infants and 12 of 14 older infants. A one-way ANOVA on the peak mu frequency with factor age group showed a main effect of age group, $F(1, 23) = 5.3019$, $p = .03$, $\eta^2 = .188$, with significantly lower peak frequency for younger infants (mean = 6.56 Hz, SD = 1.38) than older infants (mean = 7.73 Hz, SD = 1.13). These results are in line with the prior findings of a gradual increase in modal mu peak frequency from 6 to 7 Hz during the first year of life (Berchicci et al., 2011; Marshall et al., 2002).

3.2 | Post-stimulus mu rhythm modulation

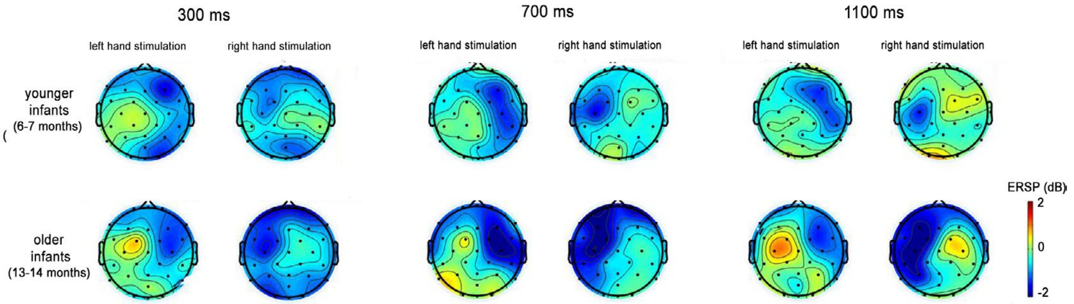
Time-frequency plots and topographic maps (Figures 3–6) indicate that the vibrotactile stimulus elicited mu rhythm desynchronization at central sites contralateral to the vibrotactile stimulation. This effect was observed in all individual participants.

A repeated-measures ANOVA (2 × 2 × 2 × 2; age Group × hand × hemisphere × region) on post-stimulus ERSP (300–1300 ms window) showed no significant main effect of age group, $F(1, 30) = 1.55$, $p = .223$, hand, $F(1, 30) = 0.09$, $p = .757$, hemisphere, $F(1, 30) = 0.193$, $p = .663$, or region, $F(1, 30) = 0.03$, $p = .863$. There was a significant interaction between hand and hemisphere, $F(1, 30) = 48.99$, $p < .001$, $\eta^2 = .156$. Post hoc tests showed that post-stimulus mu desynchronization was greater for contralateral sites than ipsilateral sites (for left-hand stimulation, right hemisphere ((mean = −1.21 dB, SD = 1.26) < left hemisphere (mean = −0.26 dB, SD = 1.11), $F = 25.537$, $p < .001$, $\eta^2 = .149$; for right-hand stimulation, left hemisphere (mean = −1.22 dB, SD = 1.5) < right hemisphere (mean = −0.17 dB, SD = 0.96), $F = 34.559$, $p < .001$. $\eta^2 = .163$).

The ANOVA also showed a significant three-way interaction between the age group (6–7 vs. 13–14 month olds), hand (left vs. right), and hemisphere (left vs. right), $F(1, 30) = 8.676$, $p = .006$, $\eta^2 = .031$. Post hoc analyses were conducted using pair-wise *t*-tests. For left-hand stimulation, older infants showed greater desynchronization in the right hemisphere (M = −1.486, SD = 0.596) compared with younger infants (M = −1.067, SD = 1.346, $t = 2.17$, $p = .034$). There was no significant difference between age groups in ipsilateral (left) ERSP (older M = 0.254, SD = 1.136, $p = .361$; younger M = −0.303, SD = 1.040, $t = 0.922$, $p = .361$). Similarly, for the right-hand stimulation, older infants exhibited greater contralateral (left) desynchronization (M = −1.955, SD = 1.225) than younger infants (M = −1.132, SD = 1.725; $t = 2.482$, $p = .016$) and there were no



(a) Pre-stimulus window



(b) Post-stimulus window

FIGURE 3 Topographic maps of alpha (5–8 Hz for younger infants, 6–9 Hz for older infants) ERSP in 400 ms intervals. The top panels (a) display alpha ERSP in the epoch prior to the tactile stimulus, which was delivered at $t = 0$ ms. The audiovisual cue was delivered at −2000 ms. The lower panels (b) show alpha ERSP evoked by tactile stimulation of the left or right hand

differences in ipsilateral (right) ERSP between older infants (M = 0.017, SD = 0.655) and younger infants (M = −0.162, SD = 1.152; $t = 0.512$, $p = .608$).

3.3 | Stimulus anticipation: pre-stimulus alpha rhythm modulation

Figure 3 shows topographic plots for alpha ERSP across the pre-stimulus and post-stimulus time windows. Figure 6 shows time-frequency plots of significant ERSP changes relative to baseline, with FDR correction, following the cue and following tactile stimulation of the right hand. As shown in these figures, alpha desynchronization was apparent in the time period prior to the onset of the tactile stimulus: Starting from around −1300 ms, an alpha-range desynchronization was present that appears to be strongest over frontocentral sites. This pre-stimulus alpha desynchronization was observed in 14 of the 17 younger infants and 13 of the 14 older infants.

For the repeated-measures ANOVA comparing pre-stimulus ERSP across age groups and conditions, there was a significant main effect of region, $F(1, 30) = 30.729$, $p < .001$, $\eta^2 = .07$, with greater desynchronization at frontocentral electrodes (M = −1.02 dB, SD = 1.14) than at central electrodes (M = −0.44 dB, SD = 0.98). There was no significant main effect of age group, $F(1, 30) = 0.048$, $p = .8277$, hand, $F(1, 30) = 1.441$, $p = .239$, hemisphere, $F(1, 30) = 0.195$, $p = .662$, and there were no significant interactions between any of the factors.

To confirm that there was a significant desynchronization from the baseline epoch to the time window prior to the onset of the tactile stimulus, mean power in the alpha frequency range

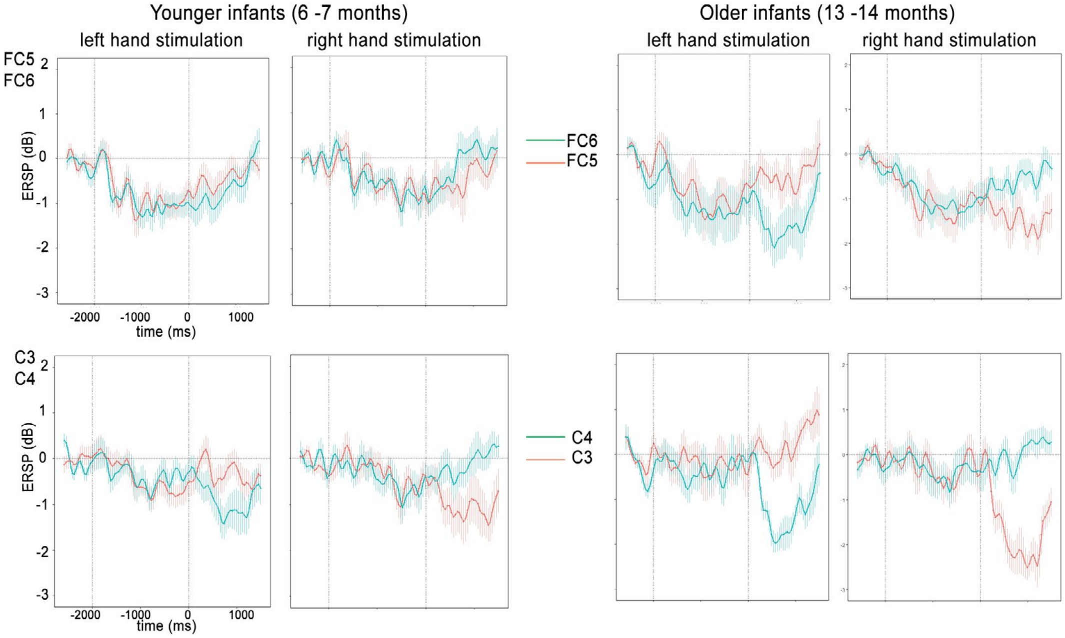


FIGURE 4 ERSP waveforms for the alpha band at FC5/FC6 (upper panel) and C3/C4 (lower panel) for younger infants (left two columns) and older infants (right two columns). The shadows around the line represent stand errors within each group. The alpha frequency range used was 6–9 Hz for older infants and 5–8 Hz for younger infants. The audiovisual cue was presented at −2000 ms (the first vertical line). Time 0 ms corresponds to tactile stimulus onset (the second vertical line)

(5–8 Hz for the younger infants, 6–9 Hz for the older infants) at frontocentral and central sites was compared using a repeated-measures ANOVA with a factor of time window (baseline: −2500 to −2100 ms; pre-stimulus window: −1300 to −300 ms). This analysis revealed a significant main effect of time window, $F(1, 30) = 22.489$, $p < .0001$, $\eta^2 = .209$, with lower power in the prestimulus window (mean = −0.73 dB, SD = 1.1) than in the baseline epoch (M = −0.13 dB, SD = 0.32).

4 | DISCUSSION

The results of the current study extend prior findings on the development of alpha-range rhythms in infancy, and further inform the understanding of infant EEG responses to tactile stimulation. This study also explored the neural concomitants of infant anticipation, applying a developmental cognitive neuroscience approach to address questions first raised in studies about behavioral anticipation.

Analyses examined alpha-band activity in the EEG signal preceding and following cued vibrotactile stimulation of the left- or right-hand in infants. Infants in two age groups (from 6 to 7 months and 13 to 14 months) were recruited to examine the developmental changes in EEG oscillations around tactile stimulation. Consistent with the prior work (Berchicci et al., 2011; Marshall et al., 2002; Thorpe et al., 2016), the mean peak frequency of the central somatosensory mu rhythm in infants increased from around 6.5 Hz in infants aged between 6 and 7 months old to 7.7 Hz at 13–14 months of age.

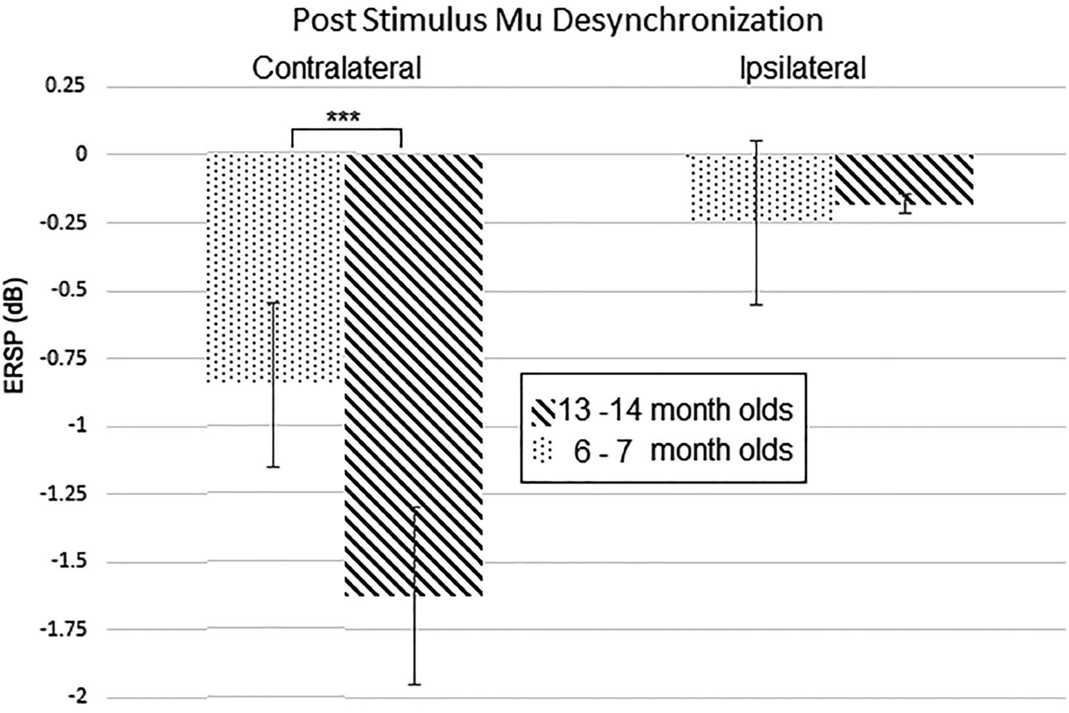


FIGURE 5 Mean alpha ERSP at contralateral and ipsilateral central sites (C3 and C4) for the 1000 ms following the onset of tactile stimulation. $^{***}p < .001$

The study of the infant mu response to tactile stimulation of the hand was restricted to stimulation of the right hand (Drew et al., 2018), whereas the current study employed stimulation of left and right hands. Contralateral desynchronization to tactile stimulation was observed for stimulation of infants' left and right hands, which adds a developmental perspective to work done with adults (Haegens et al., 2012; Van Ede et al., 2014). Although this effect was significant at both ages, older infants showed greater contralateral desynchronization than younger infants in response to the tactile stimulus, compared to younger infants. This desynchronization to the tactile stimulus did not significantly differ between frontocentral and central sites. This observation is consistent with the fact that frontocentral electrodes have sometimes been included with central sites in electrode clusters used to index infant mu (Bache et al., 2017; Stapel et al., 2010). The larger desynchronization in older infants also aligns with the findings of a larger magnitude of mu desynchronization noted during the action production in older infants (Cuevas et al., 2014). This finding can also be considered in the light of studies showing that the infant behavioral reactions to tactile stimulation of different body parts become more efficient over the first year of life (Leed et al., 2019; Somogyi et al., 2018).

The findings from the current study can be placed within the growing literature on body representations in infancy. Within the first months of life, the somatotopic organization of the basic infant body map appears consistent with that of older children and adults (Dall'Orso et al., 2018; Meltzoff et al., 2018, 2019; Saby et al., 2015; Shen et al., 2018, 2020). Work with older infants has revealed an adult-like somatotopic pattern of mu rhythm responses, observed separately during the action observation and action execution (Marshall et al., 2013; Müller et al., 2017; Saby et al., 2013). In six-month-old infants, a somatotopic pattern of mu responses was evident following

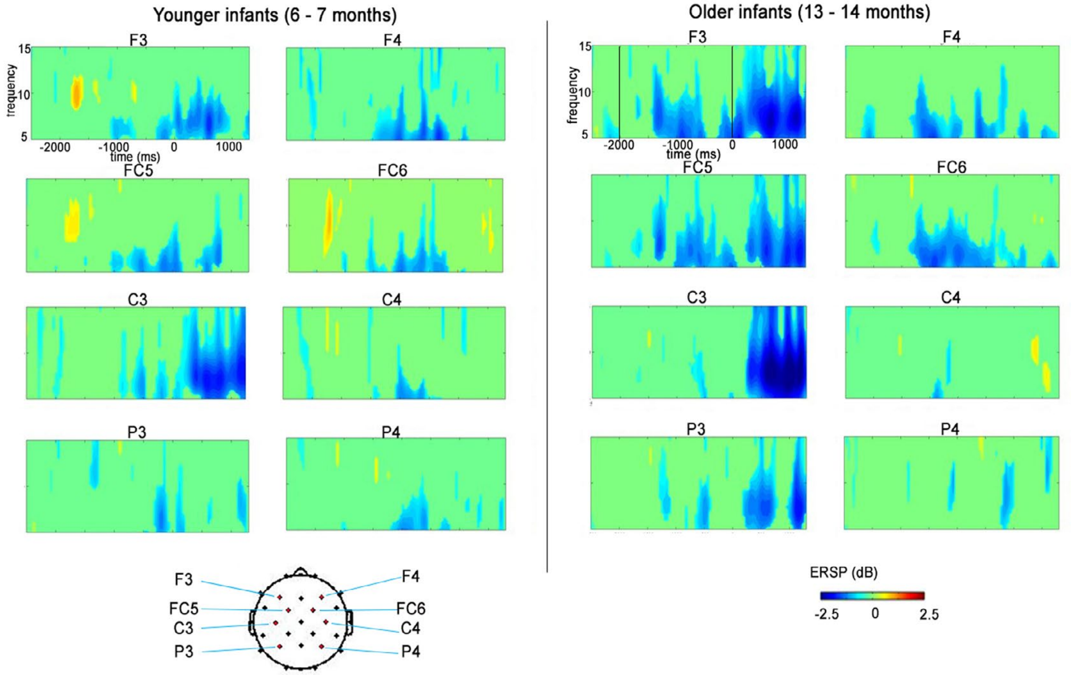


FIGURE 6 Time-frequency plots showing significant changes in alpha ERSP following right-hand stimulation relative to baseline for younger infants (left two columns) and older infants (right two columns). FDR correction was applied to all plots. Two black vertical lines in the upper left plot indicate the onset of tactile stimulation at time 0 ms and the audiovisual cue at −2000 ms. The blue in the images indicates significant decreases and yellow/red indicates significant increases of ERSP compared to baseline ($p < .05$). Green areas depict non-significant ($p > .05$) ERSP changes from baseline. The electrode array is also shown, with the labeled electrodes corresponding to the sites for which time-frequency plots are shown

tactile stimulation of the infant's hand or foot, and concurrent observation of an adult hand or foot did not modulate these effects (Drew et al., 2018). The current results add to these studies through the finding of lateralized responses following the vibrotactile stimulation.

In addition to documenting changes in the infant EEG response to tactile stimulation, a further aim of the present study was to explore alpha-range oscillatory activities prior to the onset of the vibrotactile stimulus, following a spatially informative cue that signaled the hand (left or right) to which the tactile stimulation would be delivered. Significant bilateral attenuation in alpha-range power was evident for both age groups over frontocentral sites (FC5 and FC6) in the epoch preceding the tactile stimulus. This novel finding of bilateral anticipatory attenuation of alpha-range EEG oscillations suggests that infants were able to utilize the audiovisual cue in the service of expecting the upcoming stimulus. A similar desynchronization was not apparent at central electrode sites (C3 and C4), unlike anticipatory responses preceding tactile stimulation seen in studies of adults (Anderson & Ding, 2011; Haegens et al., 2012; Jones et al., 2010) and children (Weiss et al., 2018).

The frontocentral, but not central, nature of the desynchronization prior to the tactile stimulus suggests that this response may not be specific to the tactile modality, but maybe a more general anticipatory response. Recent ERP studies have suggested that infants can generate temporal predictions about upcoming visual events from audiovisual cues (Kouider et al., 2015; Mento & Valenza, 2016), with the source of these neural responses associated with the fronto-parietal attentional networks (Petersen & Posner, 2012). It is possible that the frontocentral modulation of alpha-range power in the epoch leading up to the vibrotactile stimulus is also reflective of activity in these networks.

An additional argument against the specificity of the infant anticipatory EEG response is the lack of a lateralized response leading up to the tactile stimulation, which would have suggested a predictive response involving the anticipated location of the tactile stimulus. The current study used visual cues consistent with the spatial location of tactile stimulation (left vs. right side of the body) as well as concurrent auditory cues that were consistently associated with the side of tactile stimulation. The lack of lateralization in the alpha desynchronization during the prestimulus epoch may be a further indicator of a general anticipatory response reflecting a general association between the cue and the target stimulus. We further note that studies of anticipatory EEG responses in older children and adults also require participants to overtly respond to the target stimuli in some way, which was not possible in the current infant study and may have influenced the nature of anticipation of, or infant readiness for, the delivery of the tactile stimuli. We also note that the procedure did not include conditions where the cue and probe were incongruent, or a condition where there was no cue. Future studies could address the feasibility of including such conditions while maintaining adequate trial numbers for EEG analysis.

The lack of a lateralized anticipatory EEG response in the current study is not to say that infants cannot utilize spatially informative cues to organize responses to target stimuli. In work, using behavioral measures of infant visual attention, infants as young as 3–6 months make associations between spatially informative cues and target stimuli, as indicated by faster and more accurate eye movements to visual target stimuli that are preceded by a brief visual cue (Atkinson & Braddick, 2012; Wentworth & Haith, 1992). There is also some evidence that infants can map spatial cues across modalities (Kouider et al., 2015; Mento & Valenza, 2016), although little of this work has involved somatosensory stimuli.

Our finding of bilateral frontocentral alpha desynchronization in anticipation of tactile stimulation may reflect an endogenous, amodal shift of attention to an upcoming event. Given the increasing interest in the developing relations between the visual and tactile modalities (Drew et al., 2018; Filippetti et al., 2015; Rigato et al., 2014), further work can address how children come to map spatial cues in extrapersonal space to expected stimulation of specific body parts (Weiss et al., 2018). It would be interesting to further study how the bilateral alpha-range response that we observed at frontocentral sites during the prestimulus epoch develops into the focal anticipatory response at contralateral central electrode sites that have been reported in the studies of older children and adults involving tactile anticipation (Haegens et al., 2012; Weiss et al., 2018). Although the processes underlying such a (potential) shift have yet to be elucidated, work in adults has suggested that a shift from frontal alpha desynchronization to desynchronization of the central mu rhythm may reflect aspects of sensorimotor learning (Marshall et al., 2009) or action simulation (Coll et al., 2015). From a developmental perspective, this shift also likely involves changes from infancy to childhood in the ability of participants to complete tasks that require overt behavioral responses to the target stimulus, which would be expected to sharpen prestimulus attentional focus, which in turn would likely improve the modal specificity of the anticipatory response.

In conclusion, the present study adds to our knowledge about the developmental properties of alpha-range EEG rhythms in infants. Compared with the younger infants, older infants showed higher mu peak frequency and greater contralateral desynchronization in response to tactile stimulation of the hand. The results also suggest an anticipatory alpha attenuation in infants that occurred in advance of tactile stimulation. This alpha desynchronization was observed bilaterally over frontocentral sites, in contrast to the contralateral central response shown in somatosensory anticipation tasks in adults (Gomez-Ramirez et al., 2016) and older children (Weiss et al., 2018). Our conjecture is that the frontal alpha attenuation within the anticipatory epoch might indicate that infants can use audiovisual cues to predict the timing of an impending stimulus. There was limited evidence to support the sensory and spatial specificity of this anticipatory response. Given the potential importance of anticipation as a component of selective attention (Weiss et al., 2018), future work should continue to examine the development of anticipatory abilities over infancy and the behavioral and cognitive concomitants of these abilities.

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