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Individual differences in bodily attention: Variability in anticipatory mu rhythm power is associated with executive function abilities and processing speed

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Abstract

The ability to anticipate, attend and respond appropriately to specific stimuli is involved in the execution of everyday tasks. The current investigation examined the relations between cognitive skills measured by the NIH Toolbox and changes in the power of mu oscillations during anticipation of and in response to a tactile stimulus. Electroencephalographic (EEG) activity was measured after a visuospatial cue directed adults ($n=40$) to monitor their right or left hand for upcoming tactile stimulation. In the 500 ms prior to the onset of the tactile stimulus, a desynchronization was apparent 8 – 14 Hz at contralateral central sites, consistent with prior investigations of mu rhythm; a widespread synchronization was apparent in the 250 ms preceding delivery of the tactile stimulus. The extent of contralateral reduction in mu power was associated with speed processing ability, while ipsilateral mu power was associated with flanker performance and marginally correlated with card sort performance. Regression further probe the significance and specificity of these effects. Increases in mu power following onset of the tactile stimulus were not associated with any behavioral measures. Mu modulation during attention to a specific bodily location appears related to variability in the broader ability to regulate behavior in a goal-directed manner, and perhaps to speed of stimulus processing.

Keywords: tactile; mu; EEG; executive function; sensorimotor; oscillations; anticipation;

Introduction

Anticipation of an impending event or sensation can guide perception and action. In experimental settings, when the presentation of a visual, auditory or tactile stimulus is preceded by a stimulus-relevant cue, participants report higher rates of accurate stimulus perception and demonstrate more rapid reaction time than when a stimulus is presented without a preparatory cue (Posner, 1980; Frey et al., 2015). These behaviors suggest prior to stimulus presentation, deployment of attention in a selective, focused manner is conducive to stimulus processing (van Ede & Nobre, 2017). Exploiting the temporal precision of electroencephalogram (EEG), we can eavesdrop on the changes in neural oscillations which occur before and after the presentation of a stimulus (Cheyne et al., 2003; Engel, Fries, & Singer, 2001), with the goal of identifying how these changes facilitate perception and the regulation of behavior.

In this study we assessed individual differences in oscillatory neural responses during anticipation of a tactile stimulus and in response to that stimulus. We investigate the

association of subject-specific changes in oscillatory activity with variation in 1) reaction time in responding to the tactile stimulus, 2) general processing speed and receptive language abilities, as well as 3) executive function abilities, or the constellation of skills involved in the regulation of behavior.

The Active Role of Alpha Oscillations in Perception

Oscillatory activity in the alpha band of the EEG signal, broadly defined as activity within the 8-14 Hz frequency range in adults, has been identified as a correlate, gate and predictor of behavioral responses and cognitive functioning (Zanto & Gazzaley, 2009; van Ede & Nobre, 2017). As the most prominent oscillation in the EEG, alpha-range signals were originally associated with an 'idling' state but are now seen as more active in perceptual and cognitive processes (Klimesch et al., 1998). The oscillations apparent in the EEG signal arise from fluctuations in the polarity of cortical tissue, which reflect the shifting, homeostatic balance of postsynaptic potentials released by assemblies of excitatory pyramidal cells and inhibitory interneurons (Lopes da Silva, 2013; Cohen, 2016). The presence (or mere expectation) of a stimulus disrupts the default synchronized firing rate of postsynaptic potential which generated the rhythmic alpha activity, eliciting an event-related desynchronization (ERD) in the oscillatory signal (Haegens et al. 2011; Lopes da Silva, 2013). Changes in amplitude, phase and frequency of oscillations evoked by a discrete event can be computed using event-related spectral perturbation (ERSP), in which sinusoidal wavelets are used to estimate the shift in amplitude and phase of EEG oscillations in each successive, overlapping time window (Pfurtscheller & Da Silva, 1999; Makeig & Delorme, 2004). Thus, ERSP can quantify the changes in power of a given frequency range (relative to a baseline period), tracking the temporal sequence of postsynaptic potentials discharged synchronously from a particular neuronal population (Klimesch et al., 1998; Lopes da Silva, 2013).

To study changes in alpha power in anticipation of or in response to an upcoming event or stimulus, participants are presented with a cue that orients them to a feature of the forthcoming stimulus. In the widely-used Posner paradigm, a spatial cue indicates whether a visual stimulus will be presented to the participant's right or left visual field (Posner, 1980). During the interval following the cue but prior to the predicted onset of a visual stimulus, anticipatory ERD of

rhythmic alpha activity is observed over contralateral visual cortex, measured as a decrease in alpha power relative to baseline (Thut et al., 2006; Nobre & van Ede, 2017).

Contemporary accounts of 'top-down' or attention-related modulation of alpha-range activity rest upon the inhibition-timing hypothesis (Klimesch, Sauseng, & Hanslmayr, 2007), which explains that during rest, oscillatory EEG activity arises from the synchronized cortical firing of neurons that may limit the sampling of sensory events (Schroeder & Lakatos, 2009). When a stimulus disrupts the default state of rest or inattention, there is a reallocation of resources diverted to the local processing of the new or expected stimulus, which is facilitated by the suppression or inhibition of global neural activity. As such, widespread *increases* in alpha power from baseline reflect inhibited sampling of irrelevant sensory events, which permit concentrated cortical firing by neurons in the sensory cortex relevant to the stimulus. Focused attention and perceptual awareness of a stimulus is thus facilitated by concomitant *global increases* and *local decreases* in alpha power, indicating an adjustment in the sampling of sensory events adaptive to the expected temporal and spatial presentation of an upcoming stimulus (Frey et al., 2015; Schroeder & Lakatos, 2009; Thut et al., 2006). During anticipation, it is thought that sensory-specific alpha responses initiate the coordination of multisensory attentional control networks, enabling dynamic prediction of events across modalities and preparation for action (Engel, Fries & Singer, 2001; Sadaghiani & Kleinschmidt, 2016). In reaction to a stimulus, during rest and under most other conditions, these modality-specific alpha rhythms exhibit dissociable properties and operate independently (Mazaheri et al. 2009). Thus, the state of stimulus anticipation enables a unique opportunity for studying variability in oscillatory neural activity and centrality to behavior (Weiss et al., 2018).

Although much of the extant work on alpha power fluctuations has focused on the visual alpha rhythm at posterior occipital sites, another prominent alpha-range oscillation is the sensorimotor mu rhythm observed at central electrode sites (Jones et al., 2010; Pfurtscheller, 1989). Expectation of tactile stimulation in adults elicits changes in the mu rhythm which exhibit a somatotopic pattern (Anderson & Ding, 2011; Jones et al., 2010), in accord with the organization of the homunculus (Penfield & Boldrey, 1937). Jones et al. (2010) demonstrated reductions of mu power in anticipation of tactile stimulus, with responses lateralized according to the direction of a spatial cue (pointing left or right) as participants monitor their hands in expectation of sensation. Particularly when a distracting tactile sensation is presented simultaneous to the uncued hand, ipsilateral increases in mu power have also been demonstrated during the suppression of tactile attention (Haegens, Luther, & Jensen, 2012; van Ede, de Lange, & Maris, 2014). The utility of mu oscillatory power as an index of individual difference in behavior, beyond tactile stimulus processing to more general control of voluntary attention and action (executive functioning), has yet to be fully explored.

Anticipatory Mu Power and Tactile Processing

Across auditory, visual and tactile modalities, both contralateral alpha ERD and increases in ipsilateral alpha power during stimulus anticipation and response have been correlated with behavioral responses to stimuli (Thut et al., 2006; van Ede et al., 2014; Frey et al., 2015). In the tactile modality, the relation between mu power and behavioral indicators of tactile processing appears to differ depending on the strength and salience of the expected tactile stimulation, as well as the load on tactile attention (Haegens et al., 2012; Gomez-Ramirez, Hysaj, & Niebur, 2016). When a reliable spatial cue directs participants to expect tactile stimulation at the cued location, the magnitude of anticipatory mu ERD in electrode sites over the contralateral somatosensory cortices is linearly, inversely associated with rate of stimulus detection (Anderson & Ding, 2011; Haegens et al., 2011; Jones et al., 2010). Van Ede et al. (2012) examined anticipatory and post-stimulus mu power to parse their relative contributions to behavioral indicators of tactile processing. The authors reported that anticipatory mu ERD significantly accounted for the accuracy of participant's tactile judgements, while both the magnitude of anticipatory mu ERD and post-stimulus mu increases in mu power accounted for participant's reaction time to the stimulus. Reductions in anticipatory contralateral mu power have also been linearly associated with higher hit rates on tactile feature detection and temporal judgement tasks (Gomez-Ramirez et al., 2016).

Haegens, Handel and Jensen (2011) employed magnetoencephalography to investigate whether the lateralization of anticipatory mu oscillations varied according to how accurately a visual arrow cue relayed the location (right or left thumb) of an upcoming tactile stimulus. The authors reported that anticipatory contralateral mu power significantly distinguished between trials with above- and below-average reaction times, but not in accurate identification of the tactile stimulus (Haegens et al., 2011). This relation depended on the validity of the visual cue in predicting the location of the tactile stimulus. The authors found that the extent of oscillatory mu modulation reflects the predictability of the environment, such that differences in ipsilateral and contralateral mu power decreased under conditions with increasing uncertainty.

When tactile stimulation is expected simultaneously to a target location and another body part, it appears that variance in ipsilateral mu may index the suppression of tactile attention, partially accounting for behavioral responses to a tactile stimulus. In a subsequent MEG study, Haegens, Luther and Jensen (2012) reported that when tactile stimulation is presented simultaneously to the cued and uncued hand, both ipsilateral and contralateral mu power significantly distinguish between correct and incorrect trials. Thus, similar to the importance of increases in ipsilateral anticipatory alpha power in the visual modality in accounting for variability in stimulus response (Thut et al., 2006; Frey et al., 2015), anticipatory ipsilateral mu power may facilitate focus when tactile attention is under load.

To address inconsistencies in the literature associating oscillatory mu activity with task-specific indicators of tactile processing, we note the potential importance of subtle differences in task demands (Gomez-Ramirez et al., 2016). The dynamic adjustment of lateralized mu modulation to anticipated features of a tactile stimulus may be indicative of its sensitivity to the load on tactile attention, divided by managing competing expectancies, allocating tactile attention according to goals and bracing for potential distraction (Haegens et al., 2012).

One suggestion arising from work linking anticipatory neural responses to basic sensory responses is the proposition that ‘low-level’ indicators of attentional processing reciprocally influence, gate and cascade into individual level differences in the ‘higher-order’ ability to control behavioral responses (Engel, Fries & Singer, 2001; Gazzaley and Nobre, 2012; Sadaghiani & Kleinschmidt, 2016). We further suggest that executive function, defined by the planning, regulating and monitoring of goal-directed behavior, may partially be a manifestation of individual differences in how adults use information in their environment to anticipate upcoming sensory events and adjust their behavior to such expectancies.

The Present Study

The goal of the current investigation is to utilize an individual differences approach to the analysis of sensorimotor mu oscillatory activity during anticipation of and in response to a tactile stimulus. Our objectives were (i) to develop a subject-specific approach to identifying sensorimotor mu rhythm reactivity (ii) to examine whether mu reactivity is associated with variance in participant’s reaction time in stimulus detection (iii) to test if mu reactivity is associated with variance in a battery of cognitive skills, which includes measures of receptive language, processing speed and executive function. We employed a task in which a visual cue directed adults to focus their attention on a specific bodily location (the left or right hand) in anticipation of a tactile stimulus to that location. Using a foot pedal, participants responded to the tactile stimulus to indicate whether they detected one or two stimuli. We expected neural indicators of heightened attention (greater mu desynchronization or ERD in the contralateral hemisphere, and greater mu synchronization or ERS in the ipsilateral hemisphere) to relate to higher-order cognitive abilities (i.e., the executive function measures) and response time to target stimuli.

The logic of presenting a preparatory cue in a *different* modality from the target stimulus allows temporal and spatial differentiation of anticipatory activity (over sensory cortex relevant to the target) from neural responses elicited by the cue. There are also several strengths of employing somatosensory rather than visual targets: (i) Compared with the visual modality, tactile attention is not complicated by factors such as ocular shifts or visual preference; (ii) Neural indices of anticipation of touch are readily measurable through EEG recordings from electrodes overlying somatosensory cortex (Anderson and Ding, 2011; Haegens et al., 2011; Jones et al., 2010); (iii) The ability to focus

attention to a body part in expectation of touch may be amenable to change and enhancement via specific interventions (Jones et al., 2010).

Methods

Fifty undergraduate students received course credit in return for participation. Data from six participants were excluded from analyses due to technical issues. Four additional participants were excluded due to excessive artifact that contaminated more than 25% of trials. The final analyzed sample comprised 40 participants (mean age = 21.24 years; SD = 3.85; 37 females). All participants were right-handed according to the Oldfield Handedness questionnaire, neurologically healthy, and had normal or corrected vision. Once consented, participants were fitted with an EEG cap and tactile stimulators, seated at a table facing a computer screen, and instructed to rest their hands on their lap, out of sight.

Procedure

Participants were instructed to prepare for tactile stimulation to the index finger of the hand indicated by the direction of the arrow, and to indicate how many stimuli they detected (one or two) by pressing a foot pedal once or twice. The foot used to report stimulus detection was counterbalanced across participants. The specific sequence of visual stimuli in each trial comprised a fixation cross for 500 ms, followed by the arrow cue for 2250 ms, followed by a response screen that read “Copy with Your Foot!” (Figure 1). The tactile stimulation was delivered 1500 ms after the onset of the arrow cue, which remained on the screen for the 750 ms following tactile stimulation. The direction of the arrow was randomized, with an equal number (100) of left and right trials. Individual participant’s reaction time was retrieved from the onset of the response screen to the foot pedal press. Two tactile stimuli were delivered in rapid succession (“double stimuli”) on 20 out of the 200 trials, and 80 single-pulse trials were delivered to the right or left hands of participants. Prior to the experimental trials, 5 practice trials were presented to ensure that participants distinguished between the single and double tactile stimuli.

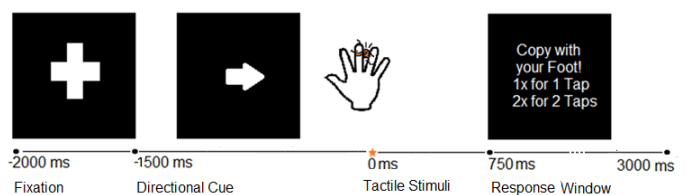


Figure 1. Trial structure: A fixation point was displayed for 500 ms, followed by an arrow spatial cue displayed continuously for 2250 ms, and the onset of the tactile stimulus occurred 1500 ms later (at 0 ms). The response prompt was displayed 750 ms after the tactile stimulus.

Tactile stimuli were delivered to the distal tip of the left and right index fingers using an inflatable membrane (10 mm diameter; MEG Services International, Coquitlam) mounted

in a plastic casing and secured with a finger clip. The membrane was inflated by a short burst of compressed air delivered via flexible polyurethane tubing (3 m length, 3.2 mm outer diameter). The compressed air delivery was controlled by STIM stimulus presentation software in combination with a pneumatic stimulator unit (both from James Long Company, Caroga Lake) and an adjustable regulator that restricted the airflow to 60 psi. To generate each tactile stimulus, the STIM software delivered a 10 ms trigger that served to open and close a solenoid in the pneumatic stimulator. Expansion of the membrane started 15 ms after trigger onset and peaked 35 ms later, with a total duration of membrane movement of around 100 ms.

EEG Recording and Processing EEG was recorded at a 512 Hz sampling rate using a stretch cap (ANT Neuro, Berlin) with electrodes placed at Fp1, Fpz, Fp2, F3, Fz, F4, F7, FC6, FC1, FC2, FC5, F8, Fz, C3, Cz, C4, CP1, CP2, CP5, CP6, T7, T8, P3, Pz, POz, P4, P7, P8, O1, Oz, O2, GND, and the left and right mastoids. Vertical EOG was recorded above and below the orbital rim of the left eye. Conducting gel was used and scalp electrode impedances were kept under 25 k Ω (values were typically lower). EEG channels were collected referenced to the vertex (Cz) and were re-referenced offline to an average mastoids reference prior to further analysis. The signal was amplified using optically isolated, high input impedance (> 1 G Ω) custom bioamplifiers (SA Instrumentation) and digitized using a 16-bit A/D converter (+/- 2.5 V input range). Bioamplifier gain was 4000 and filter (12 dB/octave rolloff) was set to .1 Hz (high-pass) and 100 Hz (low-pass).

Initial processing of the data utilized the EEG Analysis System (James Long Company) followed by analysis using the EEGLAB toolbox (Makeig et al., 2004) implemented in MATLAB. Independent component analysis was used to clear the EEG data of ocular and muscle artifact (Hoffmann and Falkenstein, 2008). Visual inspection of the EEG signal rejected epochs containing excessive remaining artifact. There was no difference in the number of usable trials between the left and right cued conditions ($p = 0.81$). Out of 80 trials, the mean number of artifact-free trials per condition was 69 (SD = 5.62).

For each single-pulse trial with a correct behavioral response, an epoch of 2500 ms was extracted (beginning 2000 ms prior to onset of the tactile stimulus and extending 500 ms after tactile stimulus onset). To avoid contamination of the anticipatory and response window by stimulus delivery, we set the initial membrane expansion as the onset of the tactile stimulus (0 ms) and the post-stimulus window to 20ms following the peak of membrane expansion. Spectral power over this epoch was estimated using Gaussian-tapered Morlet wavelets (Makeig & Delorme, 2004). Changes in power were computed as event-related spectral perturbation (ERSP) from initial visual cue presentation until after tactile stimulus presentation (i.e., -1500 to 300 ms) relative to a 500 ms baseline preceding the visual cue (i.e., -2000 to -1500 ms prior to tactile stimulation onset). For statistical analyses, a key variable was anticipatory mu ERSP, which was extracted

from mean ERSP value at C3 or C4 from 8 – 14 Hz in the 500 ms prior to onset of the tactile stimulus to the onset of the tactile stimulus (0 ms). We extracted post-stimulus mean mu ERSP by extracting the mean mu ERSP for the period from the delivery of the tactile stimulation at 20 ms to the following 270 ms.

Behavioral Measures Following the tactile task and removal of the EEG cap, four tasks from the NIH Cognition Toolbox were administered (for details, see Zelazo et al., 2013): the Flanker task, the Card Sort task, a Processing Speed task, and a picture vocabulary test that measured Receptive Language. On the Card Sort task, participants selected one of two test stimuli which matched either the shape or color of the target stimuli. In the Flanker task, participants indicated the direction of a central arrow that was presented between distracting ‘flanker’ arrows. Processing Speed was measured by the average reaction time to detecting if two images were identical. Participant’s scores on the Card Sort and Flanker tasks were calculated to reflect both accuracy and reaction time for participants who correctly identified targets on 80% of trials; accuracy alone was considered when this threshold was not met. For all four measures, we used t-standardized test scores (standardized around $\mu=100$) provided by the NIH Cognitive Toolbox.

Results

Behavioral Responses to Tactile Stimuli

Aggregated across the sample ($N = 40$), participants correctly identified the single or double tactile stimuli on 96.7% of trials. Reaction time was calculated as the duration from response screen until the initiation of the foot pedal press. Only single-stimulus trials were included in analyses.

Identifying Mu ERSP

Time-frequency plots (Figure 2) show a clear mu rhythm (8-14 Hz) ERD at the central electrode site (C3 or C4) contralateral to cue direction. In contrast, there was minimal change in mu power at the central electrode ipsilateral to the cue direction. Significant differences between contralateral and ipsilateral central sites (Figure 2) are driven by mu ERD during anticipation of tactile stimulation (-500 ms to 0 ms) at the site contralateral to the cue direction. At the left central electrode site (C3), mu ERD was apparent as participants attended to their right hand. At the right central electrode site (C4), mu ERD was present during attention to the left hand.

Quantifying Anticipatory and Post-Stimulus Mu ERSP

The envelope of the amplitude-modulated signal was computed via the Hilbert transform (“hilbert” function in Matlab), which discards phase information and reveals oscillatory power fluctuations over time. A subject-specific approach to identifying peak mu activity was used, with a peak quantified in R as the largest local maximum within the 7-14 Hz range (Goljehani et al., 2014). This value was extracted from individual participant power spectra for C3 and C4, for each condition (right/left).

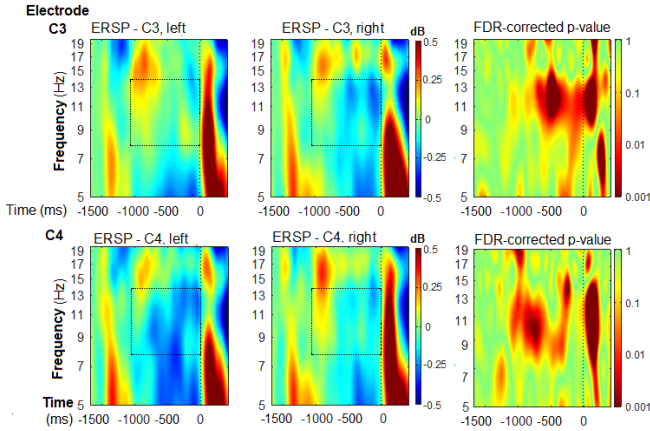


Figure 2. Time-frequency plots showing ERSP (event-related spectral perturbation) at left and right central sites (C3/C4) across a range of 5-20 Hz for the period from 1500 ms before the tactile stimulus (0 ms) to 300 ms after.

The bin with the highest number of observations was centered at 10.5 Hz. The mean alpha peak frequency across subjects was 10.1 Hz with a between-subject SD of 2.1 Hz and the median was 10.4 Hz.

A repeated-measures ANOVA was conducted, comparing anticipatory mean 8-14 Hz ERSP in the -500 to 0 ms window prior to tactile stimulation, by electrode (C3/C4) and cue direction (left/right). No main effects were observed. A significant interaction was observed between cue direction and electrode, $F(1, 39) = 25.757, p < .001, \eta^2_p = 0.398$. As suggested by the ERSP scalp maps (Figure 3), this interaction was driven by greater mu ERD at the contralateral site than at the ipsilateral site. When stimulation was expected to the left hand, greater mu ERD was observed at C4 ($M = -0.461, SD = 0.988$) than at C3 ($M = -0.022, SD = 0.984, t = 3.246, p < .001, d = .588$). When stimulation was expected to the right hand, greater mu ERD was observed at C3 ($M = -0.398, SD = 1.026$) than at C4 ($M = -0.077, SD = 0.844, t = -3.246, p < .002, d = -0.513$).

A repeated-measures ANOVA was conducted, comparing mean 8-14 Hz ERSP in the 20 to 270 ms window by electrode (C3/C4) and cue direction (left/right). No main effects were observed. A significant interaction was observed between cue direction and electrode, $F(1, 39) = 11.823, p < .001, \eta^2_p = 0.233$. Following stimulation of the left hand, mu ERSP was greater at the ipsilateral site C3 ($M = 0.308, SD = 1.337$) compared to the contralateral site C4 ($M = -0.083, SD = 1.555, t = -3.506, p = .015, d = .403$). Following stimulation to the right hand, mu ERSP was greater at the contralateral site C3 ($M = 0.393, SD = 1.545$) compared to ipsilateral site C4 ($M = 0.079, SD = 1.686, t = -2.240, p = .031, d = -.354$).

To examine the relations between mu ERSP and scores on the behavioral tasks, the dependent variables used in the previous ANOVA were collapsed into *contralateral* (mu ERSP at C3 for the right hand cue and at C4 for the left hand cue) and *ipsilateral* (mu ERSP at C3 for the left hand cue and at C4 for the right hand cue) mean *mu ERSP* values.

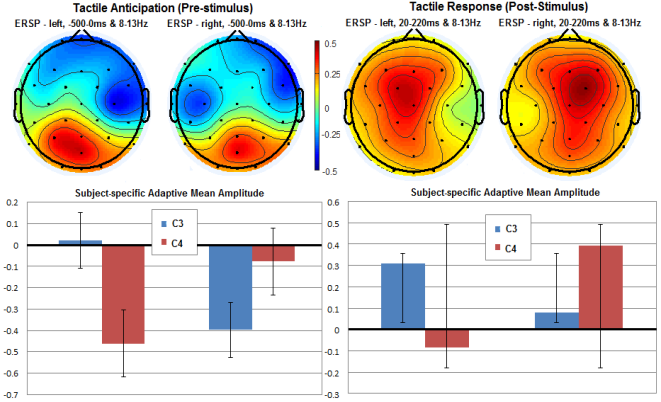


Figure 3. Scalp maps showing mean ERSP for the anticipatory period (-500 to 0 ms) and stimulus response period (20-270 ms) at each of 30 electrodes. Mu power for each participant was calculated for the subject-specific frequency band (+/- 2 Hz) at C3 and C4.

Correlation of Mu ERSP with Behavior

Pearson correlations were computed among ipsilateral and contralateral mu ERSP in anticipation of (*anticipatory*) and in response to (*post-stimulus*) tactile stimulation, and the measures from the NIH Cognitive Toolbox. Contralateral anticipatory (CL TA) mu ERSP was inversely associated with Processing Speed (PS) ($r = -.321, p = .02$), while Flanker score was significantly associated with ipsilateral anticipatory (IP TA) mu ERSP ($r = .293, p = .03$). Similarly, Card Sort was marginally associated with ipsilateral anticipatory mu ERSP, ($r = .230, p = .06$). Processing Speed ability and task-specific reaction time were significantly correlated ($r = .245, p = .02$). Language (PVT) was not significantly correlated with other measures; contralateral tactile response (CL TR) mu ERSP was marginally associated with processing speed, ($r = -.219, p = .07$), but ipsilateral tactile response (IP TR) did not relate with other behavioral measures.

Table 1. Correlation Matrix of Study Variables.

	CL TA Mu ERSP	IP TA Mu ERSP	CL TR Mu ERSP	IP TR Mu ERSP	Flan- ker (EF)	Card Sort (EF)	PS	PVT
CL TA								
IP TA								
Mu ERSP	—	.017	.718	.667	—	—		
IP TA								
Mu ERSP	—	—	.421	.511	—	—		
Flanker	.006	.293	.021	.067	—	—		
Card Sort	-.001	.230	.018	.110	.598	—		
PS	-.254	-.043	-.219	.016	.333	.421		
PVT	-.100	-.047	-.132	-.137	-.203	.079	.047	
Reaction Time	.026	.117	.052	.008	.047	.115	.245	-.092

Regressions of Anticipatory Mu ERSP with Behavior

To address our hypotheses on the relations between cognitive skills and neural indicators of anticipation, multiple regressions were conducted predicting scores on the Flanker, Card Sort, Receptive Language, and Processing Speed tasks from contralateral and ipsilateral mu ERSP. For both Flanker and Card Sort tasks, greater ipsilateral mu ERSP was associated with better EF task performance. Flanker performance was related to ipsilateral mu ERSP, $t(39) = 2.026$, $\beta = 0.531$, $p = 0.046$, but not with contralateral mu ERSP. Card Sort performance was also related with ipsilateral mu ERSP, $t(39) = 2.219$, $\beta = 0.576$, $p = 0.033$, but was not significantly associated with contralateral mu ERSP. Contralateral mu ERSP was related to Processing Speed, $t(39) = -2.418$, $\beta = -0.621$, $p = 0.021$, and marginally associated with ipsilateral mu ERSP. Receptive Language scores were not related to anticipatory mu ERSP, nor were there further significant relations detected among regressions of behavioral measures and contralateral and ipsilateral mu tactile responses. Further, variance accounted for in Card Sort and Flanker by anticipatory ipsilateral mu ERSP remained significant when the extent of mu ERSP during the response to the tactile stimulus was used as a covariate. Similarly, variance in Processing Speed accounted for by anticipatory contralateral mu ERSP remained significant when controlling for variance in post-stimulus mu ERSP.

Discussion

We were interested in whether individuals differed in their neural activity during anticipation of and in response to a tactile stimulus, and whether such differences had meaningful relations with behavior, including indicators of tactile attention relevant to the task and measures of other attentional and cognitive skills. Consistent with previous investigations, sensorimotor mu ERD was observed in the hemisphere contralateral to the expected location of a tactile stimulus, indicating that participants indeed directed their attention to the relevant hand during the anticipatory epoch (Haegens et al., 2011; Anderson & Ding, 2011; Van Ede et al., 2014). The magnitude of contralateral mu ERD was associated with how quickly and accurately participants compared the similarity of two stimuli on a separate task assessing processing speed. In turn, performance on the processing speed task was found to be related to how quickly participants pressed a foot pedal to indicate how many tactile stimuli they perceived in the EEG task. Individual differences in executive function were also associated with variation in the magnitude of anticipatory mu oscillations, but only at central electrodes sites ipsilateral to the cued hand.

Mu activity in the ipsilateral somatosensory cortices is relevant to the coordination of behavioral responses, with animal and human research indicating that somatosensory processing is distributed across bilateral primary sensory cortices (van Ede et al., 2014; Tamè et al., 2016). The dynamic adjustment of bilateral mu modulation to anticipated features of a tactile stimulus indicates that oscillations originating in the somatosensory cortices are acutely

sensitive to the load on tactile attention (Gomez-Ramirez et al., 2016; Haegens et al., 2012). In primates and humans, neural responses in bilateral somatosensory cortices may serve to simultaneously managing competing expectancies, reflecting allocation of tactile attention according to goals and bracing for potential distraction (Haegens et al., 2012; Tame et al., 2016)

In interpreting the relation of ipsilateral mu activity (rather than contralateral mu ERD) to executive function, we look to two possible explanations for the generation of alpha oscillations. Global alpha oscillations have been ascribed an inhibitory function (Klimesh et al., 1998; Mahzeri and Jensen, 2010). In past examinations of anticipation in the visual and auditory modalities, the ‘gating’ function of increases in alpha power has offered an account for the association between anticipatory ipsilateral alpha power with task-relevant stimulus detection rate and speed of behavioral responses across sensory modalities (Frey et al., 2015). Alternatively, and supported by previous investigations of anticipation in visual and tactile modalities (van Ede et al., 2014; Thut et al., 2006), the ipsilateral mu power over the relevant sensory cortices might increase or hover at baseline to suppress sampling of events at the unattended location (Shroeder and Latkos, 2009). These complementary accounts of anticipatory alpha oscillations may provide insight into how variability of neural responses contributes to individual differences in measures of cognitive ability.

The association of processing speed ability and reductions of mu power expands the existing literature focused on relations of mu modulation with task-specific reaction time. A previous investigation of children aged 6-8 found a significant association between executive function abilities and contralateral reductions of mu power (Weiss et al., 2018). There may be developmental differences in how attention is allocated in expectation of a tactile stimulus: speculatively, younger children may deliberately focus on monitoring sensation at the cued location while adults deploy effort into inhibiting sensation at the uncued bodily location. Such task-specific strategies could explain the observed patterns of lateralized mu oscillations and the difference in which hemisphere accounted for a greater share of variance in executive function skills. It is possible that attention to bodily sensations and variability in perceived boundaries between the body, peripersonal space and extrapersonal space contributed to these developmental and individual differences (Bremner & Spence, 2017), or that mu oscillations may have greater inter-individual variability than other alpha-range rhythms (Coll et al., 2017). Regardless, our findings indicate that neural responses during anticipation of a tactile stimulus index variation in stimulus processing speed, which could cascade into meaningful individual differences captured by measures of executive function (Willoughby et al., 2018).

Further studies can address the potential utility of mu oscillations as an indicator of individual differences in how attention is deployed to the body. Neural responses during anticipation of a stimulus may offer a potential source of

variation in behavioral responses and stimulus processing speed, which could cascade into individual differences in measures of executive function.

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