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The phase of prestimulus alpha oscillations affects tactile perception

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Ai L, Ro T. The phase of prestimulus alpha oscillations affects tactile perception. *J Neurophysiol* 111: 1300–1307, 2014. First published December 31, 2013; doi:10.1152/jn.00125.2013.—Previous studies have shown that neural oscillations in the 8- to 12-Hz range influence sensory perception. In the current study, we examined whether both the power and phase of these mu/alpha oscillations predict successful conscious tactile perception. Near-threshold tactile stimuli were applied to the left hand while electroencephalographic (EEG) activity was recorded over the contralateral right somatosensory cortex. We found a significant inverted U-shaped relationship between prestimulus mu/alpha power and detection rate, suggesting that there is an intermediate level of alpha power that is optimal for tactile perception. We also found a significant difference in phase angle concentration at stimulus onset that predicted whether the upcoming tactile stimulus was perceived or missed. As has been shown in the visual system, these findings suggest that these mu/alpha oscillations measured over somatosensory areas exert a strong inhibitory control on tactile perception and that pulsed inhibition by these oscillations shapes the state of brain activity necessary for conscious perception. They further suggest that these common phasic processing mechanisms across different sensory modalities and brain regions may reflect a common underlying encoding principle in perceptual processing that leads to momentary windows of perceptual awareness.

tactile; oscillation; perception; human

CONSCIOUS PERCEPTION OF IDENTICAL tactile stimuli can vary from one moment to the next. For example, we sometimes can clearly feel a mosquito landing on our skin that at other times goes undetected. This variability is most obvious for weak stimuli, which are only detected some of the time. The reason for this variability in perception has been poorly understood, but it offers a unique opportunity to better understand the neuronal mechanisms of sensory perception and awareness.

Recent studies have shown the importance of spontaneous brain oscillations for successful perception, especially those in the 8- to 12-Hz range (Bonnefond and Jensen 2012; Lundqvist et al. 2013; Sokoliuk and VanRullen 2013). These so-called mu or alpha oscillations have long been thought to represent a cortical idle state (Adrian and Matthews 1934; Pfurtscheller 1992). For example, several studies have shown that alpha amplitude decreases before the detection of an expected target, a phenomenon referred to as event-related desynchronization (Fukuda et al. 2010; Min et al. 2007; Pfurtscheller 1992, 2003).

More recently, however, several studies have shown that prestimulus alpha oscillations may play a more active and important role in subsequent stimulus perception. For example, visual target detection has been shown to decrease with increases in prestimulus alpha power (Hanslmayr et al. 2007;

Linkenkaer-Hansen et al. 2004; Mathewson et al. 2009; van Dijk et al. 2008) or has an inverted U-shaped relationship with prestimulus alpha power (Rajagovindan and Ding 2011). In tactile perception, there is also increasing evidence that these spontaneous alpha oscillations are likely to shape the brain state and are critical for stimulus processing. In electroencephalography (EEG) and magnetoencephalography (MEG) studies, detection of a weak tactile electrical stimulus shows an inverted U-shaped relationship between prestimulus alpha power and the probability of stimulus detection, suggesting an optimal level of prestimulus alpha power for tactile perception (Linkenkaer-Hansen et al. 2004; Zhang and Ding 2010).

In addition to the prestimulus alpha power, the phase of these alpha oscillations at stimulus onset is also important for subsequent target perception. Lindsley (1952) first proposed that the phase of alpha oscillations might reflect the brain state in a phasic matter. In support of this notion, we recently showed that visual perception is modulated by the alpha phase at the time of stimulus onset (Mathewson et al. 2009), an effect that has since been replicated (Busch et al. 2009; Dugué et al. 2011; Jansen and Brandt 1991; Mathewson et al. 2011). Likewise, an fMRI study showed that the blood oxygenation level-dependent (BOLD) response to a visual stimulus is dependent on the alpha phase at stimulus onset (Scheeringa et al. 2011). However, whether the phase of alpha oscillations influences perception in other sensory modalities, such as touch, remains unknown.

In the current study, we assessed whether a similar alpha power and phase relationship occurs for touch as with vision. We recorded neuronal activity over the right somatosensory cortex using EEG while near-threshold tactile stimuli were applied to the left hand. We investigated both the prestimulus power and phase at stimulus onset of spontaneous alpha oscillations and studied their role in tactile perception. Our results show power effects consistent with previous studies and a systematic effect of alpha phase on tactile perception.

METHODS

Subjects. Nine subjects (4 females; age range: 18–23; 6 right-handed) were recruited and participated after informed consent. All subjects had normal tactile perception and mobility, and they did not have any neurological disorders. The experiment was approved by the Institutional Review Board of the City College of the City University of New York.

Materials. Electrical stimuli were delivered via a pair of ring electrodes that were placed on the left middle finger. A 0.03-ms square-wave electrical pulse was delivered to the electrodes using a Grass-Astromed (West Warwick, RI) SD9 electrical stimulator. The intensity of the stimuli was set to each individual's sensory threshold level before the main experiment using the method of limits. Ascending and descending series of stimulus intensities were delivered until

subjects no longer felt the stimulus in the descending series or began to feel the stimulus in the ascending series. The threshold for each subject was defined as the average of the transition points from both series.

Experimental paradigm. Subjects sat in a wooden chair 57 cm from a 20-in. CRT monitor (Dell, Round Rock, TX) with their arms resting on a table in front of them. Figure 1 shows the time course of stimulus events for a typical trial. Each trial began with a blank interval for 250 ms, which was then followed by a fixation cross at the center of the monitor for 50 ms, the onset of which was coincident with the time of tactile stimulus onset. On half of the trials, a 0.03-ms near-threshold tactile stimulus was delivered at the onset of this 50-ms fixation cross interval, whereas no tactile stimulus was delivered on the other half of the trials. These two conditions were presented an equal number of times and in random order, but with the constraint that no more than three consecutive trials could be from the same condition. At 300 ms, a question mark was presented for 50 ms at the center of the monitor. Subjects then had to indicate whether or not they had perceived the tactile stimulus. Responses were made by the subjects using their right hand on a two-button mouse, with the left button corresponding to perceived and the right button corresponding to unperceived stimuli. No feedback regarding their accuracy was given to the subjects. To avoid anticipation and any potential phase-locking effects, random intertrial intervals were used such that each trial lasted between 2,300–2,380 ms. Each subject completed 10 blocks of 50 trials with a short break between every two blocks.

EEG and event-related potential recording and analysis. The EEG was recorded using a Grass-Astromed IP511 amplifier attached to three silver-silver chloride electrodes. The single-channel electrode was placed over the right somatosensory cortex, 1 cm posterior to C4 in the standard 10/20 system layout. The reference electrode was placed on the right mastoid, and the ground electrode was placed 1 cm posterior to P3 in the standard 10/20 system layout. We used the mastoid as the reference because it is easy to attach an electrode to it to yield low impedance measurements and it is a commonly used reference by other investigators. Electrode impedance was kept under 20 kΩ. The EEG was first filtered online with a 0.1- to 30-Hz bandpass filter and then sampled at 1,000 Hz. The continuous EEG data were epoched from −500 to 1,000 ms, time locked to the onset of the tactile stimulus.

The behavioral data were analyzed in terms of detection rate on stimulus-delivered trials. For the EEG data analyses, we used EEGLAB (http://sccn.ucsd.edu/eeglab/) and custom-written Matlab scripts. We extracted from the EEG data the alpha power and phase with a sinusoidal wavelet decomposition using a 0.5-cycle wavelet applied to overlapping Hanning-tapered time windows between −475 and −25 ms. The time windows were 50 ms in steps of 10 ms. Unlike fast Fourier transforms, which only extract frequency domain information, this wavelet analysis procedure extracts both temporal as well as frequency domain activity in the alpha band. The prestimulus and moving time windows were chosen such that the last time window was centered on −25 ms and there was no extension of this last time window into the poststimulus period. Power and phase at peak frequency in the mu/alpha-frequency range were extracted from the wavelet transform for each time point, trial, condition, and subject.
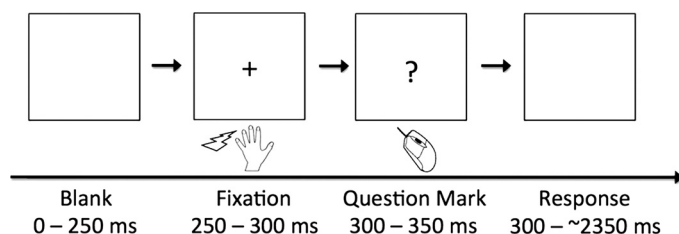
The average peak frequency for nine subjects was 9.8 Hz (SD = 0.48). The event-related potential (ERP) data were averaged over trials of the same conditions.

For alpha-power analyses, we calculated the prestimulus power from the time window between −250 and 0 ms. The average power at the peak frequency within the alpha-frequency range was calculated for each subject. Then, all trials were sorted based on the prestimulus power and divided into 10 bins with equal numbers of trials. The detection rate in each of these 10 bins was computed separately for each subject. For alpha-phase analyses, the phase was defined as the alpha phase at stimulus onset. The phase at stimulus onset of both perceived and unperceived trials was extracted separately and compared.

RESULTS

Behavior. The average detection rate for the 9 subjects on the stimulus-present trials was 51.9% (SD = 22.06%). This detection rate was not significantly different from the 50% threshold intensity level set at the start of the experiment and indicates that on average subjects perceived and missed the tactile stimulus an equal number of times (51.9 vs. 50%; Wilcoxon signed-rank test, $P > 0.05$). The average false alarm rate was 5.06% (SD = 4.65%), indicating that all subjects were able to easily differentiate target from nontarget trials. The mean reaction time for perceived trials (494.95 ms, SD = 76.61) was not significantly different from the mean reaction time for unperceived trials (495.53 ms, SD = 83.05, $t = 0.02$, $P = 0.986$).

Electrophysiology. The grand average somatosensory-evoked potentials (SEP) over the right primary somatosensory cortex for perceived and unperceived trials are shown in Fig. 2. The P1 ERP component (60–140 ms; $t = 3.131$, $P < 0.01$, two-tailed t-test) and N2 ERP component (180–250 ms; $t = 2.805$, $P < 0.05$, two-tailed t-test) were significantly larger on trials in which the stimulus was perceived than those in which it was not perceived. Figure 2 also shows that the phase of alpha was predictive of target detection. The phase of perceived trials coincides with the trough of the EEG activity at stimulus onset whereas the phase of unperceived trials coincides with the peak.

We next tested for the effect of alpha power and phase on detection rate. Trials were sorted according to the prestimulus alpha power level and then divided into 10 bins. Figure 3 shows the detection rate for these 10 alpha-power bins averaged across all subjects. An inverted U-shaped relationship between prestimulus alpha power and detection rate was measured, suggesting that there is an intermediate optimal level of alpha power for tactile perception. The solid curve in Fig. 3 was a highly significant quadratic fit ($R^2 = 0.60$, $P < 0.05$). This inverted U-shaped relationship between prestimulus alpha power and detection rate is consistent with previous studies (Linkenkaer-Hansen et al. 2004; Zhang and Ding 2010).

In the visual modality, using a metacontrast masking paradigm, we previously showed that the effect of phase was only reliable for high alpha-power trials (Mathewson et al. 2009). In our study, an inverted U-shaped relationship between prestimulus alpha power and detection rate was identified. Thus we analyzed the difference in detection rate as a function of the phase separately for the low, intermediate, and high prestimulus power trials. The detection rates of trials with positive (peak-half) and negative phases (trough-half) in one alpha

Fig. 1. Individual trial timeline with durations of each stimulus presentation. Note that the tactile stimuli were presented at 250 ms for 0.03 ms.

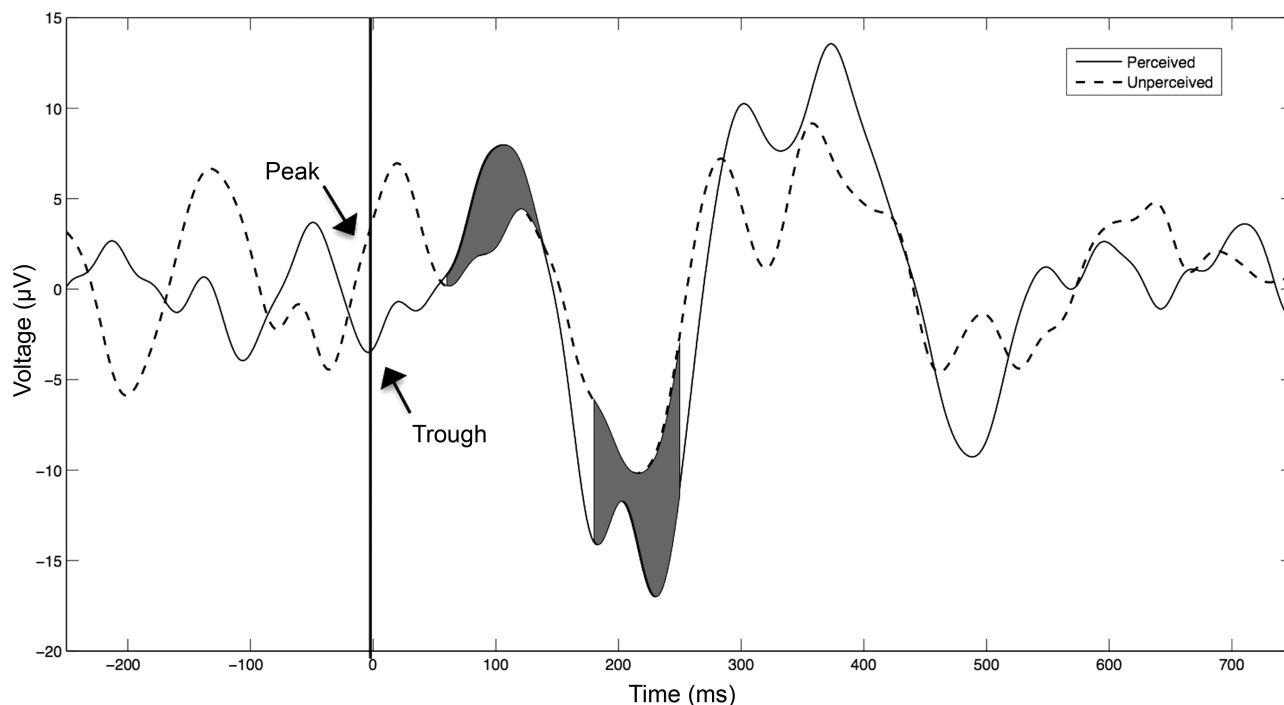| Blank	Fixation	Question Mark	Response
0 – 250 ms	250 – 300 ms	300 – 350 ms	300 – ~2350 ms

Fig. 2. Grand average somatosensory-evoked potentials (SEP) over right primary somatosensory cortex for perceived (solid) and unperceived (dotted) target-present trials. The P1 and N2 were significantly larger for perceived trials than for unperceived trials. The shaded regions indicate a significant difference between the 2 conditions. The vertical line at 0 ms represents the stimulus onset. The arrows indicate the phase for the undetected (dotted, peak) and detected trials (solid, trough) at stimulus onset.

cycle were computed for trials with low, intermediate, and high power. Figure 4*A* shows that there was no significant difference in detection rate between trials with positive and negative phases for the low prestimulus power trials (53.60 vs. 53.97, $P = 0.59$) and the intermediate prestimulus power trials (59.89 vs. 60.27, $P = 0.30$). For the high prestimulus power trials, however, the detection rate of trials with negative phase was significantly larger than those with positive phase (40.76 vs. 43.70, $P = 0.026$). The circular grand mean phase was then
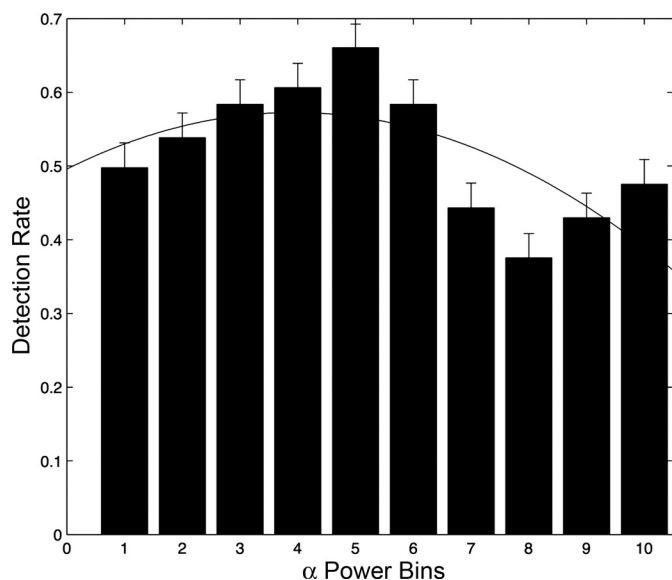
compared between perceived and unperceived trials for all alpha-power levels; there was a significant difference between perceived and unperceived trials (192.2 vs. 19.07°, $P < 0.001$).

To further show the different phase angles for perceived and unperceived conditions, a bootstrap procedure was used. In each iteration, 100 trials were randomly and independently selected from the perceived and unperceived trials and the circular grand phase mean was then computed separately for each selection of perceived and unperceived trials. Figure 4*B* shows the distribution of sample means for each condition after 10,000 iterations. A Rayleigh test shows that both distributions were not uniform ($P < 0.001$), indicating that there was a concentration of phases towards a specific angle. Direct comparison between those two distributions using Kuiper's test shows that they were significantly different ($P < 0.001$). Note that the distribution of unperceived trials was restricted to a narrow phase range (0–90°) while the distribution of perceived trials was more focused on 180–270°. This is consistent with the result that most unperceived trials were located in the phase range of 0–90°.

As Fig. 2 shows, the amplitude of P1 is an important indicator for tactile perception in that the perceived trials had larger P1 amplitudes than the P1 for unperceived trials. To further investigate the relationship between prestimulus alpha power and tactile perception, we tested the effect of alpha power on P1 amplitude. Trials were sorted by prestimulus alpha power and divided into 10 bins with equal numbers of trials. The P1 amplitude average was then calculated for each power bin. As with detection rates, Fig. 5*A* shows an inverted U-shaped function between P1 amplitude and prestimulus alpha power. The solid curve in Fig. 5 was a highly significant quadratic fit ($R^2 = 0.64$, $P = 0.02$). This result is consistent

Fig. 3. Relationship between prestimulus power and detection rate. The *x*-axis represents the alpha-prestimulus power bins, increasing in power from *left* to *right*. The black bars represent the detection rate for each power bin. The solid line represents the quadratic fit. The error bars are SE.
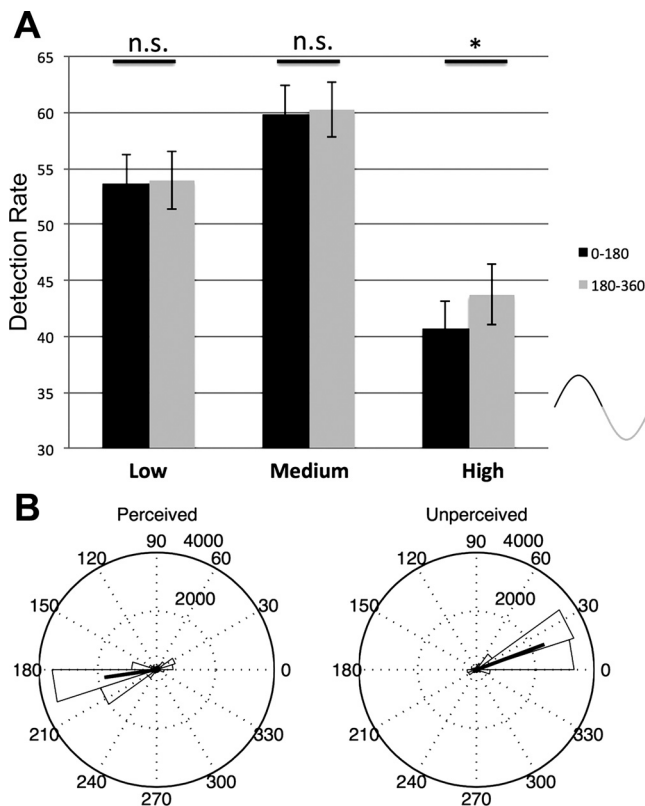
Fig. 4. *A*: detection rate for the 2 opposite phase bins in 1 alpha cycle for low, intermediate, and high prestimulus levels of alpha power. The black and gray bars represent the detection rate for the peak and the trough half of alpha cycle, respectively. The *right corner* shows 1 alpha cycle with peak half (black) and trough half (gray). The effect of phase was not reliable for the low and intermediate alpha-power trials. *B*: results of a bootstrap analysis of the grand mean phase of alpha oscillations for perceived and unperceived trials. One complete phase cycle was divided into 20 bins. The gray vector represents the number of iterations that fell into the given bin. The black line represents the mean phase vector (both direction and length).

with the relationship between prestimulus alpha power and detection rates, which further shows that there was an optimal power level for tactile perception. The N2 ERP component was also larger in perceived trials (−13.04 uV) than in unperceived trials (−9.81 uV; $t = 2.805$, $P < 0.05$, two-tailed t-test). Like the P1 component, Fig. 5*B* shows the N2 component has an inverted U-shaped relationship with alpha power ($R^2 = 0.76$, $P < 0.01$).

The difference in SEP amplitudes for perceived and unperceived trials may have partially depended on the alpha-phase difference at the time of the SEP components, as well as the alpha-phase difference at stimulus onset. If the phase of ongoing alpha influences the SEP components, the SEP amplitudes might be larger for trials with alpha in one phase than trials with alpha in the opposite phase at the time of the SEP components. To test for any influences of alpha phase on the amplitude of the SEP components, we conducted two analyses. First, a two-way ANOVA was conducted to examine the influence of ongoing alpha phase on the SEP components, with perception (perceived and unperceived) and phase angle (trough and peak) at the time of the SEP components as the two within-subject factors. For the P1 component, the main effect of perception was statistically significant ($F = 10.048$, $P = 0.002$), but the main effect of phase angle ($F = 0.940$, $P =$

0.332) and the perception by phase angle interaction ($F = 2.734$, $P = 0.098$) did not approach significance. For the N2 component, there was also a statistically significant main effect of perception ($F = 7.627$, $P = 0.006$), but the main effect of phase angle ($F = 1.775$, $P = 0.183$) and the perception by phase angle interaction ($F = 1.892$, $P = 0.169$) were not statistically reliable. These results, and in particular the lack of significant main effects of phase angle and two-way interactions, show that the SEP component differences were not exclusively due to alpha-phase differences at the time of those SEPs. However, the SEP component differences between perceived and unperceived trials might have also been biased by the prestimulus alpha phase. To address this potential influence on the later SEP components, in a second analysis we used the method proposed by Kruglikov and Schiff (2003) to subtract out the influences of prestimulus alpha phase on the SEPs. Specifically, we subtracted from the mean P1 and N2 amplitudes for perceived and unperceived trials the EEG activity
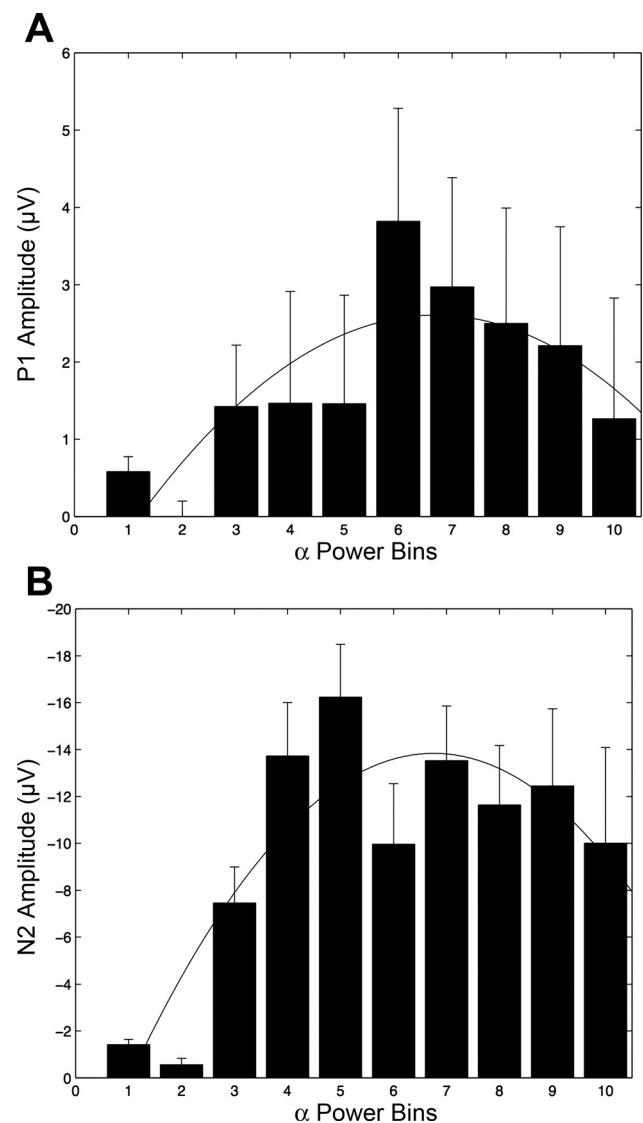

Fig. 5. *A*: relationship between prestimulus alpha power and P1 event-related potential (ERP) component amplitude. *B*: relationship between prestimulus alpha power and N2 ERP component amplitude. Black bars represent the averaged ERP component amplitude for each power bin. The solid line represents the quadratic fit. Error bars are SE.

recorded on trials with no tactile stimulus but with corresponding phase angles at the time of fixation offset. The P1 and N2 components were still significantly larger on perceived trials compared with unperceived trials even after the subtraction (P1: $P < 0.001$; N2: $P = 0.012$), indicating that these SEP differences were not confounded by differences in alpha-phase angle at the time of tactile stimulus onset.

To confirm that the relationship between detection rate and prestimulus alpha power was not a result of other factors, such as elapsed time in the experiment and intertrial interval, we also compared the detection rates and prestimulus alpha power with elapsed time in the experiment and intertrial interval. We divided all trials into 10 bins based on their elapsed time in the experiment and computed the detection rates and average prestimulus power for each bin. Neither the quadratic fit between prestimulus alpha power as a function of elapsed time in the experiment ($R^2 = 0.062$, $P = 0.32$) nor detection rate as a function of elapsed time ($R^2 = 0.09$, $P = 0.27$) was significant, indicating that elapsed time in the experiment does not share the same inverted U-shaped relationship with pre-stimulus alpha power and detection rates. Because different intertrial intervals (0, 20, 40, 60 and 80 ms) were used in this experiment, we also assessed whether alpha power might be related to these different intertrial intervals. Neither alpha power ($R^2 = 0.03$, $P = 0.63$) nor detection rates ($R^2 = 0.063$, $P = 0.18$) showed a significant inverted U-shaped relationship with intertrial interval. Thus our finding that the inverted U-shaped relationship between prestimulus alpha power and detection rates was not driven by any of these other factors.

DISCUSSION

We investigated the effect of spontaneous prestimulus alpha oscillations on the perception of near-threshold tactile stimuli. Two main results were found. First, and unlike with visual perception, there was a significant inverted U-shaped relationship between prestimulus alpha power and detection rate, which is consistent with some previous studies and suggests that there is an optimal level of alpha power for tactile perception. Second, and as with vision (Mathewson et al. 2009), there was a significant difference in phase angle concentration between perceived and unperceived trials. This phase dependency suggests a general processing principle across different sensory modalities such that when a stimulus presentation coincides with the peak of the alpha oscillation, subjects are less likely to detect the stimulus.

P1 amplitude and tactile perception. The results of this study show that the P1 and N2 ERP component is significantly higher for the perceived trials than the unperceived trials. We also found an inverted U-shaped relationship between P1 and N2 amplitude and prestimulus power. The P1 component for tactile stimuli, as in the visual modality, has been suggested to be related to attention to somatosensory stimulation (Kida et al. 2004; Rajagovindan and Ding 2011; Waberski et al. 2002) and has been suggested to be generated in secondary somatosensory cortex, SII (Frot and Mauguière 1999; Hämäläinen Kekoni et al. 1990; Hari and Forss 1999). MEG and EEG studies have shown that responses in SII increase with attention (Fujiwara et al. 2002; Hari and Forss 1999; Kida et al. 2004). Thus top-down attentional modulation may contribute to both the magnitude of P1 as well as the overall power of alpha.

Rajagovindan and Ding (2011) proposed a theoretical model in which the firing rate of neurons has a sigmoidal function and that the stimulus-evoked response follows the derivative of the sigmoidal function, which is an inverted U-shape function. In this model, in terms of the EEG, the P1 component is equivalent to the stimulus-evoked response, whereas prestimulus alpha power is equivalent to background neural activity (Rajagovindan and Ding 2011). The results from our study provide further evidence for this model by showing that the prestimulus alpha power levels and P1 component have an inverted U-shaped relationship.

Before data collection, we set the high- and low-pass filter settings on our amplifiers at 0.1 and 30 Hz. Although these filter settings are fairly standard, widely used, and sufficient for the purposes of this study, they limited our ability to accurately measure earlier and faster components of the SEP, such as the N20 component. Because we were most interested in the prestimulus alpha oscillations rather than these earlier and higher frequency ERP components, future studies will be necessary to measure the effects of alpha oscillations on these early ERP components.

Prestimulus power and tactile perception. In the present study, the prestimulus alpha power had a parabolic relationship with tactile detection rate, suggesting that there is an optimal alpha-power level for successful tactile perception. This parabolic relationship may best be explained by differences in excitability at different alpha-power levels. Previous studies have shown that spontaneous neural oscillations in the 5- to 20-Hz range can reflect cortical states that affect the integration of sensory inputs as a result of recurrent connectivity in the cerebral cortex (Destexhe 1999; McCormick et al. 2003; Shu et al. 2003). The generation of a burst of activity in a large number of pyramidal cells can lead to a state in which neurons are more responsive to stimuli, while the activation of inhibitory neurons can lead to a state in which neurons are less responsive.

Moderate depolarization, which brings the local neuron population close to firing threshold, can strongly influence the generation and timing of action potentials (Shu et al. 2003). This moderate excitation causes a remarkable increase in neuronal responsiveness to a stimulus, especially those of small amplitude. Generally speaking, when a weak exogenous stimulus is presented while moderate levels of spontaneous oscillations are ongoing, the probability of responsiveness is higher compared with those presented during weak spontaneous oscillations. Thus the absence or very low levels of spontaneous neural oscillations may fail to induce responsiveness to a weak stimulus.

In contrast, high levels of spontaneous activity may also fail to induce responsiveness to a weak stimulus by a blocking of external sensory stimulus processing (Castro-Alamancos 2009; Dehaene and Changeux 2005; Petersen et al. 2003). Higher levels of spontaneous neural oscillations may therefore result in *1*) a decrease in driving force by glutamatergic excitation and an increase in driving force by GABAergic inhibition (Petersen et al. 2003); *2*) more spontaneous action potentials, which could lead to short-term depression; and (*3*) activation of surrounding GABAergic interneurons, which results in more inhibition. Hence, there may be competition between sensory-evoked depolarization and spontaneous neural activity (De-

haene and Changeux 2005; Petersen et al. 2003), with either one being capable of preventing the other.

Our results showed an optimal intermediate level of alpha power, which provides support for this notion that there is an intermediate level of spontaneous oscillations that facilitates the perception of weak stimuli. Similar results demonstrating an intermediate level of alpha activity for successful weak tactile stimulus detection have been obtained by others with EEG and MEG.

However, the differences in alpha power, with a monotonic decrease in detection rates with increases in alpha power for vision but a parabolic detection rate function with increases in alpha power for touch, suggest that the visual and tactile system may be responding to alpha in slightly different ways. Because several studies have suggested that alpha is generated in the posterior parietal cortex (Romei et al. 2011; Thut et al. 2011; van Dijk et al. 2008), these differences suggest that alpha may be a general broadcast signal that is adapted and used locally in slightly different ways. The lack of the parabolic relationship between alpha-power level and detection rate in vision (Mathewson et al. 2009) may be also due to a higher signal-to-noise ratio level in the visual system compared with the somatosensory system, which may also be coding movement related activity. The mechanisms underlying these alpha-power differences on tactile and visual perception remain to be elucidated but may be due to different neuronal architectures being differentially responsive to the same types of signals.

Even in somatosensory perception alone, however, there are discrepancies in the literature regarding the relationship between alpha power and detection. For example, in contrast to our results and those of Zhang and Ding (2010) demonstrating a U-shaped relationship between prestimulus alpha power and somatosensory perception, Jones et al. (2010) and van Ede et al. (2012) showed that alpha power has a negative linear relationship with somatosensory perception. The exact reasons for these inconsistent results are unclear. However, although the results of Jones et al. (2010) did not show an inverted U-shaped relationship, they found that on trials with the lowest levels of alpha power, detection rates were lower compared with detection rates for trials with slightly higher alpha power. In the study of van Ede et al. (2012), subjects performed a somatosensory detection task in which the onset and spatial location of the stimuli were either auditorily cued or not. The negative linear relationship in those studies, instead of an inverse U-shaped relationship, might be a result of differential attentional modulation produced by the cues and spatial location of stimuli, which may have increased the overall levels of alpha compared with our study, in which the time and location of the tactile stimuli were always consistent. If such were the case, then those studies showing a linear relationship between alpha power levels and stimulus detection may only reflect the upper half of our inverted U-shaped function. Further studies are necessary to more systematically investigate these issues and discrepancies.

Phase and tactile perception. Separate analyses of the perceived and unperceived trials showed a significant difference in phase angle concentration. Phase angles for unperceived trials were mostly focused on one part of the cycle (0–90°), whereas those for perceived trials were not as focused and on a different part of the cycle (180–270°). These results suggest a strong link between alpha-phase angle at stimulus onset and conscious

target detection and further suggest that inhibition is not equal across the alpha cycle. Rather, the effects of alpha on perception appear to be very specific to certain parts of the cycle, generating a so-called "pulsed inhibition" (Klimesch et al. 2007; Mathewson et al. 2011; Mazaheri and Jensen 2010). According to this pulsed inhibition account, alpha activity produces bouts of inhibition that are repeated every 100 ms. These pulses of inhibition act to reduce neural firing and cognitive perception at specific peak phases of alpha. When the stimulus coincides with the peak phases of alpha oscillations, the likelihood to detect the stimulus is low. This pulsed inhibition is consistent with our phase result that the detection was low in one part of the cycle (0–90°).

Mazaheri and Jensen (2010) recently proposed an account of alpha oscillations that is different but not inconsistent with pulsed inhibition. According to their "amplitude asymmetry" theory, the peaks of ongoing oscillations may be modulated more than the troughs, which results in an asymmetric effect of alpha oscillations on perception (Mazaheri and Jensen 2010). It is this asymmetry between the magnitudes of peaks and troughs, which likely correspond to forward and backward pyramidal cell currents, that induces the amplitude asymmetry of ongoing oscillations. Similarly, Klimesch (2007) proposed an inhibition-timing mechanism that suggests that alpha reflects the inhibition that controls the exact timing of oscillations and helps to establish a highly selective activation pattern. Support for these accounts of alpha comes from a recent study that used intracranial recordings over sensorimotor cortex in a monkey performing a somatosensory discrimination task (Haegens et al. 2011). Haegens et al. showed that spikes and alpha oscillations were phase synchronized, suggesting that spiking activity was more likely to occur at the trough than at the peak.

Our results show that the effects of prestimulus alpha power and phase on tactile perception are not separate. When prestimulus alpha power is low and intermediate, there is no difference in detection rates for stimuli that are presented during the peaks or troughs. When prestimulus alpha power is high and the stimulus is presented during an alpha trough, detection rates are significantly higher than those presented during the peak. A similar trend was measured for low alpha-power levels, but this effect was only marginally significant. However, when the prestimulus power is intermediate, the ability to detect a weak stimulus is high, which overrides the difference in detection rates that are influenced by stimuli being presented during the peaks and troughs of alpha oscillations. These phase-specific results are consistent with our previous study on visual perception (Mathewson et al. 2009), and they suggest that the phase of an alpha cycle may influence perception in similar ways regardless of sensory modality.

Top-down modulation and alpha. Our study shows that the alpha oscillations in somatosensory cortex before stimulus onset play an important role in stimulus processing and perception. Top-down modulation of alpha activity may also be critical for perception, which may be a hallmark of attention (Fan et al. 2007; Worden et al. 2000). Indeed, a more recent study showed that the power of alpha oscillations can be modulated by top-down attention and can consequently influence near-threshold tactile stimuli (Zhang and Ding 2010). Another study, which manipulated attention by cueing the hand or the foot, demonstrated decreased somatosensory perception

with increases in alpha power following a cue (Jones et al. 2010). Applying transcranial magnetic stimulation over the intraparietal sulcus or the frontal eye field, both of which have been suggested to control the allocation of spatial attention, disrupted the anticipatory (prestimulus) alpha desynchronization and its spatially selective topography in parieto-occipital cortex (Capotosto et al. 2009). These results further suggest that alpha activity may be modulated by top-down attention and incorporated into local sensory and neuronal processing in slightly different ways.

The occipito-parietal region has been suggested to be the source of alpha-rhythm generation (Romei et al. 2011; Thut et al. 2011; van Dijk et al. 2008). However, given the low spatial resolution of EEG and because we did not use a high-density electrode montage for source localization, we cannot estimate the source of the alpha oscillations that we recorded using our right somatosensory area electrode. However, since other studies (e.g., Haegens et al. 2011) have shown that these more posterior alpha oscillations can affect performance in a somatosensory attentional task, and also because we used visual stimuli, we assessed whether our data may have been influenced by visual cortex activity. To test the potential influence of visual cortex activity on our parietal electrode recordings, we analyzed the EEG data evoked by the visual question mark. There were no significant differences between perceived and unperceived trails for both the P1 ($P = 0.77$) and N2 ($P = 0.60$) components when time locked to the question mark. These results suggests that the P1 and N2 time locked to the tactile stimulus onset were not significantly influenced or were at best minimally affected by the visual fixation cross.

Conclusion. This study showed a systematic influence of prestimulus alpha oscillations on subsequent tactile perception. In addition to demonstrating an optimal prestimulus power for tactile perception, we show that subjects are less likely to detect targets when their onset coincides with the peak of an alpha oscillation. Our findings suggest that spontaneous alpha oscillations in somatosensory areas exert a strong inhibitory control on tactile perception and that pulsed inhibition by alpha oscillations shapes the state of brain activity necessary for conscious perception.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: L.A. performed experiments; L.A. analyzed data; L.A. and T.R. interpreted results of experiments; L.A. prepared figures; L.A. drafted manuscript; L.A. and T.R. edited and revised manuscript; L.A. and T.R. approved final version of manuscript; T.R. conception and design of research.

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