

Prestimulus Cortical Activity is Correlated with Speed of Visuomotor Processing

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Abstract

■ Response time (RT) is an important behavioral measure of the overall efficacy of sensorimotor processing and is known to vary significantly from trial to trial. Past work on how stimulus evoked cortical responses contribute to RT variability has helped delineate the stages of neuronal information processing. Much less is known about how the state of the brain immediately preceding the stimulus onset (prestimulus) affects RT. We addressed this problem by analyzing data from three macaque monkeys trained to perform a visuomotor pattern discrimination task. Local field potentials were recorded from up to 16 bipolar surface-to-depth electrodes widely distributed over one cerebral hemisphere in each monkey. The degree of linear correlation between RT and prestimulus spectral power was determined over a wide range of frequencies. In the prefrontal cortex, prestimulus power in the beta range (14–

30 Hz) was *negatively* correlated with RT in two monkeys, suggesting a possible role of activity in this frequency range in the mediation of top-down control of visuomotor processing. In the sensorimotor cortex, prestimulus power in the beta range was *positively* correlated with RT in two monkeys, consistent with the hypothesis that oscillations in this range support the maintenance of steady-state motor output. In visual occipital and temporal lobe areas, prestimulus power in the alpha/low beta range (8–20 Hz) showed *positive* correlations with RT in three monkeys, possibly reflecting a spatially specific disengagement of visual anticipatory attention. Through measurement of prestimulus spectral coherence, it was further determined that sites showing similar patterns of correlation between spectral power and RT were also linked together in synchronized networks. ■

INTRODUCTION

Oscillatory activity is ubiquitous in the nervous system. In many mammalian species, including humans and non-human primates, characteristic rhythms have been associated with distinct neural systems and their interactions (Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007; Senkowski et al., 2007; Buzsaki, 2006). Large oscillations of the local field potential (LFP) in the 4- to 8-Hz theta frequency range, for example, are characteristic of the rodent hippocampus. Another well-known example is prominent oscillations in the 8- to 14-Hz alpha range that are commonly present in the spontaneous activity of the human occipital cortex during eyes-closed rest (Shaw, 2003). Despite many years of extensive investigation, the precise roles these neural oscillations play in cognition remain poorly understood. Progress has been made, however, by studies that examine how oscillatory activity immediately preceding the onset of a stimulus affects subsequent stimulus processing (Haig & Gordon, 1998; Brandt, Jansen, & Carbonari, 1991) and behavior (Senkowski, Molholm, Gomez-Ramirez, & Foxe, 2006; Weissman, Roberts, Visscher, & Woldorff, 2006;

Womelsdorf, Fries, Mitra, & Desimone, 2006; Gonzalez Andino, Michel, Thut, Landis, & Grave de Peralta, 2005; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Serrien, Fisher, & Brown, 2003; Winterer et al., 1999). Liang, Bressler, Ding, Truccolo, and Nakamura (2002) found that the magnitude and coherence of prestimulus beta oscillations (14 to 30 Hz) in the prefrontal cortex of a macaque monkey were negatively correlated with response time (RT). Silberstein, Song, Nunez, and Park (2004) showed that the level of prestimulus synchronization between prefrontal, frontal, and central human electroencephalogram (EEG) recordings, as assessed by partial coherence, was also negatively correlated with RT. If we consider that trial-to-trial RT variability reflects spontaneous fluctuations of expectancy and attention (with a greater level of anticipatory attention leading to shorter RTs), then these results are consistent with recent thinking that ongoing cortical activity mediates important neural functions such as attention, anticipation, and motor preparation (Engel, Fries, & Singer, 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Brunia, 1999).

Most previous reports of prestimulus activity have been limited in one or more key aspects. First, studies based on the human scalp EEG or the magnetoencephalography can only poorly indicate the locations of the underlying

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neural generators to be identified. This lack of spatial resolution adversely impacts the ability to attribute functions to specific brain systems. Second, the LFP recorded from the brains of animals, although a much more localized signal, is typically sampled from only one brain area at a time. Without access to simultaneous data from multiple brain areas, it is not possible to evaluate whether different brain areas work together to form coordinated networks. Third, data analysis has been often confined to either the time domain or a single predefined frequency band. This prevents the identification of potentially important functions associated with oscillatory activity at frequencies of hitherto unknown relevance. In the present study, we overcame these problems by analyzing simultaneous LFPs from up to 16 cortical sites distributed broadly over one hemisphere in macaque monkeys trained to perform a visuomotor task. The relation between prestimulus LFP activity and the RT was examined across a broad range of frequencies. In addition, spectral coherence analysis was applied to study the formation of synchronized oscillatory networks.

METHODS

Task and Data Acquisition

Three macaque monkeys (TI, LU, and GE) were trained to perform a visual–motor pattern discrimination task at the Laboratory of Neuropsychology of the National Institute of Mental Health (NIMH) (Ledberg, Bressler, Ding, Coppola, & Nakamura, 2007; Bressler, Coppola, & Nakamura, 1993). Animal care was in accordance with the institutional guidelines at the time. The monkey initiated each trial by depressing and holding a lever with the preferred hand. Visual stimuli appeared following a random delay after the lever depression. Each stimulus consisted of four dots arranged as a (left- or right-slanted) line or diamond on a display screen. Monkeys responded (go condition) to one visual pattern type (line or diamond) and withheld the response (no-go condition) to the other. On go trials, the monkey received a water reward if the response occurred within 500 msec. On no-go trials, the lever was depressed for 500 msec poststimulus and released thereafter. RT was defined as the time between stimulus onset and lever release. The experiment was organized in recording sessions, each consisting of approximately 700–1000 trials. Go and no-go trials occurred randomly with equal probability in each session.

LFPs were simultaneously recorded during task performance from multiple surface-to-depth bipolar Teflon-coated platinum electrodes, chronically implanted in the cerebral hemisphere contralateral to the monkey's preferred hand. Data collection began about 90 msec prior to stimulus onset and continued until 500 msec poststimulus. Data from up to 16 channels (cortical sites) were analog filtered (−6 dB at 1 and 100 Hz, 6 dB per

octave falloff) and digitized at 200 samples/sec. The approximate electrode placements as marked visually during surgery are shown in Figure 1. Electrode locations are designated by arbitrary letters, and also by anatomical or functional names. The prestimulus period was defined to be from −90 to 35 msec, which was 125 msec in duration. Previous work (Ledberg et al., 2007) had shown that the earliest stimulus evoked response occurred

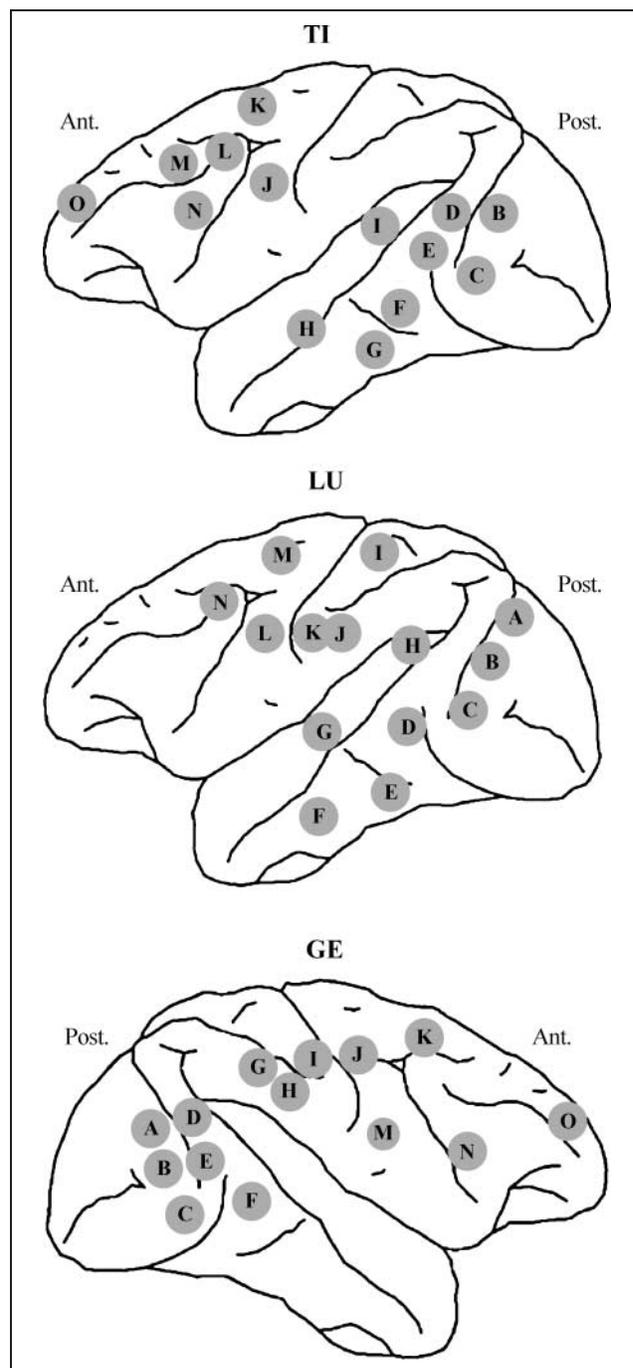


Figure 1. Approximate placement of electrodes in the three macaque monkeys used in this study, shown on schematic lateral cortical drawings. Electrode locations are designated by arbitrary uppercase letters, and also by anatomical or functional names.

around 50 msec. This observation underlined the choice of 35 msec as the end point of the prestimulus period.

Data Preprocessing

For each monkey, the data analyzed came from several recording sessions. Within each session, the RT showed sizeable variability on the order of 150 msec or more. As this study was concerned with the relationship between prestimulus neural activity and RT, only trials with correct go responses were used. The selected LFP data were preprocessed by the following procedure. First, the distribution of RT for each monkey was truncated by removing the trials with RT values less than 200 msec (random responses) or greater than 450 msec (delayed responses). Second, because the number of usable go trials in a single session was not sufficient for the subsequent subensemble autoregressive spectral analysis, it was necessary to combine trials across sessions in each monkey. However, even in the same monkey, significant session-to-session variability in the averaged event-related (local field) potential (ERP), power spectra, and RT distribution was observed. To minimize the adverse effects of such variability on the analysis, visual inspection of the wave shapes of the averaged ERP and prestimulus power spectra, as well as *t*-test evaluations of RT distributions, was employed to select sessions that had similar statistical characteristics. After rejecting outliers and bad channels, approximately 1000–1500 go trials from 14 cortical sites in each monkey were available for further analysis.

LFP Spectral Power Estimation from Multivariate Autoregressive Modeling

Correct go trials were rank-ordered by RT and then sorted into groups of 100 trials, starting with the fastest RT group and proceeding to the slowest, each group having a 50-trial overlap with the previous one. The RT values within each group were averaged to yield the group mean RT. For LFP recordings, the ensemble mean LFP value over trials at each site in a given group, at each time point during the prestimulus period, was subtracted from the single-trial LFP at the corresponding time point of the individual prestimulus time series to ensure that the time series could be treated as coming from a zero-mean (in the sense of an ensemble) stochastic process, which is essential for the autoregressive spectral analysis that was used (Ding, Bressler, Yang, & Liang, 2000). Power spectra of all channels for each group were estimated from the LFPs in the 125-msec (25 data points) prestimulus time window by the parametric method of MultiVariate AutoRegressive (MVAR) modeling (Ding et al., 2000). A model order of 8 was employed on the basis of the Akaike Information Criterion (AIC) (Akaike, 1974). The range of frequencies analyzed was from 8 to 40 Hz in 1-Hz steps. The value

of 8 Hz was determined as the lowest frequency having at least one cycle in the 125-msec prestimulus time window. This choice prevented us from examining neural activities in the theta (4 to 8 Hz) and delta (1 to 4 Hz) range which, as past work has shown (Lakatos et al., 2005), may modulate higher frequency activities considered in this work. The value of 40 Hz as the highest frequency was selected based on the observation that spectral power decreased rapidly with increasing frequency beyond 40 Hz, raising concern that power above 40 Hz might be more vulnerable to adverse influences of measurement noise.

Correlation of Spectral Power and RT

For each site and each integer frequency from 8 to 40 Hz, the group power was plotted against the group mean RT, and Spearman's rank correlation coefficient (ρ) between power and mean RT was computed and its statistical significance was tested. The number of sites times the number of frequencies give rise to a multiple comparison situation. If no correction is being made, many false positives may result. The traditional Bonferroni correction, given the large number of comparisons, leads to prohibitively small *p* values for each comparison, and may not be appropriate here because different comparisons may not be independent. Our solution is to use a permutation procedure (Nichols & Holmes, 2001) to create a null hypothesis condition which incorporates all the comparisons. The group indices for the group mean RTs were randomly permuted to generate a synthetic dataset where the correlation between spectral power and RT occurs at chance level. Spearman's rank correlation coefficients at each integer frequency (i.e., 8, 9, . . . , 40 Hz) and for each channel were then calculated for this synthetic dataset. The largest correlation coefficient, regardless of frequency and channel label, was selected. This random permutation procedure was repeated 500 times and a null-hypothesis distribution using the 500 maximum Spearman's rank correlation coefficients was created for each monkey. From this distribution, we derived the threshold corresponding to a given *p* value (e.g., .05). The original correlation values that were greater than this threshold were judged to be significant at, for instance, the $p < .05$ level.

Spectral Coherence and Assessment of Synchronized Networks

Spectral coherence during the prestimulus period was calculated for all pairwise combinations of the 14 recording sites in each monkey using the same MVAR spectral analysis method used to compute spectral power. Spectral coherence is a normalized measure of interdependence and covariation between the LFPs at two sites as a function of frequency. A peak in the coherence spectrum is indicative of phase synchronization

of two oscillatory processes within a narrow frequency band. Pairs of recording sites having coherence peaks within the frequency range of 8–40 Hz were identified, and those without spectral coherence peaks were excluded. Peak coherence values were sorted by magnitude, and maps were constructed with lines drawn between site pairs whose peak coherence fell within the top 10% and 10% to 20% of the sorted peak values. The statistical significance of these peak coherence values was determined by a random permutation procedure similar to the one above and is described in detail in Brovelli et al. (2004). The maps were investigated for the existence of functional networks of sites interconnected by synchronized oscillations. As shown in Figure 6, solid lines were used to connect pairs in the top 10% and dotted lines for the pairs in the 10% to 20%, after the coherence peak values underlying these lines were found to be significant. Each network obtained in this way was further characterized by calculating the mean frequency and magnitude of its coherence peaks and their standard deviations. The overall strength of synchronized activity within a network was assessed as the mean coherence magnitude, averaged over the site pairs of the network, within a 10-Hz-wide frequency band centered on the

mean peak frequency. The same methodology, based on the correlation between group mean coherence and group mean RT over RT-sorted trial subensembles, was used to study the possible role of synchronized networks in sensorimotor processing.

RESULTS

We first examined the relation between spectral power and RT. The objective was to determine whether spectral power was significantly correlated with RT, and if so, at which frequencies this occurred. For a given recording site, the correlation coefficient between spectral power and RT was found to be either negative or positive depending on frequency. Likewise, for a given frequency, the correlation coefficient was found to be either negative or positive depending on recording site. Figure 2 illustrates this point by showing two examples from monkey TI. On the top row are the power spectra from a prefrontal site (M) and a striate site (B). The scatterplots between group power at 16 Hz and group mean RT are shown on the bottom row. It can be seen that, whereas the 16-Hz power at site M has a significant

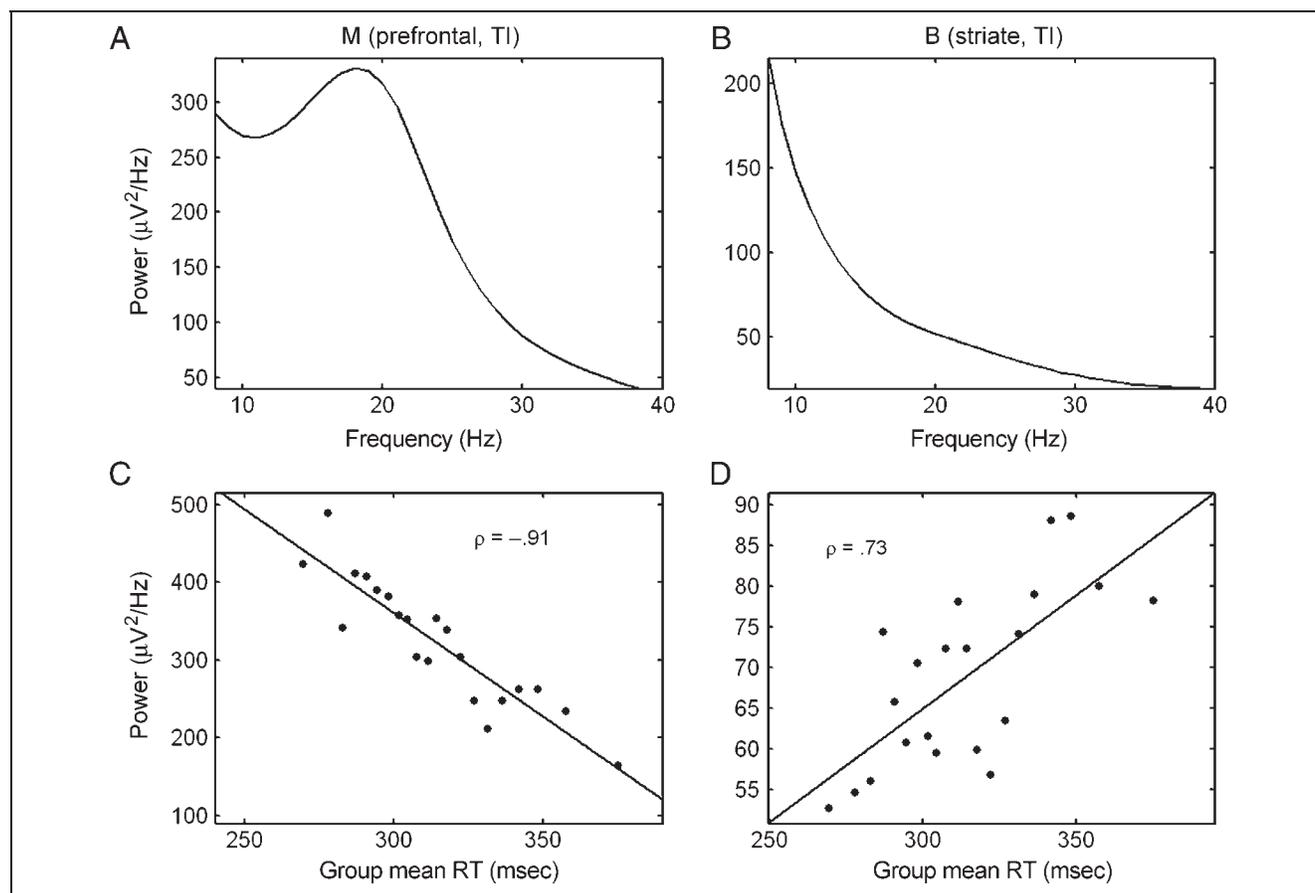


Figure 2. Power spectra and scatterplots for two recording sites (TI). (Top) Power spectra for a prefrontal site (M) and a visual site (B) during the prestimulus time period. (Bottom) Scatterplots showing strong positive or negative correlations between group spectral power and mean RT at 16 Hz. Linear least-square fits to the data are superimposed.

negative correlation ($\rho = -.91, p < .0001$) with RT, at site B it has a significant positive correlation ($\rho = .73, p < .0001$). Here the p values were computed on a single-site and single-frequency basis using the random permutation procedure described in the Methods section.

The results of the correlation analysis for all frequencies and sites in all three monkeys are summarized in Figures 3, 4, and 5. Frequency is displayed on the horizontal axis, and Spearman's rank correlation on the vertical. Shaded regions indicate frequencies having spectral power that was significantly correlated with RT at $p < .05$. These plots reveal four primary observations. First, spectral power in the prefrontal cortex was negatively correlated with RT in two monkeys (TI and GE). Specifically, in TI (Figure 3), three sites (L, M, and O) among the five prefrontal sites had significant negative correlations ($\rho < -.70, p < .05$) in the frequency ranges 16–25 Hz, 12–24 Hz, and 17–32 Hz, respectively (Figure 3). The correlations in the frequency range 20–30 Hz were also negative at prefrontal site N in TI, although these correlations did not reach significance (Figure 3). The prefrontal site O in GE also had significant negative correlations ($\rho < -.62, p < .05$) in the frequency range of 15–18 Hz (Figure 5). Monkey LU had only one pre-

frontal site (N), for which the correlation with RT was not significant (Figure 4).

The second observation concerns sites in the sensorimotor cortex, from which LFPs were recorded in all three monkeys. Two of three sites in LU (K and L) had significant positive correlations ($\rho > .61, p < .05$) over a broad frequency range from 8 to 33 Hz (Figure 4). The remaining site (M) had positive correlations over much of the same frequency range, although they did not reach significance (Figure 4). Power at the two sites in this region in TI (J and K) was not significantly correlated with RT at any frequency (Figure 3). Two (J and K) of four sensorimotor sites in GE showed significant positive correlations ($\rho > .62, p < .05$) at selected frequencies, 27–28 Hz for site J and 8–15 Hz for site K, in the range of 8–30 Hz (Figure 5).

Third, the findings in the visual cortex (i.e., at striate, prestriate, and inferior-temporal sites) were consistent across all three monkeys. As shown in Figure 3, power at all six visual cortical sites (B, C, D, E, F, and G) in TI had significant positive correlations ($\rho > .65, p < .05$) with RT, primarily in the range of 8–20 Hz. Three of the six visual cortical sites (A, B, and D) in LU had significant ($\rho > .61, p < .05$) positive correlations, mostly in the

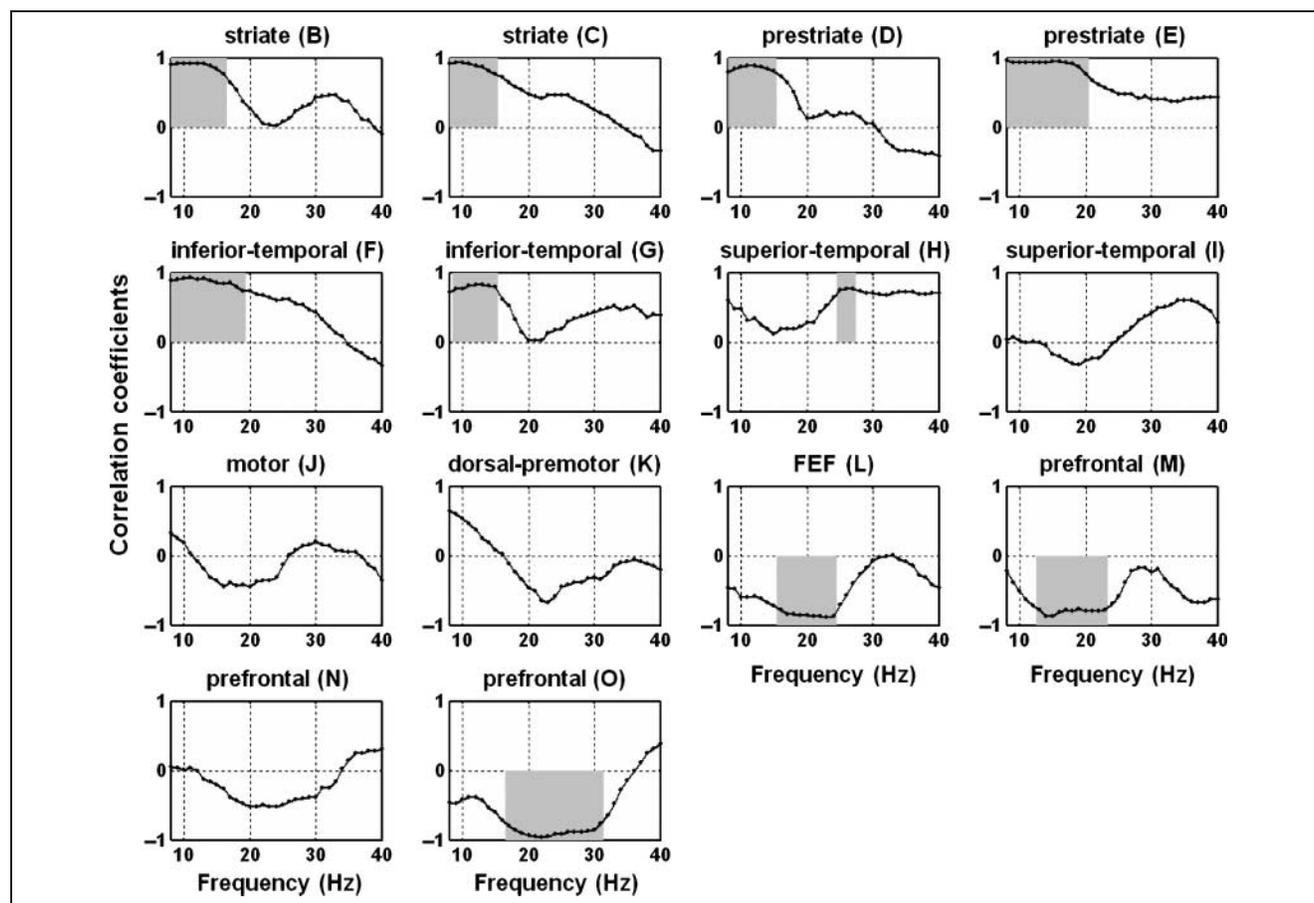


Figure 3. Correlation coefficients at each frequency in the range of 8 to 40 Hz between group prestimulus spectral power and mean RT for monkey TI. (Shaded area signifies correlations that are significant at $p < .05$.)

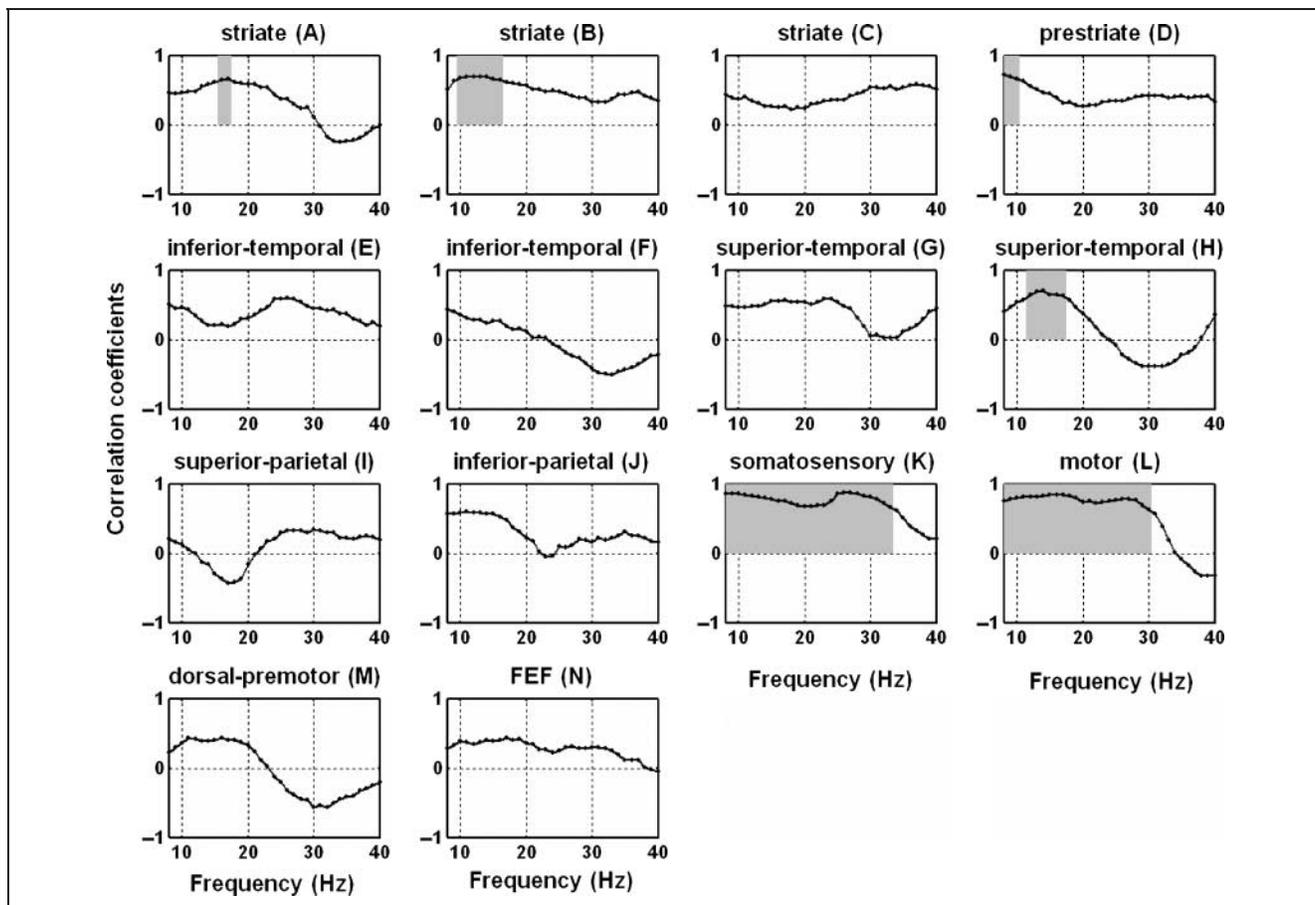


Figure 4. Correlation coefficients at each frequency in the range of 8 to 40 Hz between group prestimulus spectral power and mean RT for monkey LU. (Shaded area signifies correlations that are significant at $p < .05$.)

range of 8–18 Hz (Figure 4). Three (B, E, and F) of six visual cortical sites in GE had significant positive correlations ($\rho > .65$, $p < .05$), and this was in the frequency band of 8–18 Hz (Figure 5).

Fourth, one of the two superior–temporal sites (H) in TI showed significant positive correlation ($\rho > .73$, $p < .05$) at 25–26 Hz. Also, one of the two superior–temporal sites (H) in LU had significant positive correlations in the range of 12–16 Hz ($\rho > .62$, $p < .05$). Monkey GE had no superior–temporal recording sites.

The above findings indicated that recording sites located in the same region of the cortex tended to have significant LFP power–RT correlations at similar frequencies. This observation raised the possibility that this similarity was due to the cooperation of such sites within a synchronized functional network. We examined this issue by computing spectral coherence for all pairwise combinations of recording sites. A peak in the coherence spectrum in the frequency range from 8 to 40 Hz was taken as evidence for the existence of oscillatory communication between the pair of sites. The site pairs were sorted according to their maximum coherence peak values. Those site pairs having peak coherence values within the top 10% and 10–20% of the sorted

distribution, all of which were found to be significantly above zero at $p < .05$ level, were shown connected by lines in maps separately for monkeys TI, LU, and GE in Figure 6.

For monkey TI, 84 site pairs were found to have coherence peaks within the frequency range of 8–40 Hz. The top 10% of coherence peak values (Figure 6, top left) corresponded to nine site pairs, six of which linked six sites in the frontal lobe (J, K, L, M, N, and O), and three of which linked four visual cortical sites (D, E, F, and G). For the frontal network, the mean peak coherence frequency was 19.7 ± 2.6 Hz, and the mean peak coherence magnitude was 0.28 ± 0.14 . For the visual network, the mean peak coherence frequency was 13.3 ± 1.5 Hz, and the mean peak coherence magnitude was 0.27 ± 0.15 . Similarly, two distinct networks were found in monkey LU based on the top 10% of coherence peak values (Figure 6, middle left). The first was a sensorimotor network, involving sites G, I, J, K, and L, with a mean peak coherence frequency of 21.8 ± 2.9 Hz and a mean peak coherence magnitude of 0.18 ± 0.1 . The second was a visual network, involving sites B, C, D, and E, with a mean peak coherence frequency of 14.3 ± 3.1 Hz and a mean peak coherence magnitude of $0.14 \pm$

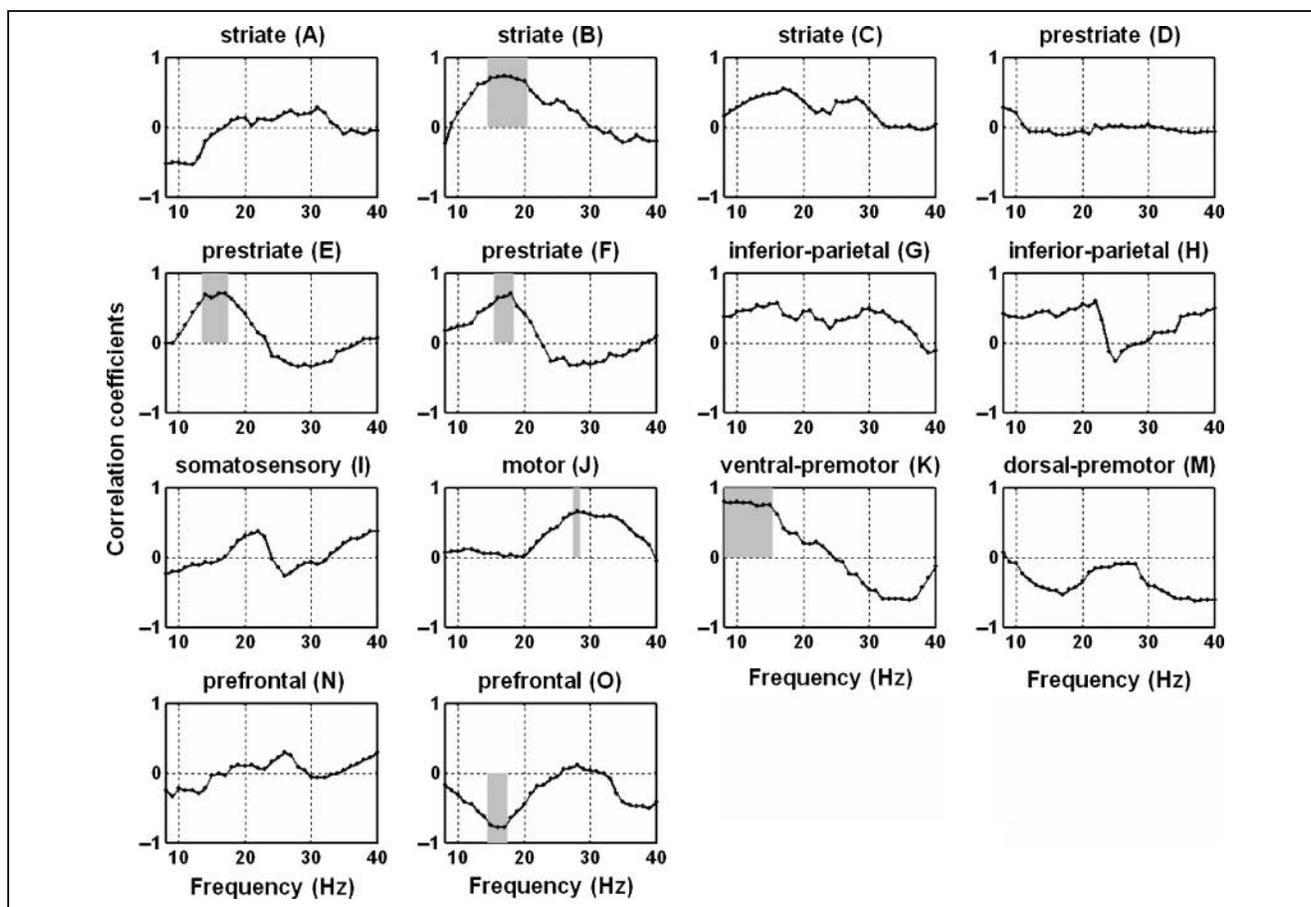


Figure 5. Correlation coefficients at each frequency in the range of 8 to 40 Hz between group prestimulus spectral power and mean RT for monkey GE. (Shaded area signifies correlations that are significant at $p < .05$.)

0.04. Finally, two distinct networks were also found in monkey GE based on the top 10% of coherence peak values (Figure 6, lower left). A sensorimotor network, involving sites G, H, I, and J, had a mean peak coherence frequency of 22 ± 0 Hz and a mean peak coherence magnitude of 0.31 ± 0.16 . A visual network, involving sites A, D, E, and F, had a mean peak coherence frequency of 16.7 ± 1.2 Hz and a mean peak coherence magnitude of 0.16 ± 0.03 . A comparison between these coherence results and Figures 3, 4, and 5 revealed that, except for the sensorimotor network in GE, the mean synchronization frequency of each network fell within the range of frequencies for which the network sites exhibited significant LFP power–RT correlation.

The above analysis suggested the existence of synchronized oscillatory networks that were relatively localized. The question of whether the degree of synchronization in these local networks, as assessed by spectral coherence, was significantly correlated with RT was next examined. Mean spectral coherence magnitude (in a 10-Hz-wide frequency band centered on the mean peak frequency) was averaged over site pairs having the top 10% of peak coherence magnitudes, and then compared to mean RT across RT-sorted groups. Figure 7 shows the relation

between group mean band coherence and mean RT as scatterplots over groups for monkey TI (A and B), LU (C and D), and GE (E and F). For monkey TI, coherence within the frontal network had a significant negative correlation with RT ($\rho = -.62, p < .005$), and the coherence within the visual network had a highly significant positive correlation with RT ($\rho = .90, p < .0001$). This finding may reflect the spectral power correlation results observed for some of the sites participating in these networks in monkey TI. In monkeys LU and GE, however, the correlations were found to be not significant.

In addition to the local networks discussed above, consisting of pairs in the top 10% of peak coherence values, Figure 6 also shows network links corresponding to the top 20% of peak coherence values (right column). Whereas the top 10% yielded networks with well-defined synchronization frequencies which lie in the functional frequency bands of the participating sites, and relatively localized to brain regions with well-defined functional and anatomical properties, connectivity patterns drawn according to the 10% to 20% (dotted lines) of peak coherence values were much more widely distributed. For example, the linked site pairs within the second decile of all three monkeys spanned multiple cortical regions and

Figure 6. Site pairs having the top 10% (left column) and 20% (right column) of peak coherence magnitudes in the range of 8 to 40 Hz are indicated by connecting lines (solid lines for pairs in the higher decile and dotted lines for pairs in the lower decile). The rows, from top to bottom, represent monkeys TI, LU, and GE, respectively.

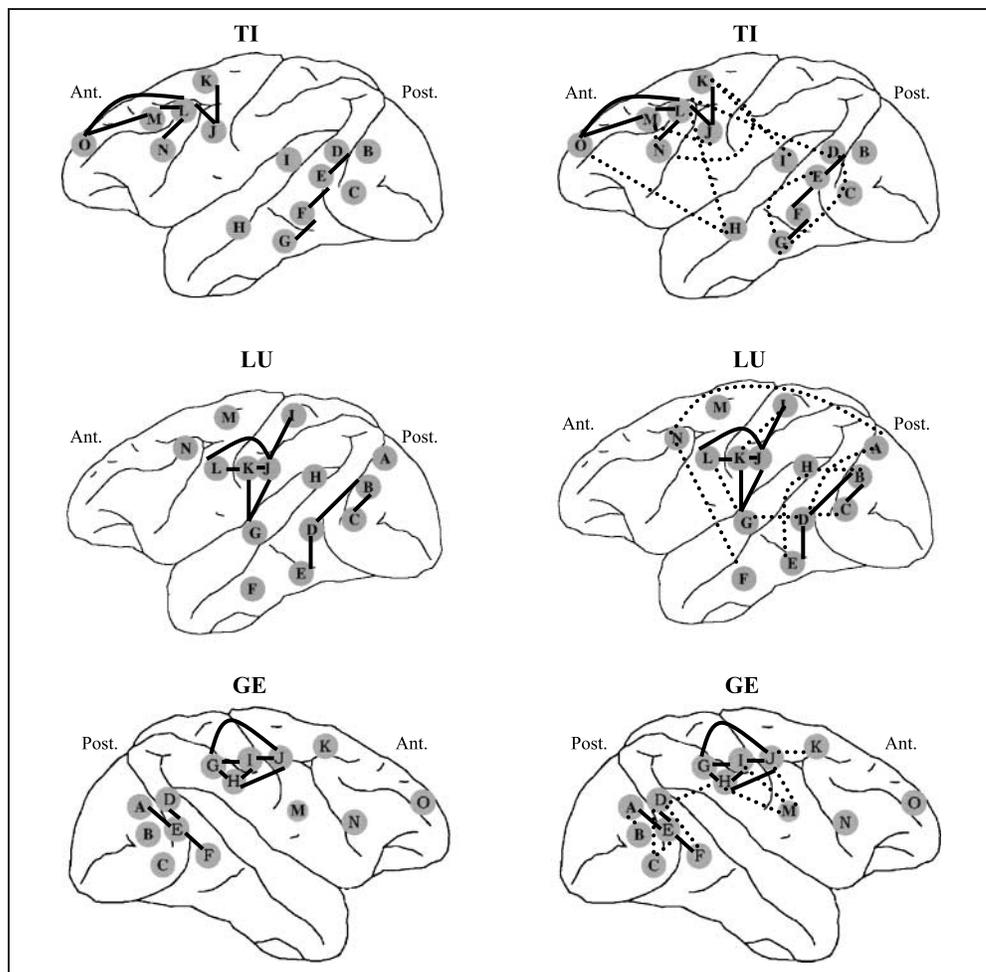
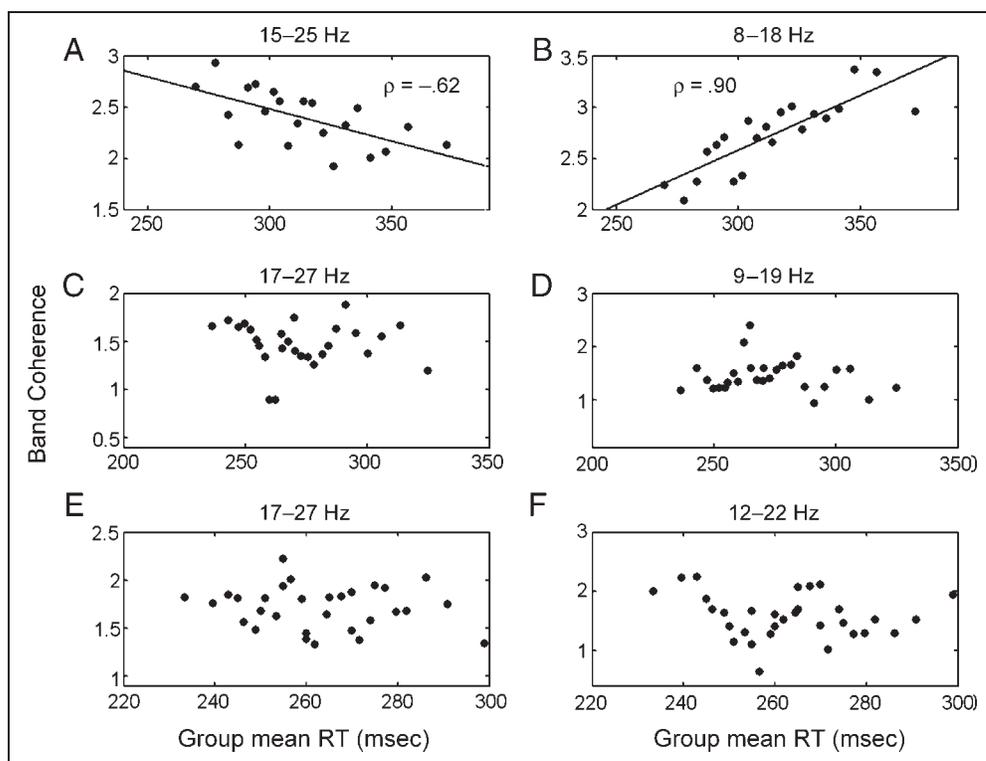


Figure 7. Scatterplots between group mean band coherence and mean RT within the frontal network (A) and visual network (B) of TI; the sensorimotor network (C) and visual network (D) of LU; and the sensorimotor network (E) and visual network (F) of GE. Linear least-squares fits to the scatterplots are shown, and Spearman's rank correlation coefficient values are displayed, for the two networks in TI.



had standard deviations of peak frequencies as high as 7 Hz. Despite being statistically significant, the mean coherence value was only 0.08 for GE and TI and 0.07 for LU. These findings suggest that functionally similar cortical sites are located close to one other and engage in communications within narrowly defined frequency bands in the 8–40 Hz range. Couplings between distant cortical sites are weaker and utilize more diffuse frequencies.

DISCUSSION

We investigated the statistical correlation of the power and coherence of prestimulus cortical LFP activity with RT. The sign of that correlation, whether positive or negative, was postulated to reflect the nature of the relation of cortical activity in a given area to visuomotor processing. Specifically, a negative correlation for the prestimulus activity in an area would indicate that the area was involved in processes, such as anticipatory attention, leading to enhanced visuomotor performance. A positive correlation, on the other hand, would suggest that the area was involved in processes that impeded visuomotor performance, perhaps by being in competition with anticipatory attention. Within this conceptual framework, our main results may be summarized as follows: (1) power in the prefrontal cortex, in the beta range (14–30 Hz), was negatively correlated with RT in two monkeys; (2) power in the sensorimotor cortex, in the range of 8–33 Hz, was positively correlated with RT in two monkeys; (3) power at visual cortical sites, in the alpha/low beta (8–20 Hz) range, showed positive correlations with RT in all three monkeys; and (4) sites showing similar patterns of correlation between power and RT were also linked together in synchronized networks.

The prefrontal cortex is considered to be situated at the highest level of the cortical executive hierarchy. Through extensive anatomical connections, the prefrontal cortex is hypothesized to direct biasing signals representing goals to the posterior sensory and motor systems that control attention, movements, and other cognitive functions (Engel et al., 2001; Fuster, 2001; Miller & Cohen, 2001; Brunia, 1999; Knight, Staines, Swick, & Chao, 1999). These biasing signals enhance the processing of behaviorally relevant input and suppress behaviorally irrelevant neural activity. In a previous report by our group (Liang et al., 2002) on one monkey (TI), negative correlations were found between prefrontal beta oscillatory activity and RT, meaning that stronger prefrontal beta oscillations in the prestimulus period lead to faster visuomotor responses. This finding has been confirmed here and strengthened by the evidence of similar effects in a second monkey (GE). The lack of significant correlation of prestimulus power with RT at prefrontal sites in the third monkey, LU, was likely due to the very sparse sampling of prefrontal cortical sites in that monkey. In sum, these observations not only are consistent with the hypothesized role for the prefrontal cortex in mediating

top-down control for anticipatory attention but also suggest that LFP oscillations in the beta range may act as a biasing signal in the modulation of lower-order sensory and motor circuits (Senkowski et al., 2006; Alegre et al., 2004; Liang et al., 2002). In a related work on coherence of the human EEG, Silberstein et al. (2004) found that the greater was the level of phase synchronization over the frontal lobes, the quicker subjects responded, a finding similar to our results for these prefrontal sites.

Synchronized oscillatory LFP activity in the alpha and lower beta ranges has been observed in the visual cortex in alert cats and monkeys (Gray & Singer, 1989; Eckhorn et al., 1988). Different models have been proposed to account for the role of these oscillations (Shaw, 2003). Some hypotheses, including cortical idling (Pfurtscheller, Stancak, & Neuper, 1996), inhibitory sensory processing (Klimesch, Sauseng, & Hanslmayr, 2007), and visual attentional disengagement (Foxe, Simpson, & Ahlfors, 1998), appear to predict that alpha activity is inversely related to cognitive activity. Our finding that prestimulus alpha activity at visual cortical sites was positively correlated with RT, meaning that higher levels of alpha activity lead to less efficient visual stimulus processing, hence, longer RTs, is in line with these hypotheses. Furthermore, Gonzalez Andino et al. (2005) reported that in more than 50% of their subjects, alpha band power had a significant positive correlation with RT.

Oscillatory LFPs in the range of 14–40 Hz have been observed in the sensorimotor cortex of nonhuman primates (Baker, Kilner, Pinches, & Lemon, 1999; Sanes & Donoghue, 1993; Murthy & Fetz, 1992). However, the role played by these oscillations remains unclear. Some authors have reported that these high-frequency (beta/gamma) oscillations provide reliable communication channels between different motor areas (Donoghue, Sanes, Hatsopoulos, & Gaal, 1998). Brovelli et al. (2004) postulated that the primary somatosensory cortex and the primary motor cortex were bound together in a beta-synchronized, large-scale cortical network in support of prestimulus maintenance of pressure by the hand on a depressed lever. By invoking a neural competition perspective, our observation of positive correlations between power and RT for sites in the sensorimotor cortex at similar frequencies can be seen to be consistent with this motor maintenance hypothesis. Specifically, as maintenance of hand pressure and visual anticipatory attention compete for processing resources, a greater allocation of neural resources to the maintenance of hand pressure, associated with larger beta oscillations, would imply a smaller allocation to visual anticipation, resulting in less efficient subsequent visuomotor processing and longer RTs. Thus, through positive correlations with RT, beta oscillatory activity helps reveal the competition between two concurrent tasks that place conflicting demands on a common neural processing resource.

Coherence is considered an index of synchronous activity between two cortical recording sites, with larger

coherence indicating stronger synchrony. Synchrony has been suggested as the basis for functional integration as well as for neural communication in the cortex. Based on the top 10% of coherence peak values, we were able to identify synchronous networks clearly localized in functionally specific brain regions. The frequency of synchronization between the participating sites in each network was in a narrow band and was consistent with the frequencies at which LFP power correlates with RT. Lowering the coherence threshold to include the links corresponding to the 10% to 20% of peak coherence values broadened the extent of the network configuration to include more site pairs which were more distributed and had more diverse synchronization frequencies. These observations suggest that functionally similar cortical sites form strongly synchronized networks, and that distant cortical sites may communicate through oscillatory activities of broad frequency content. Intriguingly, by virtue of their common correlation with RT, the prefrontal beta power should be negatively correlated with visual alpha power. Our analysis confirmed this idea (result not shown). The functional connectivity signified by the dotted lines in the right column of Figure 6 may play a role in the mediation of such coordinated activity between distant cortical sites.

Two remarks are in order. First, the spectral power values observed to have significant correlations with RT in our study did not necessarily represent peaks in the power spectrum (Figure 2). For example, spectral power at site M (TI) had one peak in the range of 16–23 Hz, whereas site B (TI) did not have any spectral peaks (see Figure 2A and B). Nonetheless, when correlation scatterplots were constructed for one frequency, 16 Hz, for both sites (see Figure 2C and D), we observed that site M had a significant negative correlation ($\rho = -.91, p < .0001$), whereas site B exhibited significant positive correlation ($\rho = .73, p < .0001$). This implies that even in the absence of prominent peaks in the power spectrum, power values may reflect characteristics of cortical processing. Second, in this study, we did not examine frequencies above 40 Hz and below 8 Hz. The reasons were noted in Methods section. Thus, how neural activities in the delta (1–3 Hz), theta (4–8 Hz), and high gamma (40–80 Hz) ranges contribute to RT variability remains to be elucidated in future experiments.

In summary, we found that the power of prestimulus oscillations was correlated with RT across a broad range of frequencies in prefrontal, sensorimotor, and visual cortical areas. The sign of correlation was found to be useful in suggesting different forms of processing at play in different cortical regions. In particular, different frequencies were found to have opposite signs of correlation with RT at the same cortical site, and vice versa for the same frequency at different cortical sites. This suggests that examining the role of ongoing brain processes in the production of RT variability is a valuable approach for determining the functional properties of the ubiquitous occurrence of oscillatory neural activities.

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