Optimal sustained attention is linked to the spectral content of background EEG activity: greater ongoing tonic alpha (~10 Hz) power supports successful phasic goal activation

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Abstract

Efficient executive control frequently requires the timely activation or re-activation of a task-goal to enable purposeful behaviour. Additionally, more generalized factors such as alertness or neurological health will influence the efficiency with which control can be implemented. Goal-directed processes have been investigated by examining event-related potentials (ERPs), but much less is known about the involvement of background or 'tonic' processes reflected in the ongoing electroencephalogram (EEG), and how these affect the phasic processes expressed in the broad-band ERP. Here, we investigate the relationship between a key attention-sensitive tonic process – the alpha rhythm – and relevant phasic processes observed during a sustained attention paradigm in neurologically healthy subjects. We report that subjects with relatively higher tonic alpha power (~10 Hz) show a larger-amplitude late positive ERP component that is thought to index goal activation and has been found to predict good sustained attention performance as defined by correct response patterns. Source localization results suggest that the neural generators responsible for oscillatory alpha activity, which are found primarily in the parietal and occipital lobes, are distinct from those giving rise to the late positive component. The results are discussed in terms of increased alpha synchrony facilitating goal-directed behaviour.

Introduction

Goal-directed behaviour depends on the efficiency of executive control processes that select and manage goals in working memory (Posner & Peterson, 1990). Additionally, background factors such as circadian rhythms (Manly *et al.*, 2002), age (Grigsby *et al.*, 1995) or neurological health (Robertson *et al.*, 1997) influence the degree to which behaviour can be controlled and purposeful. The consequences of breakdown in goal-directed behaviour can be dramatic, as seen in patients with frontal lobe damage or psychiatric illnesses such as schizophrenia. In support of goal-directed behaviour is an alertness or sustained attention system involving a right lateralised fronto-parietal network (Posner & Peterson, 1990; Sturm *et al.*, 1999). This system is essential for maintaining an intrinsic goal-directed focus in otherwise unarousing contexts where exogenous stimuli are not present to increase alertness through novelty, demand or perceived difficulty (Robertson & Garavan, 2004). The aim of the current study is to examine the relationship between short-term 'phasic' neurophysiological processes at play during a test of sustained attention and longer-term 'tonic' neurophysiological signals. The former reflect moment-to-moment cognitive events whereas the latter are more stable and reflect characteristics or traits of normal individuals that change more slowly over time.

Event-related potentials (ERPs) have been informative in understanding phasic activity during goal-directed behaviour. We have previously charted the ERP components elicited during the fixed sequence sustained attention to response task (SART$_{fixed}$; Dockree *et al.*, 2005). In this task a predictable series of single digits are presented (1–9) and subjects are required to make a response to each number (go-trials) with the exception of the number 3 (no-go trial). This task requires the activation and maintenance of a task goal, which is manifest in the ERP as a broadly distributed positivity over parieto-central areas. This goal activation component, termed late positive 1 (LP1) is observed 550–800 ms following stimulus onset on trial 2 (i.e. the digit '2') and exhibits divergence between the conditions of correct and incorrect responding on the following target (no-go) trial 3. Specifically, it was found that preceding an error, the LP1 was attenuated. Thus on a grand average level this component is most clearly indicative of successful performance on the SART and so stands out as a component of interest.

As exemplified by the aforementioned ERP component, neurophysiological processes are most commonly examined with respect to event-related, phasic changes in electro-cortical signals that occur at a rapid rate. By contrast, tonic EEG processes vary at a much slower rate and can be influenced by daily changes in circadian rhythms (Aeschbach *et al.*, 1999), fatigue (Borbely *et al.*, 1981) and mood

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states (Papousek & Schulter, 2002). Furthermore, tonic EEG signals are also associated with particular traits of individuals such as their age (Duffy *et al.*, 1984), intelligence (Klimesch *et al.*, 1998) or neurological health (Besthorn *et al.*, 1997). Tonic activity in the alpha frequency range (~10 Hz) has been informative regarding the cognitive resources available to an individual (Klimesch, 1999) and the level of alertness of an individual following the sedative effects of benzodiazepine and barbiturate administration (Feshchenko *et al.*, 1997). This evidence suggests that high tonic alpha power may be indicative of alert wakefulness and enhanced cognitive performance in healthy individuals.

Here, we examine how tonic alpha relates both to behavioural response patterns [in terms of response time (RT)] and to specific ERP components (late positive components) that augment goal-activation during the SART$_{fixed}$. In light of the abovementioned evidence, we hypothesize that subjects with high tonic alpha power will exhibit late positive ERP components of larger amplitude than subjects with lower alpha power. To help elucidate the potential functional relationships between tonic and phasic activity we conducted source dipole analysis of both the late positive ERP component and tonic alpha to determine whether the neural generators of the phasic and tonic processes under investigation were common or separate. The current study, in neurologically healthy subjects, will provide a baseline for further studies of clinical groups and their documented sustained attention deficits (Robertson *et al.*, 1997; Dockree *et al.*, 2004; O'Connell *et al.*, 2004; Mullins *et al.*, 2005).

Materials and methods

Subjects

Further analysis was conducted on 14 (six female) right-handed neurologically normal volunteers whose data was originally collected and analysed as part of a broad-band ERP study published in *NeuroImage* (Dockree *et al.*, 2005). They were paid $100 for one day of participation. Subjects were aged between 18 and 32 years (mean, 23.86, SD ± 4.24). All subjects gave written informed consent, and the Institutional Review Board of the Nathan Kline Institute approved the procedures which were in accordance with the Declaration of Helsinki. All subjects reported normal or corrected-to-normal vision.

SART paradigm and procedure

Digits were presented sequentially from '1' through '9'. For each block, 225 digits were presented sequentially (25 of each of the nine digits) over a period of ~4.7 min. Subjects undertook as many blocks as possible over the course of a day with regular breaks as required. Subjects were seated in a dimly lit, sound-attenuated, electrically shielded room approximately 1.52 m from the computer monitor. Subjects completed, on average, 24.4 blocks (range 13–30 blocks). For each trial, a digit was presented for 150 ms followed by an inter-stimulus interval (ISI) that varied randomly between 1000 and 1500 ms. A variable ISI was included to prevent subjects succumbing to a speed–accuracy trade-off that can occur when ISIs are regularly paced. Subjects were instructed to respond with a left mouse button press with their right forefinger upon presentation of each digit (go-trials) with the exception of the 25 occasions when the digit 3 (target) appeared, where they were required to withhold their response. False presses on the target were defined as commission errors.

Five randomly allocated digit sizes were presented to increase the demands for processing the numerical value and to minimize the possibility that subjects would set a search template for some perceptual feature of the target trial ('3'). Digit font sizes were 100, 120, 140, 160 and 180 in Arial text. The five allocated digit sizes subtended vertical angles of 1.39°, 1.66°, 1.92°, 2.18° and 2.45°, respectively, at a viewing distance of 152 cm. Digits were presented 0.25° above a central yellow fixation cross on a grey background. The task specifications were programmed and stimuli were delivered using the Presentation® software package (Version 0.75, http://www.neurobs.com). Figure 1 shows a schematic of the fixed sequence SART.

Measurements

High-density EEG recordings were acquired from 128 scalp electrodes (interelectrode spacing ~2.4 cm) referenced to the nasion. Electrophysiological data were recorded in AC mode with a gain of 1000 and a band pass of 0.15–100 Hz and the A/D conversion rate was 500 Hz. Recording began when electrical impedance had been reduced to less than 5 kOhms at all scalp sites. Vertical eye movements were recorded with two VEOG electrodes placed above and below the left eye, while HEOG electrodes at the outer canthus of each eye recorded horizontal movements.

Broad-band ERP analysis

The late positive ERP component LP1 was measured from scalp site POZ over parietal cortex, selected by visual inspection of overall data (Figs 3, 4, 5, 6, 7, 8, 9 and 10) as the area under the average waveform (compared to the 0 μV baseline) in the poststimulus interval between 550 and 800 ms on trial 2. Statistical tests of response-related differences (correct withhold vs. commission error) were conducted using a randomly selected set of precorrect withhold sweeps for trial 2, to equate with the lower number of pre-error sweeps. The LP1 area measures were the dependent variables for these tests.

Alpha power

The average power spectrum over the entire recording period was calculated for each participant using the discrete Fourier transform. The location on the scalp of maximum alpha power was selected for each individual, identified by inspection of topographic maps. Each participant's tonic alpha power (μV^2) was calculated as the power in the 4 Hz range centred on the individual alpha frequency (IAF) at the selected electrode site (see Fig. 2). The IAF is defined as the frequency at which the maximum peak is located within the alpha range in the power spectrum. One subject was excluded from the analysis because the alpha power for this subject exceeded the criteria for outliers (greater than two standard deviations from the mean).

Dipole source analysis

ERP components and oscillatory activity on the scalp can be related to changes in local activity of particular brain regions. Methods for localization are termed inverse solutions that provide noninvasive approximate localization of the neuronal generators. The BESA® (Brain Electrical Source Analysis; Version 5.1.6, http://www.besa.de) software package employs a four-shell ellipsoidal head model to address the inverse problem. Dipole source localization proceeds by a search within the head model for one or more electrical source generators that represents a centre of gravity for averaged data selected within a particular epoch. Dipoles ultimately rest in locations where they can explain a maximal amount of variance for the observed data at the scalp (Scherg & Von Cramon, 1985; Scherg & Picton, 1991).
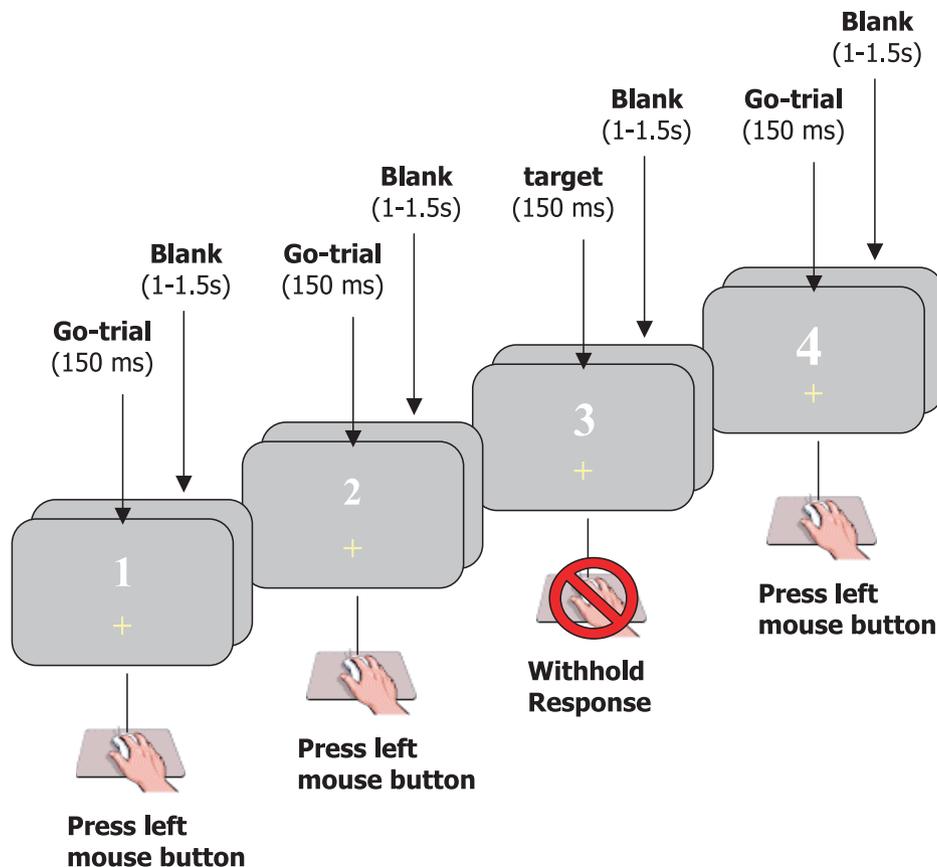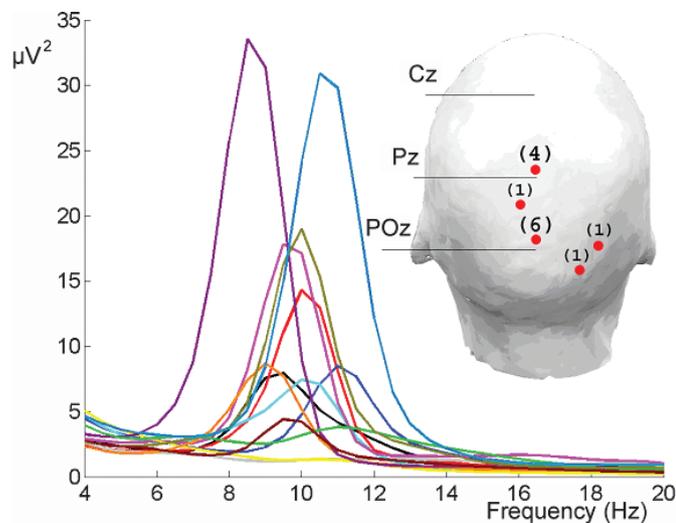
FIG. 1. A schematic diagram of the fixed sequence SART.

FIG. 2. Each participant's tonic alpha power (μV^2) was calculated as the power in a 4-Hz range centred on the individual alpha frequency (IAF) at the electrode site of maximum power on the scalp. IAFs are shown to the left and topographical sites of maximal alpha power are shown to the right. The red disks indicate the electrode locations of maximal alpha power and the numbers of subjects recorded at each location are indicated next to the disks in parentheses.

For the current data, source analysis was conducted for the LP1 component and tonic alpha. A source fitting strategy was adopted for the LP1 component by successively fitting each component in the broader epoch (from earlier sensory/perceptual ERP components to later cognitive ERP components) in a bottom-up fashion. That is, we began by progressively fitting the early components (e.g. P1, N1 and 2) before attempting to fit the later component of interest (i.e. the LP1). This strategy was constrained closely by the ERP components and their scalp topographies that are reported by Dockree *et al.* (2005). The rationale behind this approach was to localise the more anatomically distinct early componentry and attribute maximal variance in the model to these early components before proceeding to later components that possess larger field patterns on the scalp, are more heterogeneous in their morphology, and are likely to emerge from multiple and distributed sources.

To determine sources for the generation of tonic alpha a different approach was adopted. As tonic alpha is not an event-related process, it is not possible to derive its sources from an averaged ERP waveform. Rather, tonic alpha is measured in the spectral content of ongoing background EEG. Individual data were selected for two subjects (MF and TK) who exhibited the largest alpha peaks within the group (see Fig. 1). For each individual the entire continuous EEG was band-pass filtered in the 4 Hz range centred on their individual alpha frequency (subject MF, 8 Hz; subject TK, 11 Hz). A typical burst of alpha spindles was then identified in the filtered EEG data, and selected within a 400 ms epoch. A pattern recognition template was derived from the selected data using a specialized BESA® function. Using this template an automatic search was initiated in which the template is matched to similar alpha spindles throughout the entire EEG record. The cumulative matches were then averaged to represent a selection of tonic alpha. To ensure a representative selection of tonic alpha was achieved, this process was repeated twice over. On each

occasion a different alpha spindle was selected producing an alternative pattern recognition template to search for alpha. For each subject, three separate automatic search averages were generated to which a dipole source model could be applied and compared.

Correlation analysis

The LP1 area measure was averaged across all trial 2 sweeps preceding a correct withhold on the target trial. A correlation analysis was carried out between (i) the LP1 measure; (ii) response time differences in the critical target-processing period (trials 9 through 2, iii) alpha power, and as a control (iv) the early P1 component of the ERP.

Results

Behavioural results

Commission errors occurred on 2.5% (SD, 1.4) of trials. This amounted to an average of 59.8 commission errors across subjects over a full day of testing. A distinct pattern of response times (RTs) preceded the no-go trial. RTs on trials 9, 1 and 2 were compared before an upcoming correct withhold (successful run) or a commission error (unsuccessful run) on trial 3. A two-way repeated measures ANOVA was conducted. The factors were Response run (successful vs. unsuccessful) and Trial (9, 1, 2). No effect of Response run $F_{1,13} = 1.02$, $P = 0.330$ or Response run–Trial interaction $F < 1$ was observed; only a main effect of Trial was reliable $F_{2,26} = 19.01$, $P = 0.0001$. Repeated contrasts demonstrated that RT differences were as follows. RTs were significantly slower on trial 1 compared to trial 9 ($P = 0.001$) and RTs to trial 2 were significantly faster than trial 1 ($P < 0.0001$). The RT findings suggest that significant changes in stimulus processing occur in anticipation of the target stimulus (see Fig. 3).
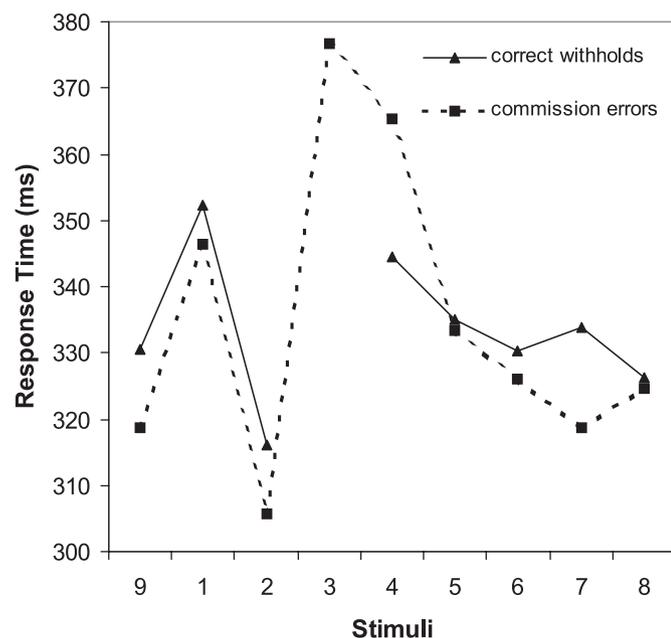

FIG. 3. Response time presented for each trial type (1–9) for averaged 'successful runs' (where target responses were correct – withhold on '3') and for averaged "unsuccessful runs" (where target responses were incorrect – false press on '3').

ERP results

Of primary interest was a sustained late positive ERP component (550–800 ms) that was maximal in amplitude over central and occipito-parietal sites. Late positive amplitude was greater at trial 2 prior to a correct withhold than prior to a commission error, $t_{(12)} = 2.36$, $P = 0.036$. The waveform plot at electrode location POZ (Fig. 4A) shows the diverging timecourses of the late positive component that reaches maximum divergence at ~600 ms and the difference topography shows a parieto-central distribution with field patterns showing a right hemisphere bias (Fig. 4B).

Correlations

To test the relationships between tonic alpha power, late positivity and RT patterns preceding the critical no-go trial, Pearson's correlations were carried out (see Table 1). A positive correlation was found between alpha power and the late positive ERP component. To verify the specificity of this relationship, a correlation between alpha power and the P1 ERP component was also carried out. (The P1 amplitude was extracted from the reference waveform (REFW), which represents the average of trials 5–8. We measured peak amplitudes at their respective occipito-parietal scalp location for each individual and grand-averaged these amplitudes to derive the P1 component.) We reasoned that alpha power might show a positive relationship with all componentry for each trial rather than to any one specific component. However, there was no relationship between the P1 component and the late positive component discounting this possibility. A positive correlation was also found between alpha and greater RT differential between trials 9–1 and trials 1–2. That is, subjects with higher alpha power showed larger shifts in response time from 9 to 1 and from 1 to 2. Further, the late positive amplitude was also positively correlated with the aforementioned RT differentials.

Source dipole localization

Source models derived for the LP1 component proved to be unreliable. Modelling was applied to (i) the LP1 at trial 2; (ii) difference waveform I (LP1 prior to a correct withhold minus LP1 prior to a commission error) and (ii) difference waveform II [LP1 prior to a correct withhold minus the reference waveform (REFW), which represents the average of trials 5–8] Three independent attempts to model the data were made by three different investigators and resulted in three different solutions, each with one or more dipoles in different subcortical regions. Although there is evidence that regions of the basal ganglia and the thalamus contribute to goal-directed behaviour as part of a broader more distributed fronto-striatal network (Sturm & Willmes, 2001; Kelly et al., 2004), it is unlikely that the LP1 is solely accounted for by subcortical activity. Moreover, a lack of precise replication across the three independent attempts to model the data suggest that the LP1, with its large topographical field pattern and dissimilar morphology between subjects, may be difficult to model accurately because it arises from multiple distributed sources.

Source modelling of tonic alpha was conducted separately for each of three automatic search averages generated for subjects MF and TK. In view of the broad posterior scalp topography for alpha in both subjects (see Fig. 5) and evidence showing that the functional correlates of the alpha rhythm have bilateral occipital loci (Hari et al., 1997) we assumed bilateral symmetrical sources in the model. For subject MF, a model was produced for the first automatic search average for tonic alpha. A two-source model with dipoles located near
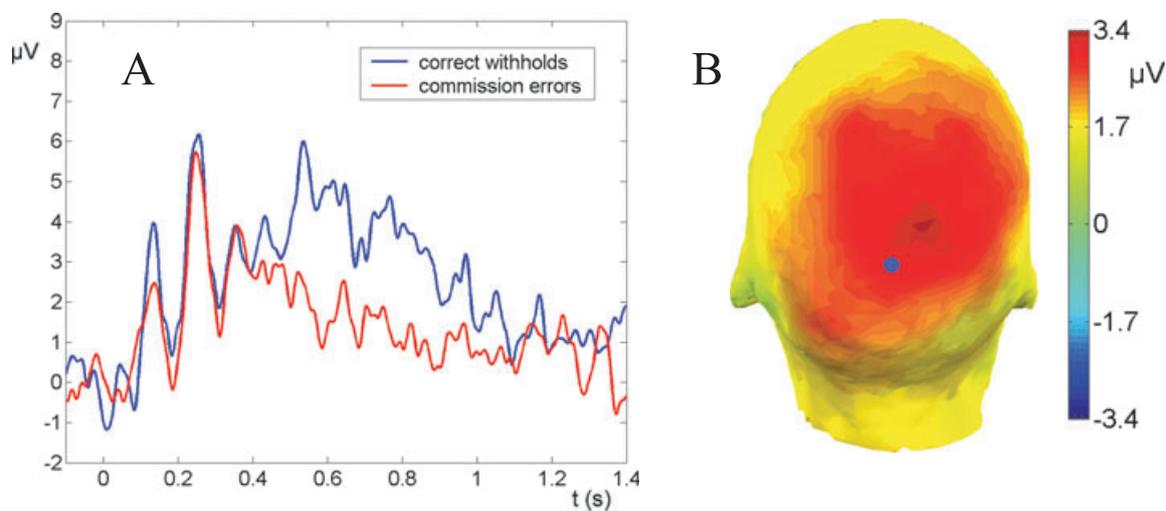
FIG. 4. (A) Waveform morphologies for the LP1 component prior to a correct withhold (blue trace) and prior to a commission error (red trace) are displayed. Scalp topographic maps (B) were produced using the EEGLAB toolbox (Delorme & Makeig, 2004). These represent interpolated field potential distributions, derived from 128-channel measurement. A topographic difference map was computed to illustrate the difference in the field distribution between a pre-correct and pre-error trial (i.e. on trial 2 immediately preceding a correct response or an error). Amplitude was integrated over the timeframe of the late positive ERP component in the computation of the topographic map. The electrode location (CPZ) is pin pointed using a blue disk.
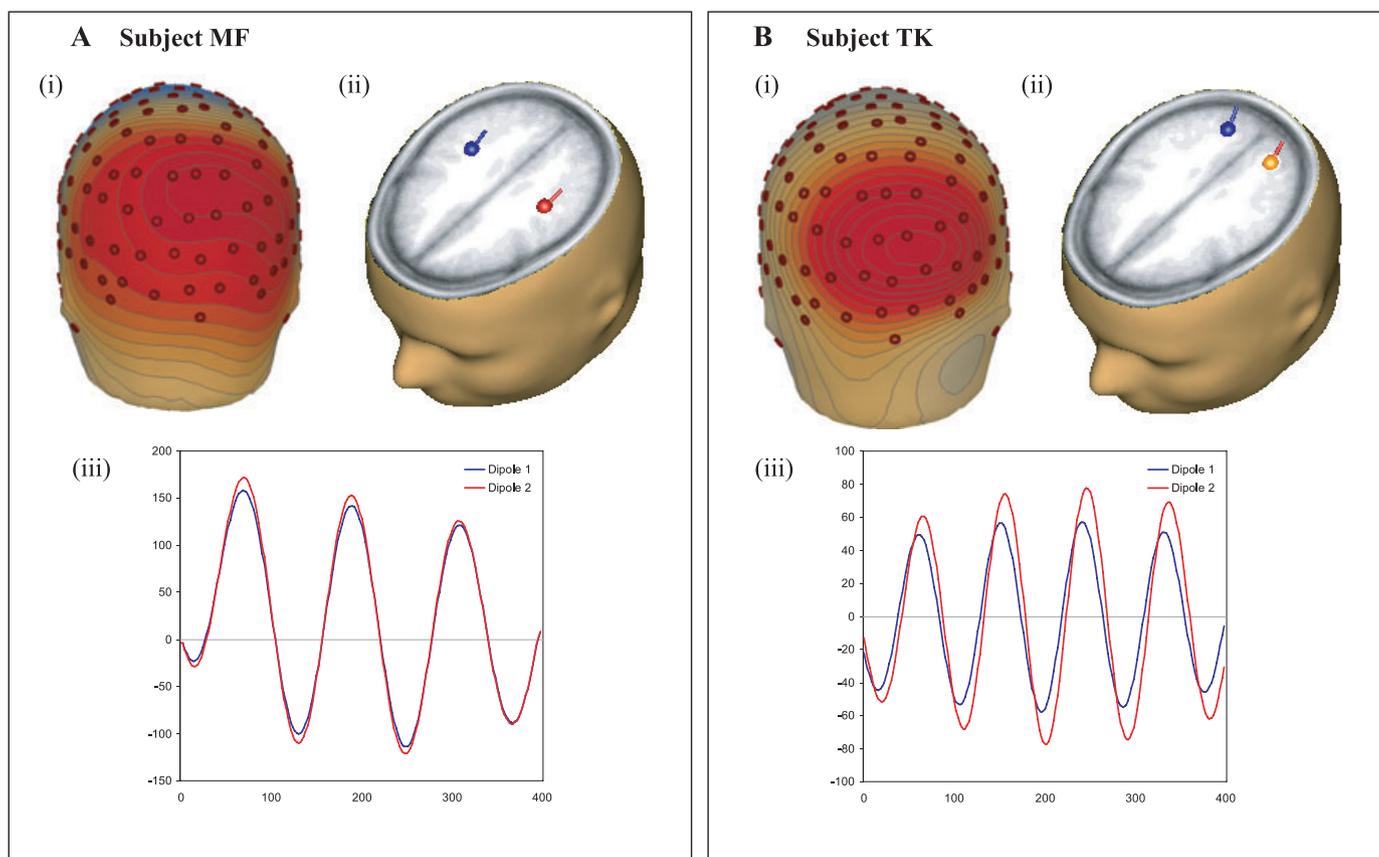

FIG. 5. Scalp topographies (i); dipole locations (ii), and source waveforms (iii) for subjects MF and TK. Alpha power (6–10 Hz) for subject MF (box A) exhibits a broad occipito-parietal topography slightly lateralised to the right. Dipoles are located bilaterally in the inferior parietal lobule and source waveforms illustrate oscillatory alpha activity. Alpha power (9–13 Hz) for subject TK (box B) shows an occipital topographic focus. Dipoles are located bilaterally in the precuneus and the alpha oscillations characterise the source waveforms. For each subject, the solutions displayed are just for the first iteration of the automatic search average. The model corresponds well to the other two iterations of our template matching exercise as outlined in Table 1. NB source waveform colour and dipole colour correspond.

TABLE 1. Pearson's *r* correlations between tonic alpha, average response time difference between trial 9 and trial 1, average response time differences between trial 1 and trial 2, late positive ERP component at trial 2 (LP1) and the P1 ERP component at the reference waveform (REFW)

	Tonic alpha	RT_difference 1–9	RT_difference 1–2	Late positive ERP component at trial 2
RT_difference1–9	0.709**			
RT_difference1–2	0.556*	0.758**		
Late positive ERP component at trial 2	0.595*	0.592*	0.611*	
P1 ERP component at REFW	−0.177	0.111	0.126	0.195

**Correlation is significant at the 0.01 level (two-tailed); *correlation is significant at the 0.05 level (two-tailed)

to the postcentral gyrus bounded by the inferior parietal lobule accounted for most of the variance (the model produced a goodness-of-fit value > 95%). The model also provided a good fit when applied to the other two automatic search averages (goodness-of-fit > 95% and > 90%, respectively). For subject TK, a two-source model was also indicated for the first automatic search average. Most of the variance was accounted for by dipoles located bilaterally in the precuneus near to the cuneus (goodness-of-fit value > 95%). For the second and third automatic search averages goodness-of-fit values for the model were > 95% and > 90%, respectively. Table 2 shows the Talairach coordinates for the bilateral dipoles and the residual variance (RV) inside the 400-ms fit interval and the RV of the best sample within the fit interval. Data are presented for each of the three automatic search averages for each subject.

In order to test whether the tonic alpha source models could account for much of the variance attributable to the LP1, each subject's model, accounting for their tonic alpha, was applied to the 550–800 ms LP1 epoch of their broad-band ERPs. For both subjects, the tonic alpha models were insufficient to account for the LP1 variance [Subject MF, RV 70.2%, BEST 43.8%; subject TK, RV 84.5%, BEST 70.2]. The goodness-of-fit values for both subjects are < 30% implying that tonic alpha and the LP1 component do not share common anatomical generators.

Discussion

The present study reveals an association between tonic alpha power and phasic properties of the ERP during a sustained attention task. We show that subjects with higher levels of tonic alpha exhibit enhanced late positive amplitudes that, in turn, predict successful goal execution during the SART$_{fixed}$. Furthermore, high tonic alpha power was also correlated with response time slowing from trials 9–1 and shortening from trials 1–2. Separately, the strong presence of this RT pattern was associated with larger late positive amplitudes, suggesting that strategic changes in RT are functionally important to the activation and maintenance of the primary task goal.

The relationship observed between tonic alpha and the LP1 raises the question of whether the networks of cortical generators are common or distinct. We addressed this through source analysis of tonic alpha, which produced stable estimates of distinct generator locations for the two analysed subjects. A number of investigations attempting to source-localise the alpha rhythm have identified multiple generators within occipital and parietal cortex. Specifically, MEG studies have identified the calcarine fissure (Chapman *et al.*, 1984; Williamson *et al.*, 1997) and the parieto-occipital sulcus (Hari *et al.*, 1997) as generators for alpha. An independent component analysis (ICA) approach employed by Makeig and colleagues using EEG data (Makeig *et al.*, 2002) corroborates the aforementioned MEG studies by identifying both lateral occipital and central occipital components of oscillatory alpha activity. Intracranial recordings have revealed tight coupling between the occipital alpha rhythm and alpha oscillations in the lateral geniculate nucleus of the thalamus. Animal experiments demonstrate that across thalamo-cortical relay cells there is strong coherence within the alpha frequency range that is associated with decreased sensory transmission (Lopes da Silva *et al.*, 1980).

A recent neuroimaging study (Moosmann *et al.*, 2003) showed that while subjects are awake with their eyes closed, increased alpha activity is correlated with decreased BOLD signal in cortical areas including the superior temporal gyrus, inferior frontal gyrus, inferior parietal lobule and postcentral gyrus. Conversely, a positive relationship has been found linking increased alpha activity with increased thalamic activity (Lindgren *et al.*, 1999; Goldman *et al.*, 2002). Oscillatory alpha activity has also been associated with a more distributed fronto-parietal network (Laufs *et al.*, 2003). Strong and widespread negative correlations between the BOLD fMRI signal and alpha power were found in lateral frontal and parietal cortices – areas

TABLE 2. Dipole model solutions for subjects MF and TK

	Talairach coordinates for dipole model solutions			Model fit for each automatic search average (ASA)	
	x	*y*	*z*	RV	BEST
Subject MF					
5 mm search range					
Left inferior parietal lobule/postcentral gyrus	−36	−28	35	4.021%	3.432% (1st ASA, 7845 samples)
Right inferior parietal lobule/postcentral gyrus	36	−28	35	4.077%	3.601% (2nd ASA, 7871 samples)
				6.126%	4.605% (3rd ASA, 15648 samples)
Subject TK					
5 mm search range					
Left precuneus/cuneus	−21	−69	34	1.951%	1.226% (1st ASA, 27774 samples)
				4.574%	2.849% (2nd ASA, 26539 samples)
Right precuneus/cuneus	21	−69	34	5.593%	3.383% (3rd ASA, 20546 samples)

Anatomical areas and Talairach coordinates for dipole locations are presented on the left. The residual variance (RV) and the RV of the best sample within the fit interval for each of the three automatic search averages and for each subject are presented on the right.

known to implement attentional control. The authors argue that alpha may serve as an EEG signature of activation in fronto-parietal structures that orchestrate goal-directed behaviour. Specifically, it was proposed that alpha oscillations signal a neural baseline with 'inattention', which would be consistent with the cortical idling hypothesis positing that synchronized neurons reflect mental inactivity (Pfurtscheller & Lopes da Silva, 1999). An alternative perspective, given the broader role of fronto-parietal structures in inhibition and interference control (Hester *et al.*, 2004) is that synchronizing alpha and associated metabolic deactivation may reflect an active gating mechanism to control competing sensory and cognitive information.

In the present study, the dipole locations for alpha, although different for each of the two subjects examined, were consistent with the abovementioned fMRI and EEG studies that have identified, among other areas, the postcentral gyrus, the inferior parietal lobule and the medial occipital lobe as associated with oscillatory alpha activity (Makeig *et al.*, 2002; Moosmann *et al.*, 2003). In applying each subject's alpha source model to their late positive waveforms we obtained a poor fit, suggesting that the centre of gravity for the tonic alpha sources are separate from the LP1 generators. It is likely that the LP1 emerges from multiple and distributed neural generators within broad fronto-striatal networks that contribute to its morphology. Although the source solutions suggest different generators contribute to tonic alpha and the LP1, a relationship exists between the two that may reflect a functional advantage.

We propose that high tonic alpha power during sustained attention performance may be indicative of an alert and receptive condition of the individual that serves to facilitate the phasic electro-cortical changes related to effective anticipation and execution of task goals. This relationship may be akin to a signal-to-noise ratio whereby the phasic signal is boosted by reduction of background tonic noise. Here 'noise' is reflected in desynchronized neuronal networks, whereas networks oscillating in synchrony reflect a more stable, noise-attenuated state. It is therefore possible that individual differences in tonic alpha may represent the setting conditions against which phasic electro-cortical changes occur. These individual differences are interesting in light of the evidence that alpha activity has high heritability with genomic variation contributing significantly to alpha peak frequency and alpha power (van Beijsterveldt & van Baal, 2002).

The notion of noise-attenuation via synchronized activity within the alpha band is not inconsistent with the 'cortical idling hypothesis' (Pfurtscheller & Lopes da Silva, 1999), which proposes that synchronized networks reflect inactivity. It is conceivable that the low cognitive demands of the SART$_{fixed}$ involve localized activation of task-specific neural populations and more global synchronous oscillations of large cell assemblies that reflect cortical inactivity. In support of this conjecture, Fassbender and colleagues found reduced cortical activation in the SART$_{fixed}$ compared to a more challenging version of the task in which the digits occur randomly (Fassbender *et al.*, 2004). In the context of the current task it is possible that subjects with relatively higher alpha power were the most effective at remaining on task and avoiding distracting trains of thought (reflected in a lack of neural synchrony) and consequently the cortical regions not necessary for task performance become less active. In contrast, subjects with lower alpha may be engaged in nontask related cognition, which may interfere with timely goal activation.

Instead of a passive role for alpha, others have interpreted band-power increases as having a more active role than the traditional cortical idling hypothesis (Lopes da Silva, 1991). Large-scale synchronization within a network may actually limit and control the extent of unwanted neural processes. Recent evidence suggests that synchronized alpha over spatio-topic visual areas reflect an active attentional suppression mechanism (Fu *et al.*, 2001). In the most recent of these experiments (Kelly *et al.*, 2006), bilateral flickering stimuli were presented during a sustained visuo-spatial attention task. An external flicker ensured that evoked alpha remained desynchronized prior to periods when subjects were required to ignore distracting letter sequences in one hemifield and attend to cued target letters in the other hemifield. The data showed large induced (i.e. not phase-locked to the stimulus) increases in alpha power over the ignoring hemisphere relative to the precue baseline implying active suppression of the irrelevant stream of letters over an 8-s period. Although during simple sustained attention tasks no external distractors are present and the task becomes ostensibly straightforward, the real challenge is to overcome the monotony of the task and to suppress task-unrelated thought (Smallwood *et al.*, 2004). Conceivably, an effective strategy during the SART$_{fixed}$ could require the deactivation of task-irrelevant cortical networks in order to gate distractible trains of thought that characterize 'drifts of attention' and lead to goal neglect. Although the abovementioned studies by Foxe and colleagues specifically investigated phasic modulation of alpha in relation to inhibitory control, it is also possible that these processes operate more generally, at the tonic level. In the current study, the subjects showing large alpha power may be the most task-orientated and/or least distractible whereas those with reduced alpha activity could be less efficient at inhibiting task-irrelevant cortical networks.

Conclusion

Our data suggest that subjects with relatively higher tonic alpha power (~10 Hz) show a larger-amplitude late positive ERP component that predicts good sustained attention performance as defined by correct response patterns. We propose that individual differences in tonic alpha may represent the setting conditions against which phasic electro-cortical changes occur. These setting conditions may reflect stable and noise-attenuated cortical networks that are not called upon directly for task-directed processing. These findings are interesting with respect to damaged cortical networks in specific clinical populations and the resultant instability and noise-interference states that could emerge. Moreover, the high heritability of alpha activity indicates that it may prove to be a useful neurophysiological phenotype that interacts with cognitive states. Alternatively, it could be speculated that high tonic alpha underlies a more active mechanism causing gating of task-irrelevant cortical activity and thus facilitating sustained attention.

Acknowledgements

Abbreviations

EEG, electroencephalogram; ERPs, event-related potentials; LP1, late positive 1; RT, response time; SART, sustained attention to response task; SART$_{fixed}$, fixed sequence sustained attention to response task.

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