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Temporal dynamics of access to consciousness in the attentional blink

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Presentation of two targets in close temporal succession often results in an impairment of conscious perception for the second stimulus. Previous studies have identified several electrophysiological correlates for this so-called ‘attentional blink’. Components of the event-related potential (ERP) such as the N2 and the P3, but also oscillatory brain signals have been shown to distinguish between detected and missed stimuli, and thus, conscious perception. Here we investigate oscillatory responses that specifically relate to conscious stimulus processing together with potential ERP predictors. Our results show that successful target detection is associated with enhanced coherence in the low beta frequency range, but a decrease in alpha coherence before and during target presentation. In addition, we find an inverse relation between the P3 amplitudes associated with the first and second target. We conclude that the resources allocated to first and second target processing are directly mirrored by the P3 component and, moreover, that brain states before and during stimulus presentation, as reflected by oscillatory brain activity, strongly determine the access to consciousness. Thus, becoming aware of a stimulus seems to depend on the dynamic interaction between a number of widely distributed neural processes, rather than on the modulation of one single process or component.

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Introduction

A central question in current neuroscience research involves the neural correlates of conscious perception (Engel and Singer, 2001; Ward, 2003). Although the concept itself is under heavy debate, researchers seem to agree that conscious perception of visual stimuli is a rather quick, fleeting phenomenon. Therefore, measures of electromagnetic brain activity with high temporal resolution have been proven useful in the scientific study of consciousness (Tallon-Baudry et al., 1997; Rodriguez et al., 1999;

Koivisto and Revonsuo, 2003; Kranczioch et al., 2003; Eimer and Mazza, 2005; Sergent et al., 2005).

The brain mechanisms controlling whether physically identical information sometimes does and sometimes does not reach awareness remain poorly understood. In the case of the attentional blink (AB) paradigm, where two temporally close targets need to be processed, the second target often goes undetected. It has been suggested that this differentiation is due to a competition between neural processes devoted to the processing of the two targets reflected in the N2 and P3 waves of the event-related potential (ERP, Sergent et al., 2005). In line with this suggestion the amplitude of the P3 component evoked by the first target was found to be related to the size of the AB, that is the number of second targets that cannot be reported (McArthur et al., 1999; Shapiro et al., 2006). The P3 evoked by the second target on the other hand was shown to be reduced, if not absent, for undetected as compared to detected stimuli (Rolke et al., 2001; Kranczioch et al., 2003). Since detected task-relevant stimuli nearly always generate a P3 response, a prediction that can be drawn from these studies is that the competition for resources should be directly reflected in an interaction between first target and second target P3 amplitudes.

Recent theoretical (Fell et al., 2002; Dehaene et al., 2003) and empirical work has highlighted the role of synchronous oscillatory brain activity in the AB: differences between detected and undetected targets in long-range neural synchrony in the beta (Gross et al., 2004) and gamma (Nakatani et al., 2005) frequency ranges have been found to emerge even before target stimulus presentation. Although the functional role of different frequencies remains a matter of discussion, these findings clearly indicate that the state of oscillatory brain activity before and during stimulus presentation has an important influence on whether the second target in the AB paradigm is consciously perceived or not.

Here we tested the assumption of resource competition in the AB by analysing both ERPs and oscillatory brain activity. We predicted that brain states before and during stimulus presentation, as reflected by oscillatory brain activity, should determine the detection of a second target stimulus in the AB interval. Furthermore, the resources allocated to the first and second target processing should be directly mirrored by the P3 component, that

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is, the successful temporal management of resources should be reflected in larger P3 amplitudes for detected target stimuli.

Materials and methods

Participants

In order to compare trials in which the second target was detected with trials in which the second target remained undetected, twenty-eight healthy right handed volunteers initially participated in the study. Only participants with a reasonably strong AB were further considered for analysis, ensuring that the number of trials in both conditions would be approximately the same. The final sample consisted of nine females and six males, with a mean age of 23.9 years (range 18–28). Before the start of the experiment written informed consent was obtained from all participants according to the declaration of Helsinki. All participants were free of current or past psychiatric or neurological disorders and received monetary compensation for participation.

Behavioural task

Target and distracter stimuli were presented at central fixation on a CRT monitor with a presentation frequency of 10 Hz and on a white background. Distracters were black capital consonants (except *F*, *K*, *Q*, *X*, *Z*). The first target (T1) was a green letter, which could either be a vowel (except *I*) or a consonant (except *F*, *K*, *Q*, *X*, *Z*). The second target (T2) was a black capital X. Each trial started with the presentation of a fixation cross for the duration of 900 to 1100 ms (mean 1000 ms). This was followed by 14 to 17 distracters before T1 was presented. In 75% of all trials T1 was followed by T2 with either no (lag 1), one (lag 2) or six (lag 7) intervening distracters. T2 lags were chosen based on previous studies showing that with the present experimental setup the AB is presented well (Kranczioch et al., 2003). The trial was completed by 7 (T1 presented as 17th stimulus, T2 presented at lag 7) to 17 (T1 presented as 14th stimulus, no T2) additional distracters, always resulting in a total of 31 stimuli per trial. After stimulus presentation two successive screens appeared indicating the subject to decide whether the green letter was a vowel and whether the black X was contained in the stimulus stream. A total of 14 practice trials were conducted before the start of the experiment and followed by 96 trials presented in randomised order for each of the four conditions. All trials were spread across seven experimental blocks of approximately 6 min duration each, with breaks of about 1 min between blocks.

EEG recordings

Subjects were seated in an electrically shielded, sound attenuated and dimly lit chamber. The computer monitor used for stimulus presentation was placed outside the chamber, at a distance of 200 cm. The EEG was recorded using an electrode cap on which 63 equidistant Ag–AgCl electrodes were mounted (EASYCAP, Herrsching, Germany). An additional electrode was placed below the right eye to monitor eye blinks and the nose tip served as recording reference. Data were recorded using a high impedance 64 channel NetAmps 200 system (Electrical Geodesics, Eugene, OR, USA). Sensor impedances were kept below 20 k Ω prior to data acquisition. Data were recorded at a sampling rate of 500 Hz with 0.024 μ V precision and analog-filtered from 0.1 to 100 Hz.

Data analysis

Data analysis was performed with EEGLAB 4.51 (Delorme and Makeig, 2004), a freely available open source software toolbox (Swartz Center for Computational Neurosciences, La Jolla, CA; <http://www.sccn.ucsd.edu/eeGLAB>) running under Matlab (MathWorks, Inc, Natick, MA), in combination with in-house developments. Downsampled (250 Hz) data were epoched into segments of 3.7 s duration (–1.7 to 2.0 s relative to T2 presentation) and screened for artefacts. Following rejection of epochs containing non-stereotyped artefacts (e.g., swallowing, cable movement, etc.) or eye blinks occurring during target presentation and epochs with incorrect T1 response, concatenated single-trial EEG data were submitted to extended infomax independent component analysis (Bell and Sejnowski, 1995; Lee et al., 1999). Independent components reflecting eye movements were identified visually and discarded by back-projecting all but these components to the data space. This procedure resulted per subject, on average, in 39.1 trials (range 20 to 74) for the lag 2 T2 detected condition and in 47.8 trials (range 19 to 71) for the lag 2 T2 not detected condition ($t=1.04$, $p=0.32$). ERPs for these conditions and the condition in which no T2 was presented were computed, the 200 ms interval before the presentation of T1 was used for baseline correction.

Time–frequency analysis was performed by convolving the single-trial data with a complex Morlet wavelet $w(t, f_0)$ having a Gaussian shape in the time (σ_t) and frequency (σ_f) domains around the centre frequency f_0 . A constant wavelet is characterised by a constant ratio $Q=(f_0/\sigma_f)$. We used nonconstant wavelets with Q increasing linearly from 4 to 12 for frequencies from 3 to 70 Hz (step size 1 Hz), which results in a relative decrease in spectral versus temporal resolution with increasing frequency. For every single trial, the absolute value of the complex result of the convolution was computed, scaled to decibels ($10 \cdot \log_{10}$), and normalised by subtracting for each frequency the mean value of the –600 to –400 ms pre-T2 interval. Single trials were averaged to obtain a measure of total activity. To derive information about the phase locking of the signal between trials, the inter-trial phase coherence (ITC) was computed. If F is the (complex) representation of the signal in the frequency space, i.e.

$$F(t, f) = w(t, f) * x(t), \quad (1)$$

where $x(t)$ is the signal and $*$ designates convolution, then the ITC is obtained as

$$\text{ITC} = \frac{\left| \sum F \right|}{\sum |F|}. \quad (2)$$

(Delorme and Makeig, 2004). The sums run over all trials, and ITC is computed for all time bins t and frequencies of interest f . The result is a value between 0 and 1, indicating for each time and each frequency analysed the degree of phase consistency, with 0 indicating a random phase distribution and 1 indicating perfect phase consistency between trials. Time–frequency analysis was run for the complete epoch length of 3.7 s to ensure that the interval of interest (–600 to 1000 ms relative to T2 onset) did not interfere with invalid edge effects, as indicated by the half length of the wavelet scales.

The phase relation of the signals at different electrodes was analysed by computing the phase locking value (Lachaux et al.,

1999). If the time–frequency transformed signal at an electrode e is written as

$$F_e = a_e \exp(i\phi_e), \quad (3)$$

the cross-spectrum of two signals at sites e_1 and e_2

$$S_{e_1e_2} = 1/N \sum F_{e_1} F_{e_2}^* \quad (4)$$

becomes

$$S_{e_1e_2} = \frac{1}{N} \sum r_{e_1} r_{e_2} \exp(i[\phi_{e_1} - \phi_{e_2}]). \quad (5)$$

Normalising the frequency representation to $r_{e_1} = r_{e_2} = 1$ before averaging yields the phase locking value

$$PLV_{e_1e_2} = \frac{1}{N} \left| \sum \exp(i[\phi_{e_1} - \phi_{e_2}]) \right|. \quad (6)$$

All sums run over trials and N is the total number of trials. Like ITC, phase locking values of 0 and 1 indicate no or perfect phase locking, but this time between the signals at two recording sites over all trials.

Statistical analysis

Statistical analysis of the P3 process was carried out using two time windows, 200–400 ms after T2 presentation for the T1-related P3 process and 450–650 ms after T2 presentation for the T2-related P3 process. Time windows were defined based on previous studies (Kranczoch et al., 2003; Kranczoch et al., 2006) and visual inspection to cover the main properties of the P3 processes. Note that the offset for the T2-related P3 relative to target presentation has been described in previous studies, particularly for short T2 lags (Vogel and Luck, 2002; Sessa et al., 2007). Neighbouring electrodes were combined into 12 topographical regions of interest (ROI) in order to avoid a loss of statistical power (Oken and Chiappa, 1986). Electrode clusters belonging to each ROI are depicted in Fig. 1A. Amplitudes were analysed with a repeated measures analysis of variance (ANOVA) with the region factors laterality (left, midline, right) and anterior–posterior (frontal, central anterior, central posterior, parieto-occipital), the condition factor T2 performance (detected, not detected) and the factor time window (P3–T1, P3–T2).

Statistical testing of condition effects in the time–frequency plane focussed on three frequencies, namely alpha, beta and gamma. The selection of frequency bands was guided by previous work in the field. Previous research has indicated that targets and non-targets presented in rapid succession, very much alike to stimulus presentation in the AB, are associated with differences in late gamma activity (Kranczoch et al., 2006). Gross et al. (2004) recently demonstrated target-related activity in the beta frequency range. Moreover, the alpha band was of particular interest as ongoing alpha activity has been associated with better performance (Ergenoglu et al., 2004; Hanslmayr et al., 2005). On the other hand, the steady state visual evoked potential, which in the present study was expected to centre at 10 Hz, was found to increase if a visual stimulus stream is attended (Müller and Hübner, 2002). To guide the selection of time–frequency windows, exploratory t -tests for the two time–frequency spectra averaged across all electrodes and subjects were used. T2 detected and T2 not detected conditions were tested against zero but not directly compared at this step to

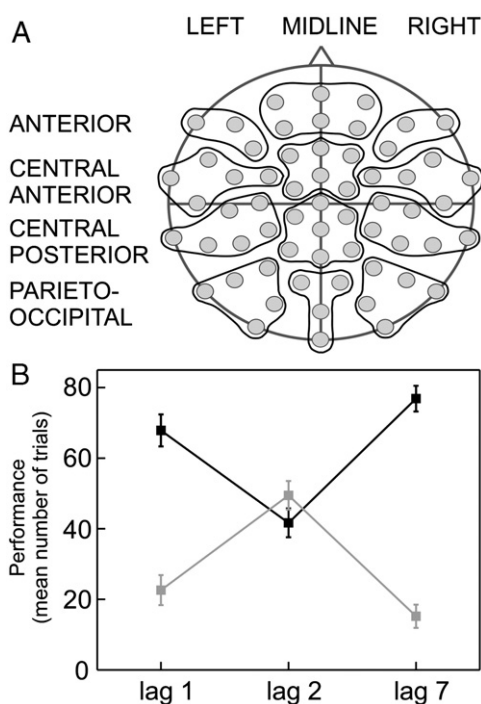
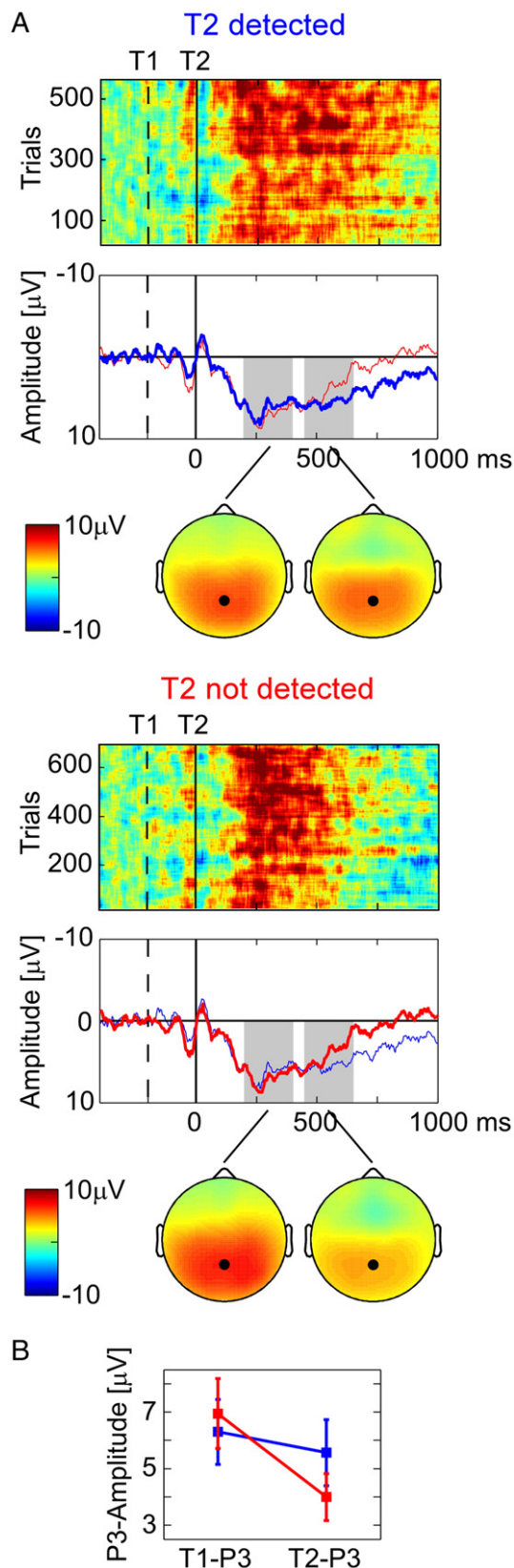


Fig. 1. (A) Schematic electrode layout. Depicted is the electrode layout together with labels for the 12 regions of interest used for statistical analysis. (B) Behavioural performance. Mean number of trials and standard error in the conditions T2 detected (black) and T2 not detected (grey). Only trials in which T1 had correctly been identified are included. The number of trials was significantly different for lags 1 and 7 (both $p < 0.001$) but did not differ for lag 2 ($p = 0.37$).

avoid undesirable dependencies between the selection of time–frequency windows and subsequent statistical analysis. The 2-D representations of t -values (times \times frequency) obtained were thresholded at $t \pm 2.145$ ($p \leq 0.025$). The two resulting t -maps showed synchronisation and desynchronisation clusters in several time–frequency windows (cf. Supplementary Fig. 1). In particular, in the alpha frequency range, clusters were found at 10 (synchronisation and desynchronisation) and 13 Hz (synchronisation), in the beta frequency range clusters centred at 20 Hz (desynchronisation), and with regard to gamma activity a late cluster was observed at about 40 Hz (synchronisation). Accordingly, seven time–frequency windows were specified to cover these clusters in the subsequent statistical analysis. These were relative to T2 presentation: –460 to –340 ms and –160 to –110 ms at 10 Hz ($\sigma_f = 1.5$), 20 to 140 ms at 13 Hz ($\sigma_f = 1.7$), –150 to –60 ms, –20 to 50 ms, and 100 to 250 ms at 20 Hz ($\sigma_f = 2.3$), and 660 to 760 ms at 40 Hz ($\sigma_f = 3.5$) (cf. black rectangles in Fig. 4). Repeated measures ANOVAs were run to test statistically whether activation in any of these time windows differed significantly between T2 detected and T2 not detected conditions. ANOVAs were based on ROI data (see above) and included the region factors laterality (left, midline, right) and anterior–posterior (frontal, central anterior, central posterior, parieto-occipital), and the condition factor T2 performance (detected, not detected). If the ANOVA revealed significant condition effects, it was followed by paired non-parametric Wilcoxon tests of ITC to determine whether differences in total activity were accompanied by ITC differences.

The interrelation between the magnitude of the significant time–frequency effects and the amplitude of the P3 process at the midline central posterior ROI was tested by Pearson correlation



analyses. Correlation coefficients are given together with one-tailed *p*-values.

Statistical analysis of phase locking focussed on exploring differences in synchronisation between T2 detected and T2 not detected conditions at the four frequencies confirmed by the *t*-test analyses of the time–frequency planes described above, i.e., 10, 13, 20 and 40 Hz. This choice of frequencies was furthermore supported by previous studies on long-range synchronisation in the AB, that report effects in the gamma (40 Hz, Nakatani et al., 2005) and beta frequency ranges (Gross et al., 2004). Note that in the study by Gross et al. frequency selection was based on the results of a time–frequency analysis pointing at about 15 Hz as the interesting frequency. In the present study time–frequency effects in the beta frequency band were evident at 20 Hz. Interestingly, in both studies the respective frequency corresponds to a multiple of the stimulus presentation frequency.

Results

Behavioural results

Trials consisted of sequences of black capital letters presented with a stimulus onset asynchrony of 100 ms. Two target stimuli were embedded in the sequence: T1, the first target, was a green letter, and T2, the second target was a black X. T1 had to be categorised (vowel or consonant) whereas T2 had to be detected (present or absent). T1 was followed by T2 with either no (lag 1), one (lag 2) or six (lag 7) intervening distracters. In addition, in 25% of all trials no T2 was presented.

The experimental manipulation resulted in the typical AB pattern for detection accuracy of T2, namely a clear decrease in the detection of T2 if presented at lag 2 if compared to lags 1 and 7. Fig. 1B shows the behavioural performance as reflected in the mean number of trials across subjects where T2 was detected or missed, given that T1 had correctly been identified. For lag 2, the mean number of trials before artefact correction was 41.7 (range 20–75) for condition T2 detected and 49.5 (range 19–72) for condition T2 missed, which did not differ significantly ($t(14)=0.97, p=0.38$).

Event-related potentials

All analyses of the electrophysiological data were centred on lag 2 trials, analyses were furthermore focussed on differences between the T2 detected and T2 missed conditions. Target stimuli evoked a prolonged centro-parietal positivity strongly resembling a typical P300 ERP component that contained both T1- and T2-related P3. The peak amplitude of this positive deflection was increased for trials in which T2 remained undetected (Fig. 2A,

Fig. 2. Event-related potential results for T1- and T2-related P3. (A) Event-related potential image (ERPimage), ERP and voltage maps for the T1-related P3 window (200–400 ms) and the T2-related P3 window (450–650 ms) for detected (top, blue) and undetected (bottom, red) T2 stimuli. Note that ERPs are respectively shown for both conditions to allow for a direct comparison. The thick line always corresponds to the condition for which ERPimage and voltage maps are shown. T1 presentation is indicated by the dashed line, T2 presentation by the solid line. Grey areas in the ERP indicate time windows of P3 data analysis. The ERPimage represents a colour-coded view of single-trial EEG amplitudes (trials sorted by time-on-task). (B) Statistical interaction of the factors T2 performance and time window.

bottom). However, as shown in Fig. 2A, for these trials the positivity returned faster to baseline than for T2 detected trials (Fig. 2A, top). This pattern was not only evident in the ERP, but also in the single-trial EEG as reflected in the ERPimage (Fig. 2A). The repeated measures ANOVA (condition factor T2 performance (detected, not detected), factor time window (P3-T1, P3-T2), region factor laterality (left, midline, right), and region-factor anterior–posterior (frontal, central anterior, central posterior, parieto-occipital)) revealed a significant interaction of the factors T2 performance and time window ($F(1,14)=5.25, p=0.038$). This interaction indicates that the T1-related P3 process is larger for trials in which T2 is missed, whilst the T2-related P3 process is smaller in these trials (Fig. 2B). A significant interaction of the region factors with the factors T2 performance and time window ($F(6,84)=4.42, p=0.004$) showed that this effect was not uniform across regions of interest (ROIs), but restricted to the six central posterior and parieto-occipital ROIs.

In a previous study it has been shown that the divergence between detected and undetected T2 starts around 270 ms after T2 presentation with a left-lateralised negativity (Sergent et al., 2005). Therefore, we also tested our data for the presence of a similar effect. When the condition in which no T2 was presented was subtracted from the T2 detected and T2 undetected waveforms, a negative deflection (ND), maximal over the left parieto-occipital ROI, became apparent between 260 and 300 ms post T2, in particular for the T2 detected condition (Fig. 3). An ANOVA with the factors T2 performance (detected, not detected) and ERP (T1-related P3 at ROI posterior central midline, T2-related ND at ROI posterior–occipital left) resulted in a significant interaction $F(1,14)=5.23, p=0.038$, indicating that a larger T1-related P3 in T2 not detected trials was associated with a smaller, less negative ND.

The ERP also showed a number of negative and positive deflections in the time interval 200 ms before to 100 ms after T2 presentation (cf. Fig. 2A). No significant effects involving the factor T2 performance were found for any of these deflections (all $F \leq 3.1$, all $p \geq 0.1$).

Time–frequency analysis

Fig. 4 shows the time–frequency spectra averaged across electrodes and subjects for the conditions T2 detected and T2 not detected. The plots show total activity, resulting from single-trial computation of the wavelet transform and subsequent averaging in the frequency domain. Significant condition effects were found for four of the seven time–frequency windows analysed (for time windows and topographies cf. Fig. 4 and the section on statistical analysis). For the -460 to -340 ms 10 Hz time window a main effect of the T2 performance factor ($F(1,14)=15.48, p=0.001$) and an interaction of T2 performance and the region factor anterior–posterior ($F(3,42)=6.12, p=0.005$) indicated that alpha activity was significantly reduced for the T2 detected condition, particularly at the six central posterior and parieto-occipital ROIs. The second significant condition effect was found for the 13 Hz, 20 to 140 ms window where activity was enhanced for the T2 detected condition (main effect T2 performance, $F(1,14)=9.45, p=0.008$). Analysis of the three 20 Hz time windows revealed that the total activity was significantly reduced in the T2 not detected condition only between -20 and 50 ms (main effect T2 performance, $F(1,14)=5.57, p=0.033$). Finally, ANOVA of the 40 Hz 660 to 760 ms time window revealed a significant tendency of the factor T2 performance ($F(1,14)=4.15, p=0.061$) that was accompanied by a significant interaction of the factors T2 performance and laterality ($F(2,28)=3.83, p=0.034$). This interaction indicates that 40 Hz activity was enhanced significantly for the T2 detected condition at midline and right hemispheric ROIs. The only significant ITC difference was found for the -460 to -340 ms 10 Hz time window. Wilcoxon tests indicated that at the midline central posterior and midline parieto-occipital ROIs ITC was significantly enhanced for the condition T2 not detected ($Z \leq -2.2, p \leq 0.027$).

Possible interrelations between the magnitude of the significant time–frequency effects and the amplitude of the P3 process at the midline central posterior ROI were tested by correlation analyses.

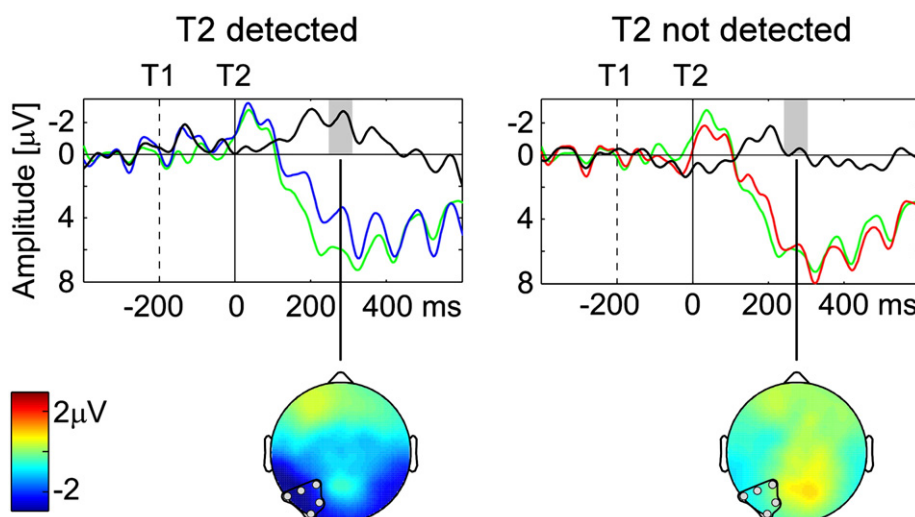


Fig. 3. Event-related potential results for the T2-related negative deflection (ND). ERPs and difference waveforms (top) and voltage maps of the difference waveforms at time window 260 to 300 ms (bottom) for detected (left) and undetected (right) T2 stimuli. The top panel shows the T2 detected condition in blue, the T2 not detected condition in red, and the condition in which no T2 was presented in green. The respective difference waveforms are shown in black. T1 presentation is indicated by the dashed line, T2 presentation by the solid line. Grey areas indicate the time window used to derive the voltage maps and for ND data analysis. ERP and difference waveforms show data averaged across the five channels making up the left parieto-occipital ROI, ROI and channels are outlined in the voltage maps.

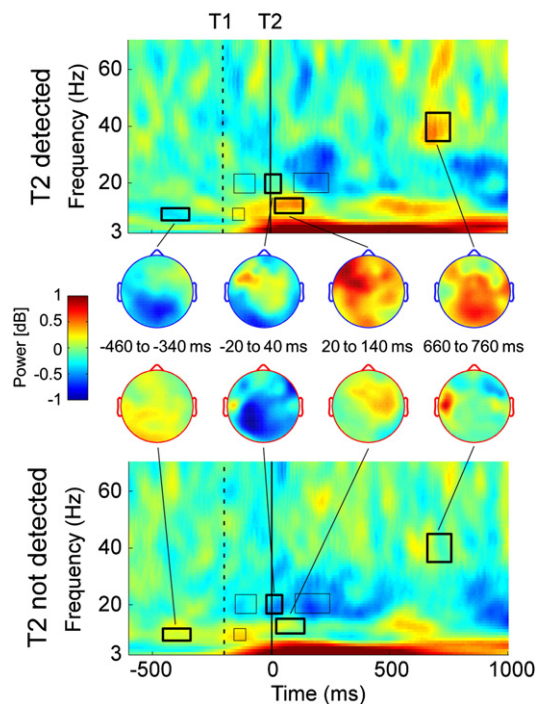


Fig. 4. Results of the time–frequency analysis. Time–frequency plots for T2 detected (top) and T2 not detected (bottom) conditions, averaged across subjects and electrodes. The dashed line indicates presentation of T1, the solid line presentation of T2. Black boxes specify the time–frequency (TF) regions for which *t*-tests indicated significant differences from zero in either condition (cf. Supplementary Fig. 1). The height of the indicated TF regions reflects the frequency resolution (centre frequency $\pm\sigma_f$) of the respective wavelet scale used for subsequent statistical analyses. Boxes are bold for those time–frequency ranges for which statistical tests revealed significant differences between conditions. The two middle panels show the topographical maps corresponding to these time–frequency regions.

For the T1-related P3 process and the 10 Hz time window a negative correlation of $r=-0.38$, $p=0.018$ was found for central posterior ROIs. A negative correlation was also obtained for activity in the 40 Hz time window averaged across all ROIs ($r=-0.35$, $p=0.029$) and the T1-related P3 window. This negative association was mainly observed for five ROIs, namely the central posterior ROIs and the left and midline central anterior ROIs (all $r\leq-0.309$, all $p\leq 0.048$). No significant correlations were found for the remaining two time windows. With regard to the T2-related P3 window, a negative correlation was observed with the activity in the 10 Hz time window averaged across all ROIs ($r=-0.31$, $p=0.05$). The effect was mainly obtained for the parieto-occipital and the midline and right central posterior ROIs (all $r\leq-0.313$, all $p\leq 0.046$). Finally, the 13 Hz time window averaged across all ROIs correlated positively with the T2-related P3 process ($r=0.308$, $p<0.049$), which was mainly due to the ROIs left frontal, left central anterior, midline frontal and midline parieto-occipital (all $r\geq 0.323$, all $p\leq 0.041$).

Phase locking

Statistical analysis of phase locking focussed on possible differences in synchronisation between T2 detected and T2 not

detected conditions at 10, 13, 20 and 40 Hz. Figs. 5A–D shows the time course of the phase locking value averaged across all electrode pairs for these frequencies. Furthermore, the figure illustrates representative examples of the topographical distribution of condition effects, i.e., electrode pairs where synchronisation was significantly enhanced in one of the two conditions as compared to the respective other condition (Wilcoxon test $p<0.05$). During most of the time prior to appearance of T2, phase locking at 10 Hz prevailed for the T2 not detected condition (Fig. 5A). In particular, synchronisation was increased between left and right temporoparietal and occipital and frontal electrode sites. At around 100 ms after T2 presentation the pattern reversed and now 10 Hz synchronisation in the condition T2 detected prevailed. This was in clear contrast to the time course observed for the phase locking at 13 and 20 Hz. At 13 Hz, phase locking steadily increased for the T2 detected condition starting with T1 presentation until approximately 200 ms after T2 presentation (Fig. 5B). The topographical pattern of differences changed dynamically from enhanced synchronisation for the T2 detected condition at primarily right hemispheric sites at -100 ms to an increasing involvement of left hemispheric sites. 188 ms after T2 presentation, when the averaged phase locking value reached its climax, a global enhancement in synchronisation was evident, leaving out only electrodes covering frontal midline scalp regions. Similarly, phase locking at 20 Hz was also increased for the T2 detected condition before and after the presentation of T2 (Fig. 5C). Electrode pairs with significant condition differences overlaid right temporoparietal and left frontal brain regions. This pattern disappeared at around 100 ms after T2 presentation. In the averaged phase locking values, at 40 Hz the prevalence in synchrony seemed to alternate between T2 detected and T2 not detected conditions (Fig. 5D). However, only few electrode pairs displayed significant condition effects and no coherent topographical pattern emerged.

Discussion

The present results clearly support the main hypothesis that P3 activity reflects restricted resources for which T1 and T2 processing has to compete in the AB. By demonstrating an interaction between T1- and T2-related P3 components and T2 detection, the study reports for the first time direct evidence in favour of resource competition as a possible cause of the AB. Moreover, our results demonstrate significant differences in oscillatory brain activity before and during target presentation. In particular, synchronisation in the beta range and a decrease in alpha synchronisation were associated with successful target detection. Finally, an increase in left frontal alpha activity following T2 presentation and enhanced long-range synchronisation also distinguished between detected and missed targets. Accordingly, our study demonstrates that becoming aware of a stimulus involves a complex set of changes in neural dynamics before, during and after target presentation.

ERPs and resource competition

T1- and T2-related P3 components displayed the characteristic centro-parietal topography, but differed in amplitude depending on whether T2 was detected or not, as did the T2-related ND. This result supports and goes beyond previous findings of a relation between T1- and T2-related P3 components irrespective of T2 detection (e.g., Martens et al., 2006; Sessa et al., 2007). It directly

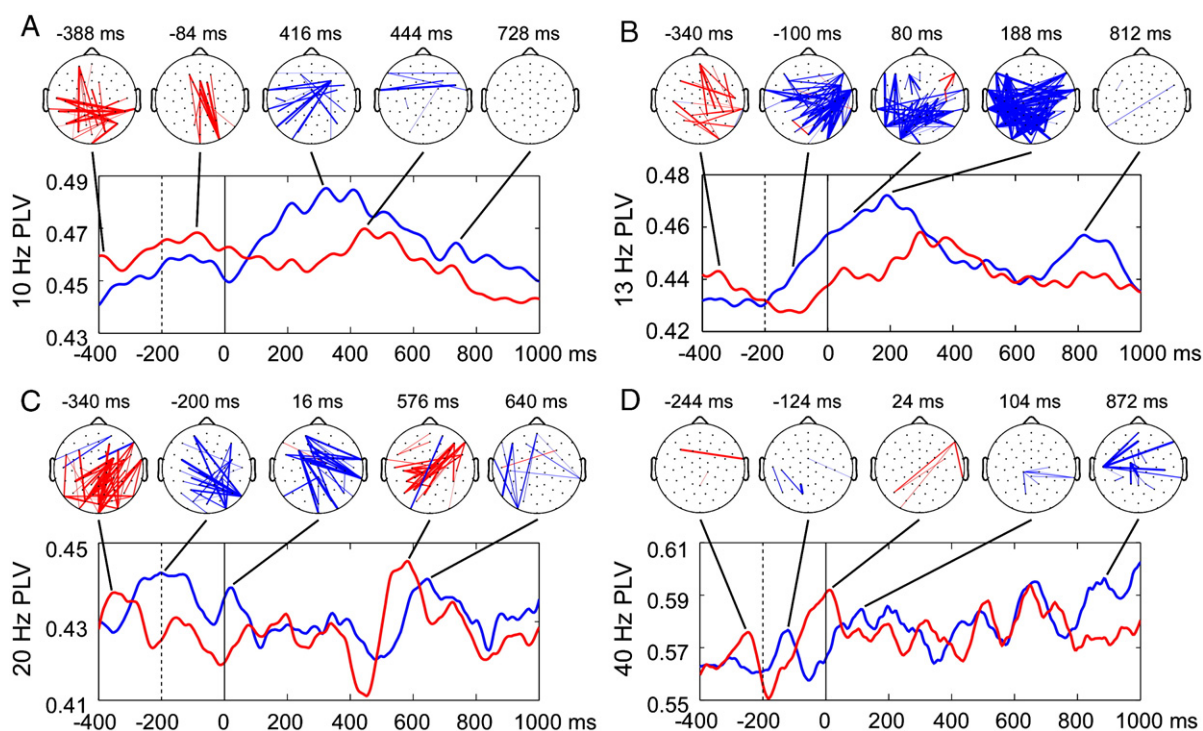


Fig. 5. Results of the phase locking analysis. Phase locking values (PLV) averaged across all electrode pairs irrespective of significant differences, and topographical distribution of significant differences between the conditions T2 detected (blue) and T2 not detected (red) for frequencies 10 Hz (A), 13 Hz (B), 20 Hz (C) and 40 Hz (D). Topographies are shown for times at which the averaged phase locking value indicated synchronisation peaks. Times were chosen based on visual inspection. In the topographical depictions electrode pairs were only included when a significant difference (Wilcoxon test $p \leq 0.05$) between conditions was observed. The significance level is specified by the line thickness, with smaller p -values indicated by thicker lines. In the topographical plots, lines are displayed in blue if the PLV was stronger in the respective time window for the T2 detected condition, and in red if phase locking was enhanced in the T2 missed condition.

supports the assumption that investing fewer resources into detecting T1 leaves more resources for processing T2. It also supports the finding that, in the ERP, conscious detection of T2 is first reflected in a parieto-occipital negative wave that has previously been referred to as N2 (Sergent et al., 2005).

One suggestion is that whether T2 is successfully processed depends on stochastic variations in the strength or duration of the T1-related P3, and the competition of the neural processes underlying the T1-related P3 and the T2-related N2 (Sergent et al., 2005). An alternative account is that in some trials more attentional resources are allocated to T1 than necessary, which then interacts with resources available for T2 processing (Shapiro et al., 2006). An implication particularly of the first suggestion is that differences in neural activity prior to the T1-related P3 should not occur. Our results provide contrary evidence and suggest that differences in processing start before the T1-related P3 can be measured at the scalp surface. This argues against the view that the neural process underlying the T1-related P3 causes the AB (Fell et al., 2002; Sergent et al., 2005) and supports the proposal that resource allocation to T1 takes place before the target is presented (Shore et al., 2001).

The early differences observed at 10 Hz support an attention-related account of differences in the T1-related P3: The desynchronisation might reflect a more efficient suppression of distracter stimuli which, thus, take up less attentional resources. This idea is in accordance with findings of enhanced steady state visual evoked potentials for attended stimulus streams (Müller and

Hübner, 2002). On the other hand, it could reflect a change in pre-stimulus power in ongoing alpha activity, which has been associated with better performance and increased ERPs (Ergenoglu et al., 2004; Hanslmayr et al., 2005). Attentional shifts towards targets have been related to decreased alpha activity in early visual areas, possibly reflecting a state change that is rendered active by top-down processes prior to relevant visual input (Engel et al., 2001; Yamagishi et al., 2005). A decrease in the BOLD signal in secondary visual areas has been associated with detecting T2 (Kranczioch et al., 2005). Our present results provide evidence for either interpretation: the enhanced phase consistency when T2 was missed suggests changes in phase locking. However, additional analyses of the evoked fraction of oscillatory activity (Herrmann et al., 2005) did not show significant differences between conditions, so that the observed changes in the 10 Hz range could also partly be attributed to power changes of spontaneous alpha oscillations.

Dynamics of oscillatory brain activity

Differences between detected and undetected T2 were observed for the total activity at 10, 13, 20 and 40 Hz. Before, after and simultaneously to the total 10 Hz activity increases discussed above, inter-electrode coherence for the T2 missed condition was augmented. Thus, particularly in this condition, large-scale coherent brain activity seemed to be strongly determined by phase locking to the distracters. Hence, one aspect of the AB might be the insufficient suppression of synchronous neuronal activity induced

by the distracter stimuli. This is supported by the observation that the presence of a task-irrelevant distracter stream increases the AB (Visser et al., 2004). However, in parallel to the discussion of 10 Hz total activity it also needs to be considered that differences in synchronisation might reflect internally rather than externally driven neuronal activity.

A left frontal increase of activity at 13 Hz was observed in T2 detected trials, immediately after T2 presentation. The positive correlation with the T2-related P3 suggests that this increase is more closely related to successful processing of T2 than T1. Bursts of alpha activity evoked by sensory stimulation are assumed to derive from a phase resetting of alpha oscillations measured over sensory cortices (Brandt, 1997; Schürmann et al., 1997; Klimesch et al., 2000; Makeig et al., 2002; Makeig et al., 2004). The left frontal topography of the observed activity renders an origin in visual cortex unlikely, and no associated ITC differences were found. Increases in non-phase locked alpha activity over frontal electrode sites and increased inter-regional coherence have been described for internally directed attention shifts (Petsche et al., 1997; Cooper et al., 2006) and working memory tasks (Sauseng et al., 2005). In line with these observations alpha activity has been considered an indicator of top-down processing (Siegel et al., 2000; von Stein et al., 2000; von Stein and Sarnthein, 2000), and left frontal brain areas have previously associated with the reallocation of attention to T2 (Kranczoch et al., 2005). Hence, the increase in 13 Hz activity and long-range synchronisation may reflect the successful, top-down driven internal reorientation of processing resources. Interestingly, behavioural studies have suggested that the AB may be caused by the temporary loss of control over the prevailing attentional set (Di Lollo et al., 2005).

Undetected T2s were associated with reduced 20 Hz activity, particularly during the presentation of the target. Even before the presentation of the targets differences in synchronisation appeared: detecting T2 was associated with increased phase locking between right temporo-parietal and left and right frontal electrodes. This synchronisation pattern bears a striking resemblance with a recently proposed visual attention network (Gross et al., 2004). Here it was similarly found that the degree of synchronous beta activity in the network differentiated between detected and undetected T2 before T1 was presented, and also considerably after T2 presentation. Thus, our results support the idea that synchrony in the beta band, in particular prior and during stimulus presentation, plays an important role in attentional processes, vigilance and visual detection (Wrobel, 2000; Liang et al., 2002; Gross et al., 2004; Kessler et al., 2006; van der Togt et al., 2006).

We did not observe increased inter-electrode coherence at 40 Hz prior to the presentation of the targets for the T2 detected condition (Nakatani et al., 2005). The only difference occurred rather late for total 40 Hz activity and can thus be excluded to be a precursor of successful target processing. In correspondence with other studies (Tallon-Baudry et al., 1998; Gruber et al., 2001; Kranczoch et al., 2006) the late 40 Hz activity may reflect active retrieval of target- and/or response-related information in preparation for the delayed response requirements.

Conclusion

Our study provides evidence that becoming aware of a certain event is characterised by the dynamic interaction of several processes. Desynchronisation and synchronisation in specific frequency ranges may act to prepare the thalamocortical network by

inhibiting task-irrelevant information, activating visual cortex areas and by linking spatially distant members of the network together that are needed for the most efficient processing of information. In the AB, these processes may enable the relatively effortless processing of the first target and the internal reorientation of resources to the fleeting image of the second target. If the interplay between desynchronisation and synchronisation fails, distracter interference increases, the system is less well prepared to process task-relevant information, and more resources need to be invested in processing the first target, sparing little for T2 processing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2007.05.044](https://doi.org/10.1016/j.neuroimage.2007.05.044).

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