

Anticipatory control of long-range phase synchronization

Joachim Gross,¹ Frank Schmitz,¹ Irmtraud Schnitzler,¹ Klaus Kessler,¹ Kimron Shapiro,² Bernhard Hommel³ and Alfons Schnitzler¹

¹Department of Neurology, Heinrich Heine University, Duesseldorf, Germany

²University of Wales, Bangor, Wales, UK

³Leiden University, Leiden, the Netherlands

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Abstract

Everyday human behaviour relies on our ability to predict outcomes on the basis of moment by moment information. Long-range neural phase synchronization has been hypothesized as a mechanism by which ‘predictions’ can exert an effect on the processing of incoming sensory events. Using magnetoencephalography (MEG) we have studied the relationship between the modulation of phase synchronization in a cerebral network of areas involved in visual target processing and the predictability of target occurrence. Our results reveal a striking increase in the modulation of phase synchronization associated with an increased probability of target occurrence. These observations are consistent with the hypothesis that long-range phase synchronization plays a critical functional role in humans’ ability to effectively employ predictive heuristics.

Introduction

Quite some headway has been made in the cognitive neurosciences to identify and locate the neural systems underlying human performance. However, much less is known about how these systems interact with each other, how they communicate and collaborate in generating human cognition. Several approaches have speculated that neural coherence, and phase synchronization in particular, may play an important role in this communication and may even represent the ‘neural language’ in which the communication takes place (Engel *et al.*, 2001; Fries, 2005; Schnitzler & Gross, 2005). Indeed, only recently we (Gross *et al.*, 2004) were able to demonstrate that human performance in an attentional task can be predicted from the dynamics of phase synchronization measures.

This finding suggests that neural synchronization serves as a communication medium to exchange information and, perhaps, control signals between members of the network. The observation that attentional processing of targets was accompanied by increases of synchronization, and the exclusion of non-targets by decreases, might suggest that controlling the amount of communication in the attentional network represents an important way to regulate information processing: relevant events are selected by ‘heavily discussing’ them in the network, while irrelevant events are ‘passed over in silence’. This scenario would nicely fit with the global workspace approaches to human consciousness of Baars (Baars, 2005), and Dehaene and co-workers (Dehaene *et al.*, 1998). However, given the correlative nature of the evidence, converging evidence is necessary to bolster this view. The present report sought for such converging evidence by testing whether phase synchronization is affected by manipulations of cognitive top-down factors.

We used a so-called attentional blink (AB) task (see Gross *et al.*, 2004). This task requires participants to identify two targets from a

stream of briefly presented symbols. The striking finding is that identifying one target is relatively easy but a second target is often missed if it appears in an interval of about half a second after the first (Raymond *et al.*, 1992; Duncan *et al.*, 1994; Shapiro *et al.*, 1994) – as if visual attention ‘blinks’. Apparently, processing the first target draws on some attentional resources that are unavailable for the second target until the first target is completely processed. Functional magnetic resonance imaging (fMRI) studies provide evidence that the attentional network implied in the AB comprises bilateral frontal, temporal, posterior parietal areas, and includes cingulate and occipital areas (Nobre *et al.*, 1997; Hopfinger *et al.*, 2000; Marois *et al.*, 2000; Corbetta & Shulman, 2002). The same areas were implied in our previous magnetoencephalography (MEG) study (Gross *et al.*, 2004) (Fig. 1), which in addition to the ‘activation’ of these components found evidence of ‘phase synchronization’ within this network in the beta band (about 15 Hz). Synchronization was contingent on successful target processing (and report) and beginning approximately 260 ms after target onset. In the present report, we analysed the synchronization–desynchronization pattern as a function of the temporal predictability of the first target.

If synchronization mediates communication between incoming sensory information and higher-order associative areas, and if this interplay would therefore be under top-down control, we would expect the amount of communication in the attentional network (i.e. synchronization among its members) to depend on the strength of target predictability, that is, on expectation. In the present study we tested this hypothesis by performing additional analyses on the previously published work described above (Gross *et al.*, 2004).

Materials and methods

Subjects, paradigm and recordings

Recordings were obtained from 10 healthy, right-handed subjects. All subjects gave their informed consent and the study was performed

Correspondence: Dr J. Gross or Dr A. Schnitzler, as above.

E-mail: jgross@uni-duesseldorf.de or

schnitz@uni-duesseldorf.de

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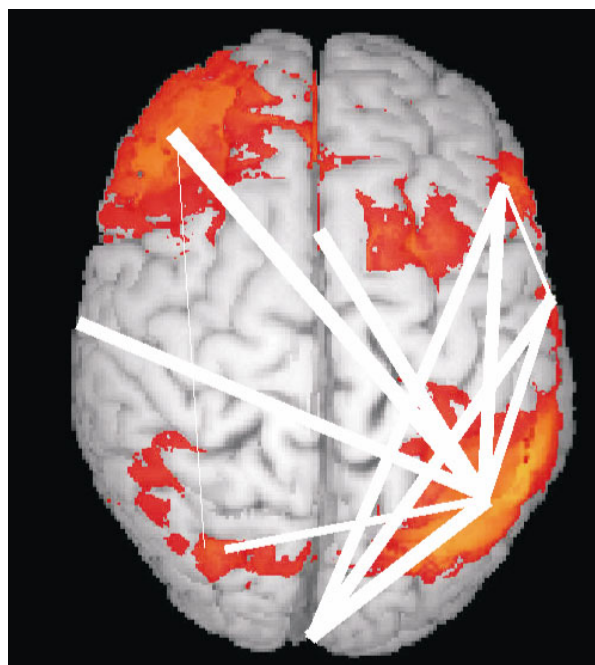


FIG. 1. Connections in the target-related network. Functional maps of oscillatory power in the beta-band were computed for each subject. The functional maps were spatially normalized using SPM99 and a permutation analysis using SnPM99 was performed. Only areas with a significance below $P = 0.05$ (corrected) are shown. Lines mark connections for which the phase synchronization is significantly modulated by target presentation. The displayed connections form the target-related network.

according to the Declaration of Helsinki, and with the approval of the Heinrich-Heine University Ethics Committee.

Subjects were comfortably seated in a reclining chair in front of a visual back projection screen. Each experimental trial consisted of 15 capital letters that were visually presented as a rapid serial visual presentation stream. Zero, one or two of these letters were pre-specified targets, 'X' and 'O' for half of the subjects, and 'L' and 'T' for the other half. The task of the subject was to report (using a button-press device) after each trial whether any target was presented and, if so, which target(s) and in which order. The response was temporally separated from the visual stream to avoid an effect of motor preparation on the data.

Each letter was presented with a visual angle of 3.72 degrees at a distance of 1.2 m. Stimulus duration was 44 ms and the interstimulus interval was 102 ms. Twenty seven to thirty blocks each containing 72 trials were obtained. Trials with zero, one or two target letters were equally probable and randomly intermixed. The subjects were not instructed about the positions of possible target presentations. The first target could occur at position 4, 5 or 6. Accordingly, if a distractor appeared at position 4, the probability for a target presentation increased relative to the probability of its appearance at position 4, with a further increase in probability if another distractor appeared at position 5 (Fig. 2). To the degree that expectations increase proportional to the increasing probability of target occurrence, we predicted that target-locked synchronization would show a commensurate increase as well. Conditional probabilities were 0.25, 0.33, 0.58 for the occurrence of a target at position 4, 5, 6, respectively, given that it has not occurred before (counting only the behaviourally relevant trials).

Neural activity was recorded with a Neuromag-122 whole-scalp neuromagnetometer (Ahonen *et al.*, 1993) in a magnetically shielded

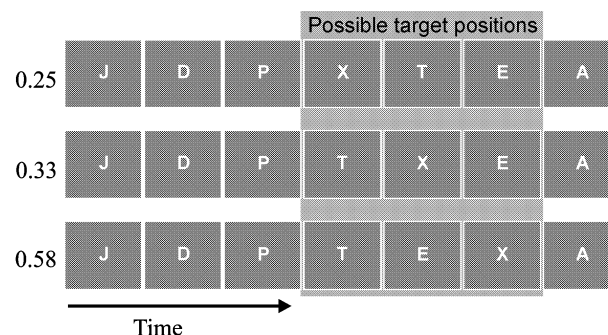


FIG. 2. Schematic representation of predictability of target occurrence. The figure shows the first seven stimuli of the rapid serial visual stream. A target (in this case 'X') could occur at position 4 (see top row), 5 or 6 with equal probability. If a distractor is presented at position 4 (see middle row) the probability is increased for a target to appear at position 5. Presentation of another distractor at position 5 (see bottom row) further increases the probability for target occurrence at position 6. Numbers to the left of each row represent the conditional probability for target occurrence at position 4 (top), 5 (middle) and 6 (bottom), given that no target was presented up to this position [only behaviourally relevant trials (i.e. trials with target) were considered].

room. MEG signals were recorded with pass-bands of 0.03–170 Hz and digitized with 514 Hz. The exact position of the head with respect to the sensor array was determined by measuring magnetic signals from four coils placed on the scalp. High-resolution T1-weighted MRIs were obtained for each subject. Anatomical landmarks (nasion, preauricular points) were localized in each individual and used for the alignment of the MRI and MEG coordinate systems.

Analysis

Synchronization analysis based on the wavelet transform was performed for the frequency band of 13–18 Hz that showed task-dependent modulation and for the following network of cortical brain areas identified in Gross *et al.* (2004) (see Fig. 1): occipital, frontal left, frontal right, temporal left, temporal right, posterior parietal left, posterior parietal right, cingulum. Phase synchronization (SI) quantifies the phase coupling between two areas. It is computed as the absolute value of the sum of the complex phase differences of two signals divided by the number of epochs and is bounded between 0 (indicating no phase locking) and 1 (indicating perfect phase locking). SI computation was based on sensor groups that are most sensitive to a given region and was performed separately for the trials in which the first target was presented at position 4, 5, 6, respectively. To identify the most sensitive sensors, the following procedure was employed. The forward problem was solved for each region of interest. The 10 sensors with the strongest absolute value were chosen for further analysis. To obtain one SI time-course, mean phase differences from two sensor groups were computed. As a control the same computation was performed for trials containing only distractors. The SI time-courses were band-pass filtered (2–10 Hz) and the difference of the 11 points surrounding the maximum (at about 260 ms) and the minimum (at about 114 ms) was computed and subjected to an ANOVA with position (4, 5, 6) and stimulus type (target, distractor) as factors. Both factors showed a significant main effect and interaction ($P < 0.001$).

The connection between left frontal and right posterior parietal areas (Fig. 1) shows the strongest target-related synchronization. To further investigate the evidence for top-down processing the phase difference between both areas in the 15 Hz frequency band was computed and averaged across subjects.

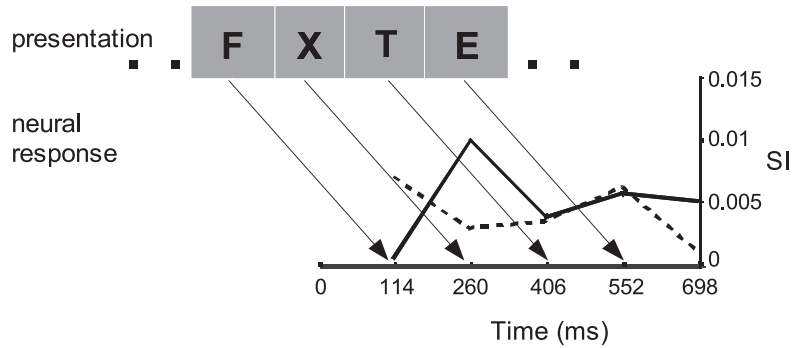


FIG. 3. Modulation of phase synchronization (SI) by targets as compared with distractors. The solid line shows the SI in trials where a target occurs, whereas the dashed line shows the SI in trials with only distractors. The x-axis specifies time relative to target onset. Each point represents the mean SI in a 60-ms-long window centred at 260 ms after the respective stimulus. For illustration, part of a possible letter sequence (with target X) is shown in the upper part of the figure. Synchronization values at 260 ms quantify the network synchronization to the target. At 114 ms a reduced synchronization is evident. This may represent the network response to a distractor that is followed by a target. The figure illustrates that target X is already partly processed at 114 ms and obviously affects the processing of the distractor by reducing the synchronization.

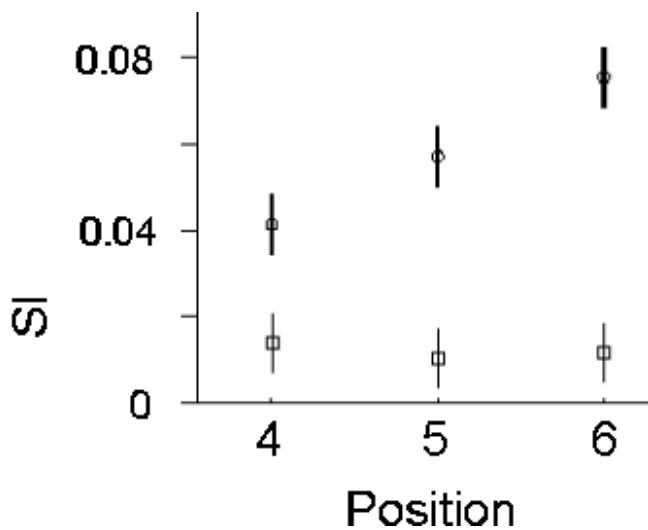


FIG. 4. Modulation of phase synchronization (SI) by targets at different positions in the presentation stream. The mean of 11 points surrounding the maximum (at about 260 ms) and the minimum (at about 114 ms) was computed for all subjects and connections of the target-related network for targets (circles) and distractors (boxes). Lines extending from the mean indicate the standard error. The modulation (difference of synchronization and desynchronization) increases with the position only for target trials.

Results

Figure 3 illustrates the differential synchronization within the network (see Fig. 1) to targets and distractors. The network responds to targets with a synchronization that is preceded by a desynchronization. Part of a possible stimulus sequence (with target X) is shown in Fig. 3. It illustrates that the network response at 114 ms is likely affected by the target (that is presented at time 0), which apparently induces a desynchronization of distractor processing. Evidence for direct competition between succeeding stimuli has been consistently found in behavioural (e.g. Hommel & Akyurek, 2005; Potter *et al.*, 2002) and electrophysiological studies (Kessler *et al.*, 2005).

More important for present purposes, we tested whether the synchronization–desynchronization pattern depended on predictability of the target. To do so, we analysed the difference between target-related desynchronization (at 114 ms) and synchronization (at 260 ms) as a function of the temporal position of the target (presented

TABLE 1. Synchronization index (SI) for targets and distractors

	Time (ms)	Position 4	Position 5	Position 6
Desynchronization				
SI for target	114	−0.01	−0.016	−0.02
SI for distractor	114	−0.01	−0.006	−0.012
Synchronization				
SI for target	260	0.01	0.018	0.02
SI for distractor	260	0.008	0.011	0.004

at positions 4, 5 and 6 in the stimulus sequence; see Fig. 4). This combined representation of the synchronization–desynchronization pattern seemed appropriate, as there were no differential effects, i.e. synchronization and desynchronization increased equally with target positions (Table 1). Two means with non-overlapping lines in Fig. 4 are significantly different ($P < 0.05$, Tukey–Kramer correction for multiple tests). Target trials are shown with a circle representing the mean, whereas the mean in distractor trials is marked with a square. Target trials show a significantly stronger modulation (i.e. stronger desynchronization and stronger synchronization) compared with distractor trials. In addition, the amount of modulation in target trials increases with the conditional probability. No increase is evident in distractor trials, which rules out that the observed effect is simply due to the stimulus position. Given all possible combinations of the strength of desynchronization and synchronization in the three conditions (targets at position 4, 5, 6, respectively), the probability for the observed effect to occur by chance is 0.0014.

Furthermore, phase differences in the interaction between left frontal and right parietal cortex revealed evidence for top-down and bottom-up processes. Within the first 400 ms following target presentation mean phase delays reversed from 20 ms (left frontal cortex leading right parietal cortex) to −20 ms (right parietal cortex leading left frontal cortex).

Discussion

Recently, Gross *et al.* demonstrated 8 Hz long-range synchronization among cerebellum, thalamus, primary and premotor cortex, which correlated with 8 Hz fluctuations of slow finger movements (Gross *et al.*, 2002). This synchronization is likely to represent the communicative link within a neural network that uses incoming

sensory feedback from the movement to predict the consequences of previous motor commands and to match them against the actual consequences. Similarly, but in the domain of perception, multiple cell recording studies in the cat have revealed expectation-induced synchronization within the visual cortex (von Stein *et al.*, 2000), as well as between visual and parietal, and parietal and sensorimotor areas (Roelfsema *et al.*, 1997; Fries *et al.*, 2001). In addition, a close correlation between hazard rate and cortico-muscular coherence in the gamma band has been demonstrated (Schoffelen *et al.*, 2005).

If long-range synchronization implements top-down control, it should change with the temporal anticipation of a target. Indeed, we found that the processing of a target event is associated with a particular pattern of neural synchronization (to the target) and desynchronization (to competing distractors), and that this pattern is more pronounced for targets that are more predictable. This suggests that expecting a target is associated with the implementation of a kind of attentional set that makes targets accessible to all members of the attentional network but prevents distractors from getting access to the network. In the words of Baars (Baars, 2005) and Dehaene and co-workers (Dehaene *et al.*, 1998), anticipated targets are granted a (more) privileged access to the 'global workspace' that allows several systems to work on the same event. This global workspace may be created by the communication between neural systems and exist only to the degree that global communication exists. Considering that targets are to be reported, which requires conscious representation, whereas non-targets do usually not reach consciousness, our findings are consistent with the idea that the degree of conscious representation and the amount of neural synchronization are systematically related (Baars, 2005).

The strongest connection in the attentional network implied in the AB task was evident between left frontal and right parietal areas. Phase differences between these two areas are consistent with neural conduction velocities and might be taken to indicate the exchange of control signals, that is, of the interaction of bottom-up and top-down processes. Whereas temporo-parietal areas have strongly been linked to attentional operations for both spatial and temporal tasks (cf. Shapiro *et al.*, 2002), frontal areas have been implicated to mediate working memory operations required to maintain target-defining templates during the AB task. The present findings are thus an important link in implicating synchronization as the mechanism by which these two cortical areas interact in performing a task such as the AB, which requires both top-down and bottom-up processing.

It seems reasonable that, during the more than 2000 trials presented in our experiment, subjects implicitly extracted the rules underlying target presentation (i.e. 'when' targets are likely to appear), and applied them to configure top-down attentional control systems. However, given that the letter stimuli were separated by a mere 146 ms, updating this configuration to reflect the current presentation probability must proceed very rapidly. Our results argue for a plausible mechanism – synchronization – that can operate within the necessary temporal constraints. In support of this contention, evidence suggests that orienting attention in time can take place as soon as 100 ms after a cue (Griffin *et al.*, 2001; Nobre, 2001).

In summary, we suggest that synchronization within a network of cortical structures mediating a given behavioural task provides a viable mechanism by which the human brain is able to link rapidly changing perceptual information with predictions about future events.

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Abbreviations

AB, attentional blink; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; SI, synchronization index.

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