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Prestimulus oscillations predict visual perception performance between and within subjects

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In the present study, the electrophysiological correlates of perceiving shortly presented visual stimuli are examined. In particular, we investigated the differences in the prestimulus EEG between subjects who were able to discriminate between four shortly presented stimuli (Perceivers) and subjects who were not (Non-Perceivers). Additionally, we investigated the differences between the subjects perceived and unperceived trials. The results show that Perceivers exhibited lower prestimulus alpha power than Non-Perceivers. Analysis of the prestimulus EEG between perceived and unperceived trials revealed that the perception of a stimulus is related to low phase coupling in the alpha frequency range (8–12 Hz) and high phase coupling in the beta and gamma frequency range (20–45 Hz). Single trial analyses showed that perception performance can be predicted by phase coupling in the alpha, beta and gamma frequency range. The findings indicate that synchronous oscillations in the alpha frequency band inhibit the perception of shortly presented stimuli whereas synchrony in higher frequency ranges (>20 Hz) enhances visual perception. We conclude that alpha, beta and gamma oscillations indicate the attentional state of a subject and thus are able to predict perception performance on a single trial basis.

Keywords: EEG; Oscillations; Prestimulus; Phase coupling; Perception; Alpha

When a visual stimulus is flashed shortly into observers' eyes, the single observers differ largely in whether they correctly perceive the stimulus, or not. Moreover, the same observer may perceive the same stimulus on some occasions but not on others. The present study searches for the prestimulus brain mechanisms that mediate this variability. Such mechanisms should differentiate between perceiving and non-perceiving observers and should also differentiate between a single observer's perceived and unperceived trials. The variability in perception performance is likely to stem from the subjects' attention capabilities which should be reflected in ongoing oscillatory brain activity, already present prior to stimulus presentation.

Basically, an oscillation can be described by two parameters: amplitude and phase. In EEG oscillations, the amplitude (or power) of an oscillation in one electrode is regarded to be a measure of synchrony between local neuronal assemblies, whereas phase coherence across two electrodes can be used to measure synchrony between distant neuronal assemblies (Varela et al., 2001; Fries, 2005). Ongoing oscillations in the alpha frequency range (around 10 Hz) are linked to attention processes (Ray and Cole, 1985; Klimesch et al., 1998; Worden et al., 2000; Thut et al., 2006). In particular, several studies have shown that the amplitude of ongoing alpha oscillations exert a big influence on visual perception performance (Ergenoglu et al., 2004; Hanslmayr et al., 2005a). These studies demonstrated a negative relationship between alpha power and perception performance (Hanslmayr et al., 2005a; Ergenoglu et al., 2004; Thut et al., 2006), indicating that low prestimulus alpha power promotes good visual perception performance. Alpha amplitudes have also been found to increase when subjects shift their attention inwards (Ray and Cole, 1985; Cooper et al., 2003) and decrease if a stimulus is expected (Worden et al., 2000; Sauseng et al., 2005a; Thut et al., 2006). Moreover, alpha power may increase contralaterally to the hemifield where a visual stimulus has to be ignored (Rihs et al., 2007; Kelly et al., 2006). Taken together, these and other findings have led to the suggestion that alpha oscillations represent an active filter mechanism (rather than passive idling) indicating that the brain is inhibited when alpha oscillations are high in amplitude (Klimesch et al., 2007).

With respect to phase coupling, several studies showed that stimulus-induced phase coupling in higher frequency ranges (>15 Hz) is critically related to perception and binding processes (Rodriguez et al., 1999; Gross et al., 2004). A recent study by

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Melloni et al. (2007) showed that stimulus-induced long-range gamma synchrony (around 40 Hz) was positively correlated with conscious visual perception. Several studies, however, have linked synchrony in the gamma frequency band not only to perception and binding processes, but also to mechanisms of attention and expectation (see Engel et al., 2001 for a review). For example, the phase-locking of evoked gamma activity predicts subsequent reaction times (Fründ et al., 2007). Furthermore, the expectation of a stimulus modulates gamma activity (von Stein et al., 2000) and long range synchrony is already enhanced when a stimulus is only expected and enhanced further after stimulus presentation (Roelfsema et al., 1997). With respect to the alpha frequency range, it has been shown that an increase in phase coupling indicates a top-down shift of attention towards a relevant stimulus (von Stein et al., 2000) or a spatial shift of attention towards a cued location (Sauseng et al., 2005a). Thus, it may be hypothesized that both amplitude and phase of ongoing oscillations in the alpha and higher frequency ranges (>20 Hz) indicate the state of attention or expectation and thus modulate the perception of visual stimuli presented at perception threshold (Arieli et al., 1996).

So far, a number of studies have investigated the role of prestimulus amplitude for perceptual performance, but to our knowledge no one has considered the relationship between prestimulus phase coupling and perceptual performance. Also, some studies sought for differences between subjects (e.g. good vs. bad performers), whereas others sought for the differences within subjects (correct vs. false responses). The aim of this study was to investigate the role of prestimulus synchrony as measured by amplitude and phase coupling for visual perception. First, we investigated the mechanisms which differentiate between subjects who are able to perceive the stimuli and those who are not. Second, we investigated the mechanisms which differentiate between the perceived and unperceived trials within subjects. In addition, we explored the question whether prestimulus oscillations can be used to predict perception performance on a single trial basis. Doing so, we used a masked perception task in which four different letters (p, q, b, d) were presented very briefly (57 ms; see Fig. 1) and the subjects' task was to press one of four buttons, indicating which letter the subject perceived.

Materials and methods

Subjects

Thirty-five subjects participated in the experiment. Five subjects were excluded, either because their EEG was heavily contaminated by movement artefacts, or because their performance was significantly below chance level (<17%; $p<0.01$), indicating that they did not follow task instruction. From the remaining 30 subjects (21 females; mean age: 23.07; range: 20 to 36), 26 were right-handed. All subjects gave written informed consent, had normal or corrected to normal vision, and reported no history of neurological disease.

Fig. 1. Example of one trial. After a fixation cross appeared for 1500–1700 ms, a target stimulus was shown very shortly (57 ms). Thereafter, a mask which consisted of an overlay of all four target stimuli (p, q, b, d) appeared. The subjects were instructed to respond as fast as possible to the four target stimuli by pressing one of four buttons.

Procedure

In the perception task, four different letters (p, q, b, d) had to be discriminated. The letters were shown on a computer screen (70 Hz refresh rate) for 57 ms. After the target stimulus, a mask which consisted of an overlay of all 4 target letters appeared for 500 ms. During the interstimulus interval (ISI) a fixation cross appeared on the screen. The ISI was jittered between 1500 and 1700 ms to avoid expectancy effects. The structure of one single trial is shown in Fig. 1. Participants were instructed to indicate on a conventional computer keyboard which of the four target letters they had perceived by pressing one of four buttons with their dominant hand. They were told to respond as fast as possible and to guess if they did not perceive the target letter. The perception task consisted of 160 trials, 40 trials per letter. The sequence of the letters was randomized separately for each subject.

EEG recording

The EEG was recorded from 64 Ag–AgCl electrodes positioned according to the extended 10–10-system. EEGs were recorded against a reference electrode placed at FCz and were later re-referenced against a common average reference. The vertical and the horizontal electrooculogram (EOG) were recorded from two additional channels to control for eye movements and blinks. Impedances were kept below 10 kΩ. A Brainamp MR+ amplifier (Megis, BrainVision, Gilching, Germany) was used for data acquisition. Sampling rate was 500 Hz. Frequencies between 0.15 and 70 Hz with a Notch-filter at 50 Hz were recorded. Prior to data analysis, EEG-data were corrected for EOG artefacts using calibration data to generate individual artefact coefficients and the PCA method (Ille et al., 2002). Remaining artefacts were excluded by visual inspection.

Statistical analysis

On the basis of their performance level, subjects were split into two groups, using a binomial test. According to this procedure, participants were split into subjects with performance significantly above chance level (more than 33%; $p<0.01$), termed Perceivers ($N=15$; mean performance: 58%), and subjects who were at chance level, termed Non-Perceivers ($N=15$; mean performance: 26%).

To avoid influences from outliers, and because some variables failed to be normally distributed (Detection Performance, Alpha Power), non-parametric statistical methods were used throughout the whole analyses. For between-subjects comparisons, Mann–Whitney *U*-tests were calculated. Non-parametric correlations were calculated with Spearman correlations. For within-subjects comparisons, non-parametric Wilcoxon-tests were carried out. Because Non-Perceivers showed a perception performance at chance level, the data from these subjects were skipped for the correlation and the within-subjects analyses.

To calculate power and phase coupling, the software package BESA (© MEGIS Software BESA v5.1.6) was used. The data was filtered in a time-window of 1 s pre-stimulus to 1 s post-stimulus and a frequency range of 4 to 70 Hz. Time–frequency resolution was set to 25 ms and 2 Hz for the lower frequency bands (4–30 Hz) and to 10 ms and 5 Hz for the higher frequency bands (30–70 Hz). This was done to pick up best the activity of each frequency (analogous to a Morlet Wavelet). Prior to statistical comparisons, the time–frequency data were collapsed over a pre-stimulus interval of 500 ms (−500 ms to 0 ms) and for six different frequency bands (4–8 Hz, 8–12 Hz, 12–20 Hz, 20–30 Hz, 30–45 Hz, and 55–70 Hz). Power was calculated for each electrode, and thereafter pooled for parieto-occipital electrode sites (PO7, PO3, POz, PO4, PO8, O1, Oz, O2) because differences were greatest at these locations (Fig. 3a).

Phase coupling was calculated for each electrode pair with the Phase Locking Value (PLV). The PLV is a measure of phase coupling between two electrode sites and ranges from 0 (no phase coupling) to 1 (perfect phase coupling; see Lachaux et al., 1999, for details). The PLV is computed by calculating the phase difference between two electrode sites (Δ phase) for a certain time point and single trial (Fig. 2a). Thereafter, the circular mean of Δ phase is calculated across all single trials (Fig. 2b). This yields a vector with a certain direction, representing mean Δ phase, and a certain length, representing the PLV. If phase coupling is low, the length of the mean vector is close to 0, and if phase coupling is high, the length of the mean vector is close to 1 (Fig. 2b). Because it is known that unequal trial numbers have detrimental effects on phase measures, the number of correct and false response trials were held constant for each subject. This was achieved by selecting a random sample of trials for the condition with more trials. E.g., if one subject had 67 correct response trials and 82 false response trials, a random sample of 67 false response trials was chosen. Because we wanted at least 25 trials to remain for analysis for each subject, one subject (17 false response trials) was excluded from this analysis. To account for multiple testing, a two-stage randomization procedure was carried out. At first, Wilcoxon-tests were calculated for each electrode pair to investigate which electrode pairs show a significant difference between the two conditions ($p<0.005$; two-tailed). Second, a randomization test (Blair and Karniski, 1993) based on 5000 permutation runs was carried out. This procedure evaluates whether a given number of electrode pairs, exhibiting a significant difference between two conditions (perceived vs. unperceived), is expected by chance. If the p-value (p_{corr}) of this randomization test is below 0.05, less than 5% of the permutation runs exhibited equal or more electrode pairs with a significant difference between the two conditions.

To determine whether phase coupling can be used to predict perception performance on a single trial basis, the following procedure was carried out. (i) The mean phase difference (Δ phase) was calculated across all single trials (Fig. 2a). (ii) The deviation from the mean Δ phase was calculated for each single trial, frequency band, and time point. Deviation from mean Δ phase was calculated using the circular variance procedure (see Fisher, 1993). This measure yields a value between 0 and 1, where values close to 0 indicate low deviation and values close to 1 indicate high deviation from mean (see Fig. 2c). (iii) Deviation from mean Δ phase was collapsed for the prestimulus interval (−500 to 0 ms). Thereafter, the single trials were grouped into 10 bins (from lowest deviation to highest deviation). (iv) In a final step, perception performance was calculated separately for each bin (percent hits). This calculation was carried out only for those frequency bands and electrode pairs showing significance in the PLV analysis. To determine phase, a Gabor transformation (for details see Gruber et al., 2005) was used. Again time–frequency resolution was adjusted differently for each frequency band.

Results

Between-subjects analysis

Mean detection rate in the perception task was 42% with high variability ranging from performance at chance level (around 25%) to nearly perfect performance (90%). Perceivers showed a mean detection rate of 58% and Non-Perceivers showed a mean detection rate of 26%, which is around chance level. Analysis of power in the range of 4 to 70 Hz revealed that Perceivers showed significantly less pre-stimulus alpha power (8 to 12 Hz) than Non-Perceivers ($Z=-2.261$; $p<0.05$). No significant effects were observed in the other frequency ranges (4–8, 12–20, 20–30, 30–45 and 55–70 Hz). The difference in alpha power was most evident at parieto-occipital electrode sites during the time window of 500 ms prior to stimulus presentation (Fig. 3a). In addition, prestimulus alpha power was functionally related to Perceivers' perception performance, as indicated by a negative non-parametric correlation between alpha power and perception performance ($r=-0.59$; $p<0.025$; two-tailed; see Fig. 2b). To investigate whether the subjects already differed at the level of their resting alpha power, the power-spectra of a resting condition with eyes open, which was recorded before the experiment started, were compared. Similarly to prestimulus alpha power, Perceivers showed significantly less resting power in the alpha range than Non-Perceivers ($Z=-2.136$; $p<0.05$; Fig. 2c). No differences were found in the other frequency ranges.

Within-subjects analysis

Because Non-Perceivers showed a performance at chance level, only the data of the Perceivers were used for the analysis between perceived and unperceived trials. The results of the prestimulus phase coupling analysis are plotted in Fig. 4. The Perceivers' ongoing pre-stimulus EEG (500 ms prior to stimulus onset) revealed reduced phase coupling in the alpha frequency range (8 to 12 Hz) when the subjects perceived the stimulus and stronger phase coupling when the subjects failed to perceive the stimulus ($p_{\mathrm{corr}}<0.01$; Figs. 4a and c). The inspection of the topography of this effect shows that mainly fronto-parietal electrode sites contributed to this effect (Fig. 4a). Interestingly, the opposite pattern was observed in the higher frequency ranges (20–45 Hz). More prestimulus phase coupling in the beta (20–30 Hz; $p_{\mathrm{corr}}<0.01$) and gamma (30–45; $p_{\mathrm{corr}}<0.05$) frequency range was present in those trials, in which the subject successfully perceived the stimulus (Figs. 4b and c). No significant effects were found for the other frequency ranges as tested by a non-parametric randomization test (see Materials and methods). Perceivers and Non-Perceivers did not differ in phase coupling, and no differences between perceived and unperceived trials were found in prestimulus alpha power, showing that the results in alpha phase coupling were not artificially created by power effects. Thus, good perception performance was related to reduced prestimulus alpha and enhanced beta and gamma phase coupling.

To determine whether prestimulus phase coupling was predictive of the subjects' perception performance on a single-trial basis, the prestimulus deviation from the mean phase difference (Δ phase) was calculated for each subject and single-trial (see Materials and

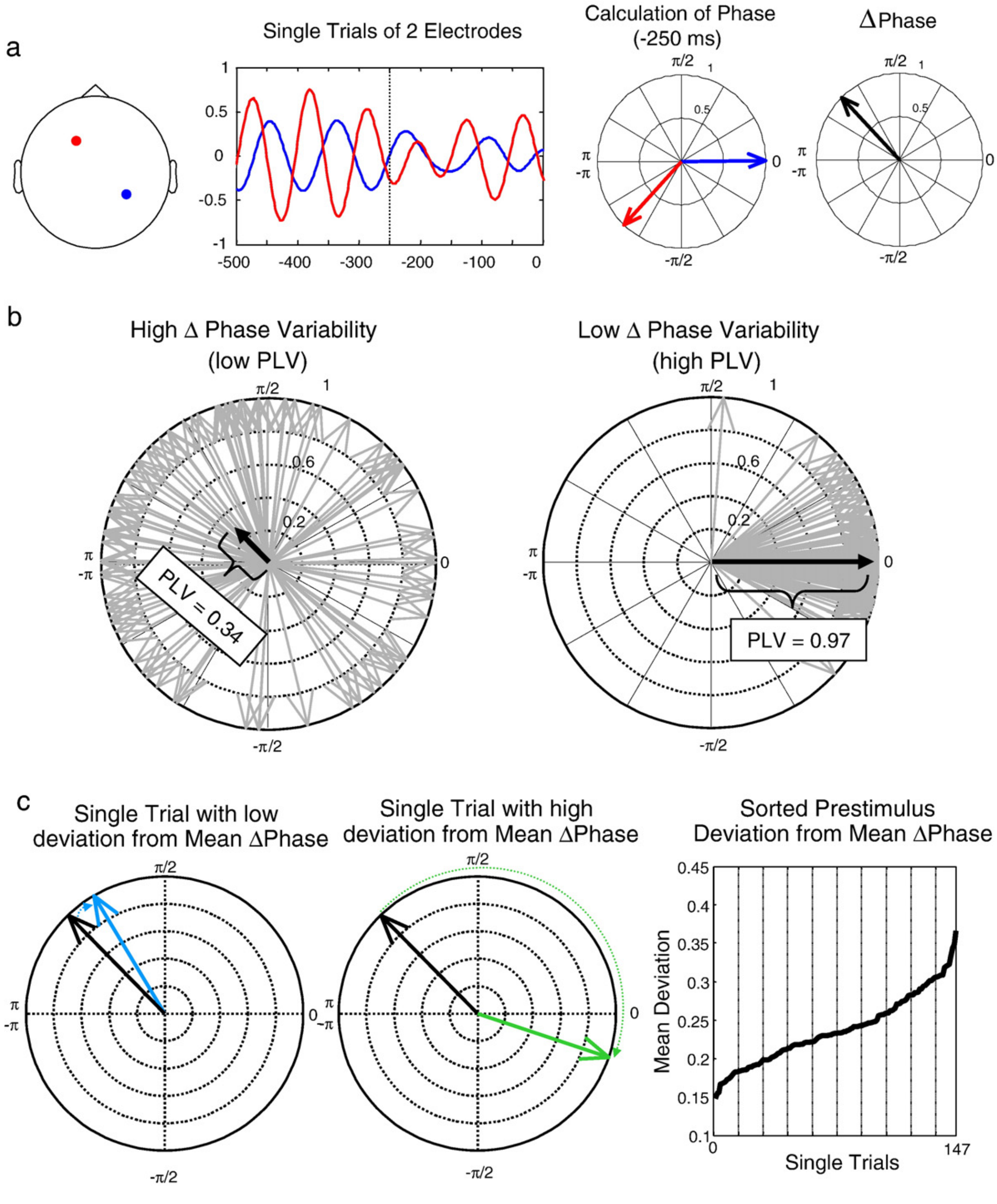

Fig. 2. (a) The calculation of the mean phase is plotted. As an example, two Gabor filtered single trials (10 Hz) of a frontal (red line) and a parietal electrode (blue line) are shown for the prestimulus interval (−500 to 0 ms). The phase of these two single trials is extracted for each time point (e.g. −250 ms). Thereafter, the phase difference (Δ phase) is calculated (black arrow). (b) Phase differences (grey arrows) and the mean phase difference (black arrow) is plotted for two sets of single trials. The example on the left plots a set of single trials with high Δ phase variability which results in a short mean vector (low phase locking), and the example on the right plots a dataset with low variability and a long mean vector (high phase locking). (c) The deviation from mean phase is plotted for two single trials. The example on the left depicts a single trial with low deviation (light blue vector) and the example in the right shows a single trial with high deviation from mean Δ phase (light green vector). The diagram on the right plots the phase deviation data of one subject. Deviation from mean Δ phase is scaled on the *y*-axis and the single trials are scaled on the *x*-axis. The vertical lines indicate the 10 bins which were used for calculation of perception performance.

methods). Thereafter, the single trials were grouped in 10 bins from lowest phase deviation (1st bin) to highest phase deviation (10th bin) and detection performance was calculated separately for each bin. The PLV analysis suggests that the detection of a stimulus is related to low alpha phase coupling, thus the single-trial analysis should reveal that perception performance increases monotonically with increasing deviation from mean Δ phase. The results are plotted in Fig. 4d showing that mean perception rate increases in a linear

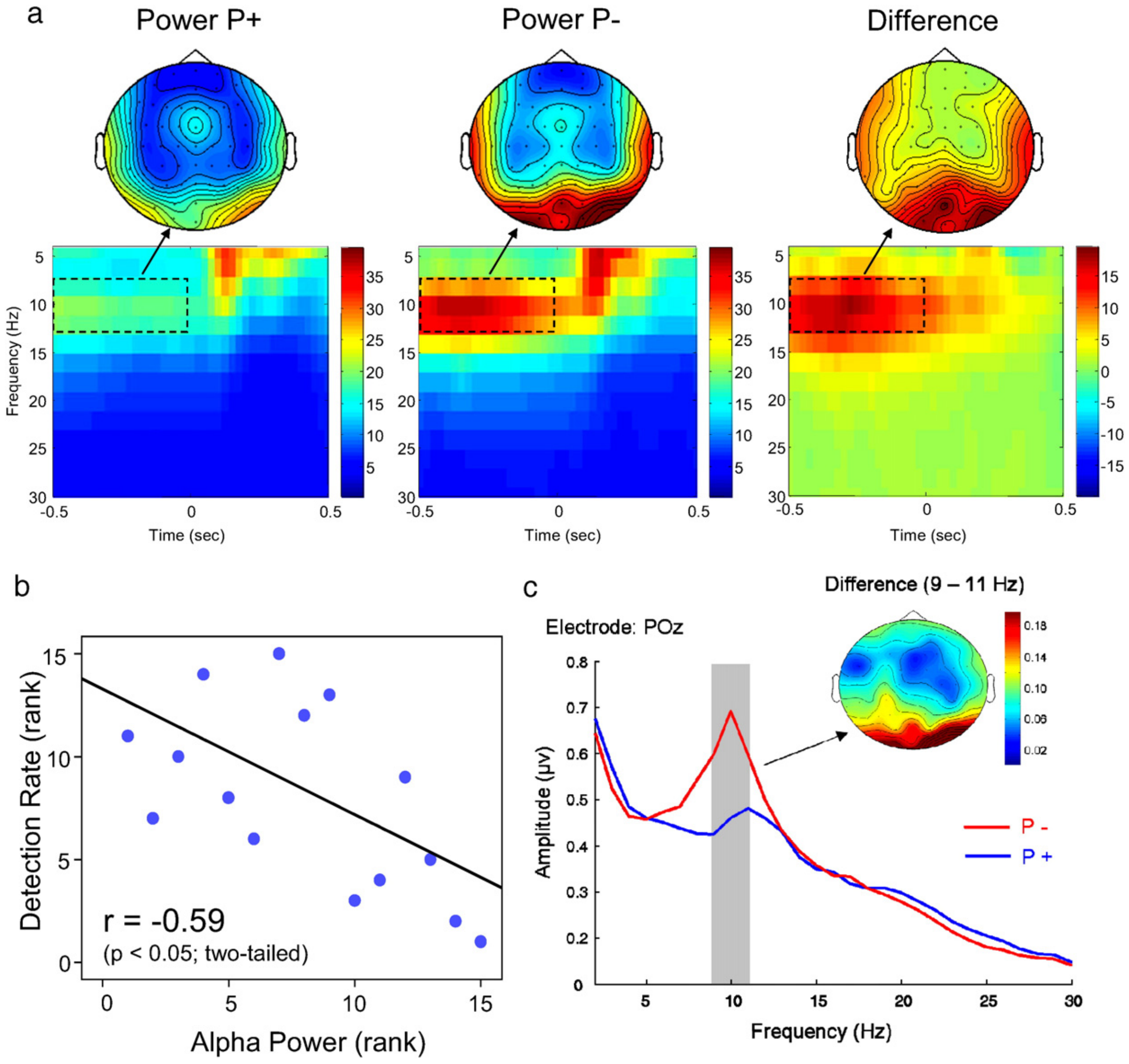

Fig. 3. The results of the between-subjects analysis (Perceivers vs. Non-Perceivers) are plotted. (a) Time–frequency plot of power is shown for the electrode O2 exemplarily. Stimulus is presented at time 0. Differences between Perceivers (P+) and Non-perceivers (P−) are most evident in the alpha frequency range (8–12 Hz) in the time window of 500 ms prior to stimulus presentation. The scalp maps indicate that alpha power was strongest at parieto-occipital electrode leads. The square indicates the time window which was used for statistical comparison. (b) The scatterplot between rank transformed alpha power (*y*-axis) and perception performance (*x*-axis) is shown. Alpha power was collapsed for parieto-occipital electrode sites. (c) Power spectrum of the resting condition with eyes open is plotted for electrode POz exemplarily. The resting condition was recorded prior to the start of the experiment. Perceivers (P+) showed significantly lower alpha amplitudes than Non-Perceivers (P−). The grey bar indicates the frequency window that was used for statistics (9–11 Hz). Power spectra were calculated using a Fast Fourier Transformation (FFT).

manner with increasing alpha phase deviation (as revealed by regression analysis; $F_{1,8}=100.51$; $p<0.001$). Perception performance increased from 37% (lowest deviation) to 76% (highest deviation) which was supported by a significant non-parametric Friedman test ($\mathrm{Chi}^2=78.21$; $p<0.001$; two-tailed). In contrast, beta and gamma phase deviation analysis should reveal that perception performance decreases monotonically with increasing deviation from mean Δ phase. The results of this analysis are plotted in Figs. 4e and f. Regression analysis revealed highly significant results for the beta ($F_{1,8}=539.68$; $p<0.001$) and gamma frequency band ($F_{1,8}=499.72$; $p<0.001$). For both, the beta and gamma band, perception performance was nearly perfect (above 90%) for the bin with the lowest deviation and decreased to chance level (around 20%) for the bin with the highest deviation from mean Δ phase. These results were also supported by non-parametric Friedman tests for both the beta frequency range ($\mathrm{Chi}^2=116.24$; $p<0.001$) and the gamma frequency range ($\mathrm{Chi}^2=119.89$; $p<0.001$).

Discussion

The main findings of this study are that ongoing alpha, beta, and gamma oscillations predict perception performance between and within subjects. Different measures of these oscillations were related to perception performance, though in different ways. Whereas alpha power distinguished between subjects who were able to perceive the stimulus and the subjects who were not, alpha,

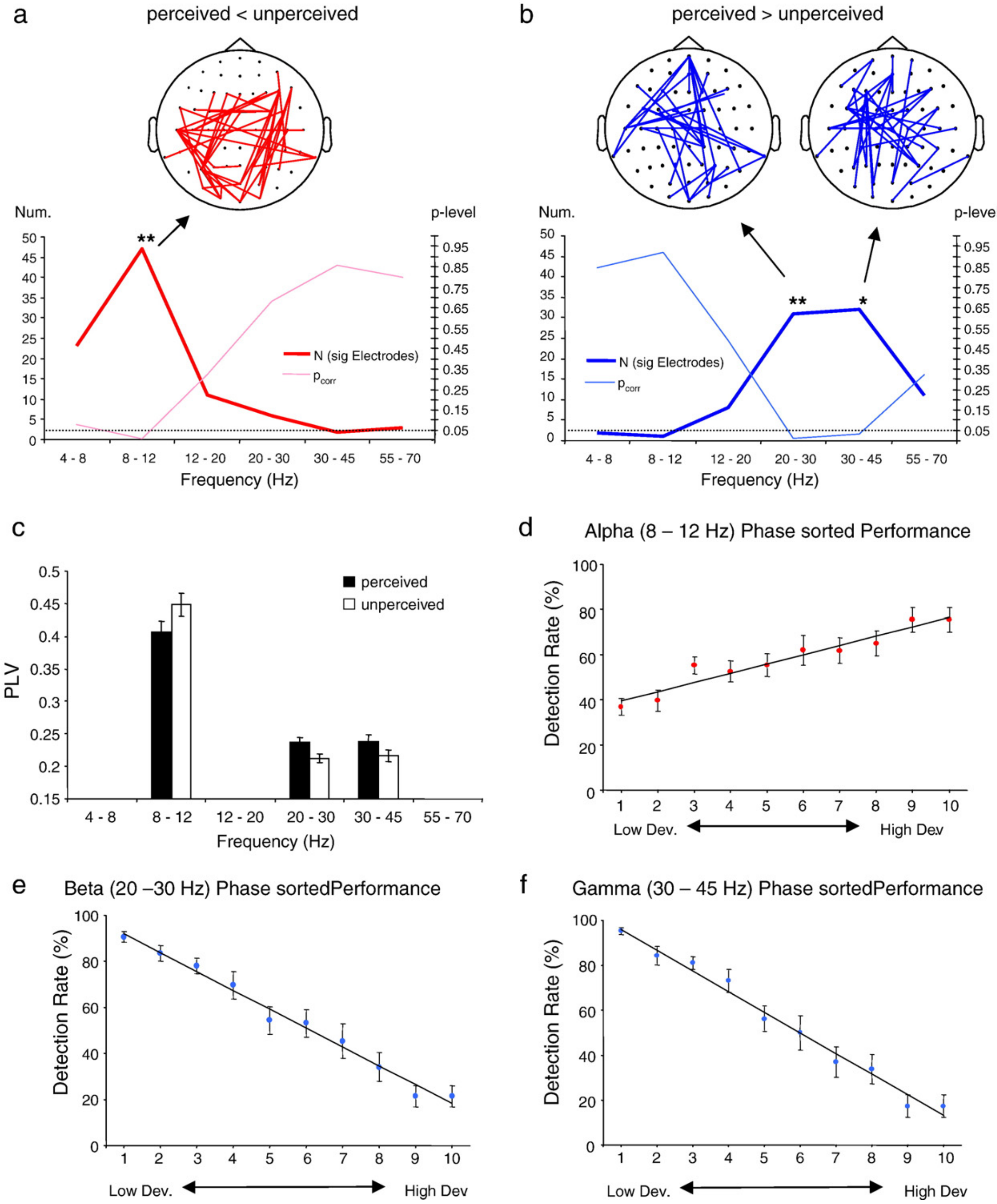

Fig. 4. The results of the within-subjects analysis are shown. Perceived trials show decreased prestimulus (−500 to 0 ms) phase coupling in the alpha frequency range (a), but increased phase coupling in the beta (20–30) and gamma (30–45 Hz) range (b). The scalp maps display the topography of the electrode pairs where phase coupling is significantly decreased (red lines) and where phase coupling is significantly increased (blue lines) for perceived trials. The diagrams show the results of the phase coupling statistics for each frequency bin (scaled on the *x*-axis). The thick red (a) and blue (b) lines (scaled on the left *y*-axis) show the number of electrode pairs revealing significant difference between perceived and unperceived trials ($p < 0.005$; Wilcoxon-test). The light red (a) and blue (b) lines show the *p*-level of the randomization test (scaled on the right *y*-axis). (c) Mean PLV is plotted for those frequency bands and electrode pairs exhibiting significance in the randomization test. The error bars indicate standard errors. (d) The results of the single trial phase coupling analysis are plotted for the alpha frequency range. Mean perception performance (scaled on the *y*-axis) increases linearly with increasing prestimulus alpha phase deviation (*x*-axis). For the beta and gamma frequency range, the opposite pattern is observed (e and f, respectively) where perception performance decreases with increasing prestimulus phase deviation. The error bars indicate standard errors.

beta, and gamma phase coupling was capable to predict perception performance within subjects on a single trial basis.

A possible explanation for the present power findings may be that tonic alpha power refers to the subject's level of performance in general. This is supported by the fact that Non-Perceivers already showed a higher level of alpha power in a resting condition, which was recorded before the experiment started. This result also replicates prior findings showing that good perception performers show low alpha power, whereas bad performers show high alpha power prior to stimulus presentation (Hanslmayr et al., 2005a). Using a selective spatial attention paradigm, Rihs et al. (2007) found increased alpha power for electrode sites contralaterally to the visual field which had to be ignored by the subjects. These and other findings led to the conclusion that alpha power reflects an inhibitory filter mechanism (see Klimesch et al., 2007, for a review). Thus, in specific visual tasks inhibition might play a functional role and help task execution in preventing distracter stimuli to interfere with target processing. In contrast, high prestimulus alpha power makes it hard for very shortly presented stimuli to be perceived, because these stimuli are likely to be filtered out. Such an interpretation also fits with several clinical studies investigating patients who suffer from schizophrenia. These patients, who are assumed to have serious problems with attentional filter functions (for a review, see Mirsky and Duncan, 1986), have lower alpha power than normals (Sponheim et al., 2000) and gain therapeutically if alpha power is induced by repetitive transcranial magnetic stimulation (rTMS; Jin et al., 2006). On a single trial level, however, alpha power was not related to perception performance as reported in other studies (e.g. Ergenoglu et al., 2004; Thut et al., 2006). One reason might be differences in the employed paradigms or task procedure. For example, Ergenoglu et al. (2004) tuned the stimulus intensity for each subject separately in order to yield a mean detection rate of 50%. Thus, the data of all subjects could be analyzed for differences between detected and undetected trials, whereas in our study the subjects with high alpha (Non-Perceivers) were excluded from the single trial analysis. An objection which could be raised against the between subjects differences is that the Non-Perceivers did not engage attentively in the task because they did not perceive the stimuli which might have led to increased alpha power. This interpretation, however, is very unlikely for two reasons. (i) The Non-Perceivers already showed higher alpha power during the resting condition (Fig. 3c), and (ii) alpha power was also related to perception performance within the Perceivers who performed above chance level (Fig. 3b).

At first glance, the present alpha findings seem to disagree with those from other studies in which high alpha power was found to be good for perceptual performance (Linkenkaer-Hansen et al., 2004; Babiloni et al., 2006). Linkenkaer-Hansen et al. (2004) for example, reported that the perception of low-threshold somato-sensory stimuli was related to high parietal alpha power. Babiloni et al. (2006) reported that conscious visual perception of a cue stimulus in an orienting shifting paradigm was related to high prestimulus power in the lower alpha frequency range (6–10 Hz). These results, however, may be reconciled with our findings. In the first case (Linkenkaer-Hansen et al., 2004), an alternative interpretation would suggest that the perception of a sensory stimulus benefits from an inhibited parietal cortex, because otherwise parietal activation could interfere with the processing of the sensory stimulus in central regions. In the second case (Babiloni et al., 2006), there are several differences in the paradigm to the one used in this study. Babiloni et al. (2006) presented a cue stimulus at perception threshold after which a target stimulus was presented on which the subject had to react. Thereafter, the subjects indicated whether they had seen the cue stimulus or not based on self-report. Subjects gave their response around 2.5 s after presentation of the critical stimulus, which suggests the involvement of a memory component. These differences make the results of that study hard to compare with the present one. Besides, however, one could argue that the ability to consciously perceive a stimulus and to keep this information in mind, profits from high selectivity which is reflected in high alpha power (Klimesch et al., 2006; Hanslmayr et al., 2005b).

While alpha power may reflect the subject's level of performance in general, alpha, beta, and gamma phase coupling may reflect the subject's current state of attention or expectation. The attention of a subject performing a visual discrimination task is not always at the same level, but rather fluctuates between more attentive and less attentive states which influence perception performance. Our results suggest that these states may be captured by ongoing phase dynamics of alpha, beta, and gamma oscillations. Our results further show that perception performance can be predicted on a single trial basis using phase synchronicity between electrode sites. Interestingly, a dissociation between the alpha and the higher frequency ranges (>20 Hz) occurred. Whereas synchronous activity in the alpha frequency band inhibited the perception of the stimulus, synchrony in the higher frequency ranges enhanced visual perception. Interactions between alpha and gamma oscillations have been reported by several other studies (Fries et al., 2001; von Stein et al., 2000). Using intracranial recordings in the macaque visual cortex, Fries et al. (2001) have shown that attention decreased synchrony in lower frequency bands and increased synchrony in higher frequency bands. Thus, a possible interpretation of our results is that decreased alpha synchrony and increased beta and gamma synchrony reflect states of enhanced attention which facilitate the perception of shortly presented stimuli.

Several studies reported that increased alpha oscillations reflect top-down processing (Sauseng et al., 2005b; Siegel et al., 2000). In their seminal work, von Stein et al. (2000) showed that phase coupling in the alpha and gamma range represent different aspects of stimulus processing. Their results revealed that alpha oscillations reflect the internal representation of the stimulus (top-down processing), whereas gamma oscillations were related to the feed-forward or bottom-up processing of the stimulus. Therefore, alpha and gamma phase coupling could indicate whether the subject is currently in a bottom-up (high beta and gamma synchrony) or top-down (high alpha synchrony) driven processing mode. Because the order of the stimuli was completely random, any expectation about a certain stimulus would be detrimental and the subject would fail to see the stimulus. Thus, the subject would benefit from a bottom-up processing mode (high beta and gamma, and low alpha synchrony).

Consistent with this interpretation, other studies showed that top-down processing can induce inattentional blindness to shortly flashed stimuli (Todd et al., 2005). In their review, Palva and Palva (2007) conclude that phase synchrony in the alpha frequency range between fronto-parietal networks belong to the neural correlates of consciousness. Our results are in line with this assumption and add to the theory that high fronto-parietal alpha phase synchrony in the prestimulus interval inhibits visual perception. Note, however, that top-down processing can also guide visual perception, as demonstrated in spatial cueing paradigms in which participants shift their attention to a specific location and alpha phase coupling is increased (Sauseng et al., 2005a).

Increased phase coupling in the gamma frequency range is usually observed during visual perception of a stimulus, and has been interpreted to reflect the binding of several features into an object (Varela et al., 2001). In this study, however, gamma phase coupling already differed in a broad time window prior to stimulus presentation and was positively associated with perception performance. Since no stimulus was presented at that time, this effect most probably relates to mechanisms of attention. It has been demonstrated that gamma oscillations are strongly linked to attention processes (Debener et al., 2003; Fell et al., 2003; Herrmann and Knight, 2001; Tallon-Baudry, 2004; Tiitinen et al., 1993). Our results shed new light on the significance of gamma phase coupling and suggest that increased prestimulus synchrony in the beta and gamma frequency band reflects states of enhanced attention which guide visual perception performance.

In summary, this study shows that prestimulus oscillations can be used to predict perception performance between as well as within subjects on a single trial basis. However, different frequency bands were related to perception performance in different ways. Whereas synchrony in the alpha frequency band, as measured by power and phase coupling, inhibited visual perception, synchrony in the beta and gamma frequency band supported perception performance. These results suggest that ongoing oscillations in the alpha, beta, and gamma frequency range indicate the fluctuation of attentional states and that alpha power distinguishes between the attentional capabilities of subjects.

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