

# Early electrophysiological markers of visual awareness in the human brain

Kathrin Ohla,<sup>a,b</sup> Niko A. Busch,<sup>b</sup> and Christoph S. Herrmann<sup>b,\*</sup>

<sup>a</sup>*Institute of Psychology I, University of Leipzig, Seeburgstr. 14-20, 04103 Leipzig, Germany*

<sup>b</sup>*Institute of Psychology II, Department of Biological Psychology, University of Magdeburg, PF 4120, 39106 Magdeburg, Germany*

Received 23 February 2007; revised 30 May 2007; accepted 7 June 2007

Available online 18 June 2007

The present study investigated neuronal correlates of stimulus processing leading to conscious perception of a task irrelevant global structure in a visual display. To study the underlying neuronal processes, participants were presented different types of dot patterns (Glass patterns) either forming a global structure or forming no global structure while EEG was recorded. Participants were naive about the pattern types and performed a demanding colour discrimination task. Following the experiment, the degree to which participants acquired awareness of the global visual structure was assessed. Early  $\gamma$ -frequency band responses (gamma, 25–100 Hz) over occipital, parietal, and central areas were enhanced to circular Glass patterns as compared to random dot patterns at 90 ms post-stimulus. This effect was observed exclusively in participants who were subjectively aware of the global pattern structure. In this group of observers, the pattern effect built up gradually during the course of the experiment. The significance of enhanced early gamma responses to global patterns for the production of awareness of the pattern might lie in the increased impact of information conveyed by well synchronised neuronal assemblies to upstream cortical areas.

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**Keywords:** Visual awareness; Conscious perception; EEG; Gamma-frequency band activity; Oscillations

## Introduction

Visual awareness is widely believed to be the aspect of consciousness that is the most accessible for empirical research (Koch, 2004). A common approach in this line of research has been to contrast neural correlates of stimulus processing that results in awareness against neural correlates of stimulus processing that do not result in awareness (e.g. Schurger et al., 2006; Burgess and Ali, 2002). In this context, awareness is defined by most authors operationally as the ability to veridically report the presence or the

quality of a stimulus. Since perception and awareness are distinct phenomena, the question arises how visual perception is transformed into visual awareness. It has been proposed that attention is necessary for awareness by acting as an access control mechanism determining which stimuli will or will not enter consciousness (Baars, 1997). Attention has been shown to enhance neuronal synchrony in animals (Fries et al., 2001). According to Fries (2005), attention selectively enhances the impact of neuronal responses conveying information about relevant sensory attributes by increasing local and long range neuronal synchronisation. Stronger synchronisation of neuronal cell assemblies is thought to enhance the efficiency of information transfer to upstream areas. Hence, attending to a visual stimulus enhances the probability of the perception entering awareness by facilitating perception through more efficient neuronal communication. A growing body of evidence associates attentional processes with neural oscillations in the  $\gamma$ -frequency band range (Womelsdorf et al., 2006; Busch et al., 2006b; Tallon-Baudry et al., 2005; Gruber et al., 2004; Debener et al., 2003; Herrmann and Knight, 2001; Müller et al., 2000; Desimone and Duncan, 1995; Tiitinen et al., 1993). In particular, selective attention enhances oscillatory activity and synchrony in the  $\gamma$ -frequency band range towards attended stimuli in monkeys (Fries et al., 2001; Taylor et al., 2005) and humans (Tallon-Baudry, 2004). Also alpha ( $\alpha$ ) oscillations have been proposed to contribute to attentional processes (Palva and Palva, 2007).  $\alpha$  oscillation have been suggested as an “idling” rhythm indicating deactivation of sensory cortical areas (Pfurtscheller and da Silva, 1999). In line with this, Sauseng et al. (2005) reported a decrease of anterior  $\alpha$  associated with executive functions. Other results suggest that  $\alpha$  event-related desynchronisation plays an active role for inhibitory control (Klimesch et al., 2007).

Attention and neural oscillations have also been proposed as solutions to the so-called “binding problem” (Treisman, 1999), which is closely related to the question of how visual awareness is achieved. It is the problem of how the unity of visual awareness is achieved by distributed activities of the visual system. Thus, visual awareness is closely related to attentional selection and binding, and neural  $\gamma$ -frequency band activity has been proposed as a substrate of each of these phenomena. Data supporting this

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\* Corresponding author. Fax: +49 391 6712222.

E-mail address: christoph.herrmann@nat.uni-magdeburg.de (C.S. Herrmann).

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connection have been provided predominantly by animal studies (Bichot et al., 2005; Engel and Singer, 2001; Fries et al., 1997; Singer and Gray, 1995). However, studies that demonstrate an association between awareness and  $\gamma$  activity in humans are scarce (see Palva et al., 2005, for an exception).

In the present study, random dot stimuli were presented to evaluate human electrophysiological responses to different global pattern types in participants who were either aware or unaware of these global patterns structures. Three different types of coloured dot patterns were employed: suprathreshold circular patterns (yielding a salient global structure), parallel patterns (yielding an intermediately salient global structure), and random patterns (providing no global structure).

Since perception of the global form requires the integration of multiple neuronal assemblies coding the local stimulus features, we expected that synchronised neuronal activity in the  $\gamma$ -frequency band should be enhanced, but only in those participants who were aware of the different patterns. We focused on electrophysiological responses in the  $\gamma$ -frequency band range (25–100 Hz) to assess the neural correlates of perceptual awareness in the human brain. We furthermore investigated lower frequency bands, i.e. the  $\theta$  (theta, 4–7 Hz),  $\alpha$  (alpha, 8–12 Hz), and  $\beta$  (beta, 13–20 Hz)-frequency band. We present reliable electrophysiological evidence that high frequency oscillations differentiate as early as 90 ms after stimulus onset between aware and unaware processing.

## Methods

### Participants

The study protocol conformed with the local ethics guidelines and the Declaration of Helsinki. Sixteen healthy, university students (8 female; 15 right-handed; aged 20–29 years, mean 23.6) either received class credit or were paid for participation. All had normal or corrected to normal vision, they were free of current or past neurological or psychiatric disorders, and they were naive as to the purpose of the study. Participants signed informed consent prior to the start of the experiment.

### Stimuli and procedure

We presented three types of coloured Glass patterns (Glass, 1969): suprathreshold circular patterns (salient global structure),

parallel patterns (intermediately salient), and random dot patterns (no global structure; see Fig. 1).

Participants were naive as to different pattern variations throughout the experiment and were instructed to perform a difficult colour discrimination task instead. In particular, a forced-choice response task required participants to press a button with the index finger of one hand when the pattern was red and to press another button with the other hand when it was violet. Response hand was counterbalanced across participants and gender. Participants were instructed to respond as quickly as possible. After the experiment, we assessed the degree of awareness of the different pattern types acquired during the experiment by means of a structured post-experimental interview. Glass patterns were constructed using an overall pattern density of 4800 dots. Dots were arranged pairwise (2400 pairs or dipoles) in a circular window of  $3.4^\circ$  radius. Using a constant distance within a dipole makes these stimulus patterns different from the original Glass pattern (Glass, 1969), such that the gap between dots in the original study increased with increasing distance from center to periphery of the pattern. Dot pairs were 100% signal dots and either arranged in randomised fashion, by vertical translation, or along an arc length (rotation) resulting in three stimulus conditions. The stimuli were presented in isoluminant colours of dark red (rgb 120, 10, 60) and violet (rgb 90, 20, 100) on a white background. Isoluminance (mean  $3.5 \text{ cd/m}^2$ ) was not equated perceptually for each subject but tested by a chromameter (Minolta). Fig. 1 illustrates the stimuli and indicates that all patterns were identical with respect to most physical parameters such as number of dots, dot size, and distance between dots. Patterns and colours were presented in pseudo-randomised order resulting in a pattern probability of 0.33 and a colour probability of 0.50, with 70 stimuli presented for each combination of pattern (random, parallel, circular) and colour (red, violet) condition resulting in a total of 420 stimulus presentations. Stimuli were presented centrally for 1000 ms, with a randomised variable inter-stimulus interval of 1500, 1600, or 1700 ms in which a fixation cross was shown on a 19-inch computer monitor placed at a distance of 1 m.

### Electrophysiological recordings and data analysis

The experiment was conducted in an electrically shielded and sound-attenuated recording booth. The stimulation monitor was placed outside this cabin behind an electrically shielded window.

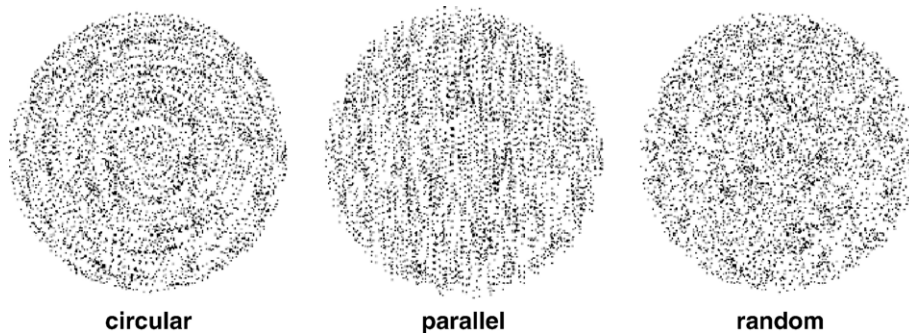


Fig. 1. A circular (left), a parallel (middle), and a random Glass pattern as used in this study. All pattern types underly the same construction mechanism including the same number of dot pairs, the same dot size, and the same distance within dot pairs and between dots, respectively. In the experiment, patterns were presented in two isoluminant colours (dark red [rgb 120, 10, 60], violet [rgb 90, 20, 100]) on a white background. Thus, the patterns were identical with respect to most physical parameters.

All devices inside the cabin were operated on batteries to avoid interference of the line frequency (50 Hz in Germany). Monitor refresh rate was 60 Hz. Stimulus onset was synchronised to the vertical retrace of the monitor. EEG was recorded with a BrainAmp amplifier (Brain Products, Munich) using 32 sintered Ag/AgCl electrodes mounted in an elastic cap (Easycap, Falk Minow Services, Munich) and placed according to the 10–10 system, with a nose-tip reference and ground electrode between Fz and Cz. Electrode impedances were kept below 10 k $\Omega$ . Data were sampled at 500 Hz and analog filtered between 0.016 and 250 Hz during recording. Electrooculogram (EOG) was recorded to control for eye movements and blinks. An automatic artifact rejection excluded trials from averaging if the standard deviation within a moving 200-ms time interval exceeded 40  $\mu$ V. All epochs were also visually inspected for artifacts and rejected in case of eye-movements or electrode drifts.

### Wavelet analysis

Spectral changes in oscillatory activity were analyzed by means of a Morlet-based wavelet transform with a “width” of 12 cycles in order to provide a continuous measure of the amplitude of a frequency component (for details, refer to Herrmann et al., 2004). In brief, Morlet wavelets can be thought of as “band-pass filters” with a Gaussian shape in the time domain and in the frequency domain around their central frequency. This method thus provides a time-varying magnitude of the signal in each frequency band, leading to a time-by-frequency representation of the data. Usually, the characteristics of a wavelet are denoted as  $2\sigma_t$  and  $2\sigma_f$ . The standard deviation  $\sigma_t$  of the Gaussian temporal envelope is reciprocally related to the frequency  $\left(\sigma_t \approx \frac{1}{f}\right)$ . The standard deviation in the frequency domain is given by  $\sigma_f = \frac{2\pi}{\sigma_t}$ . The time resolution of this method thus increases at higher frequencies, while the frequency resolution decreases at higher frequencies. Here we applied wavelets with a constant ratio  $\frac{f_0}{\sigma_f} = 2\pi$ , which corresponds to a temporal wavelet duration  $\left(2\sigma_t = \frac{2}{f_0}\right)$  of two cycles at the wavelet’s center frequency  $f_0$ , and a frequency bandwidth of  $2\sigma_f = \frac{f_0}{\pi}$ . Accordingly, a wavelet with a center frequency of 40 Hz employed in this study had a wavelet duration of  $2\sigma_t = 50$  ms and a spectral bandwidth of  $2\sigma_f = 12.71$  Hz.

Conventional terminology distinguishes between evoked and induced  $\gamma$  activity, but this distinction has been used with at least two different meanings. This dichotomy sometimes refers to the latency of the signal (i.e. evoked referring to an early signal, at approximately 90 ms; induced referring to a late signal after 200 ms) and sometimes to the method of signal analysis used to extract the signal (i.e. evoked=wavelet transform of the average of all trials; induced=average of transforms of single trials). In the following, we present a detailed description of our methodological approach and the respective nomenclature of the signal. To reveal the evoked fraction of  $\gamma$  activity, the wavelet transform was performed on the averaged evoked potential. In order to also analyse activity, which is not strictly phase-locked to the stimulus, the wavelet transform was performed for each single trial, and the absolute values of the resulting transforms were averaged. This measure reflects the total activity for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. We

will refer to this measure as total  $\gamma$  response in order to make explicit that it comprises both the evoked and induced part of the  $\gamma$  response (the same measure has been used previously for the estimation of only the induced part; Tallon-Baudry and Bertrand, 1999).

The degree of phase locking was calculated by means of the so-called phase-locking factor (Fischer, 1993; Herrmann et al., 2004; Tallon-Baudry et al., 1996). To this end, the phase of the complex wavelet decomposition in each single trial was represented as a point on the unit circle irrespective of amplitude. Averaging these points yields values between 0 for randomly distributed phases and 1 for phases that are strictly phase-locked to stimulus onset across trials. Suppose we recorded  $N$  trials  $\{x_n(t)\}_{n=1}^N$ . The instantaneous phase around frequency  $f$  and time  $t$  (estimated by the wavelet transform) is denoted as  $\phi_n(f, t)$ . Based on these quantities, the phase-locking factor is defined as mean resultant length of the instantaneous phase:

$$\text{PLF}(t, f) = \frac{1}{N} \left| \sum_{n=1}^N \exp(i\phi_n(t, f)) \right|$$

Phase-locking and event-related amplitude dynamics in single trials (i.e. induced activity) can exhibit different effects. For instance, effects on late induced activity are usually not accompanied by effects of the phase-locking factor (Tallon-Baudry et al., 1996). Vice versa, some effects on early evoked activity can result from effects on phase locking without variations of signal amplitudes in single trials (Fründ et al., 2007). Hence, by considering phase locking and activity in single trials, it is possible to discern whether effects in evoked activity result from effects of phase-locking, amplitude effects in single trials, or a combination of both.

Since the exact frequency of the  $\gamma$  response varies considerably between participants, the frequency of  $\gamma$  activity used for statistical analyses was determined individually for each subject. The procedure was as reported in Busch et al. (2006a): (1) The time–frequency transform was computed on the average of all trials (see above), irrespective of experimental condition, for every channel. (2) After subtraction of the baseline, time–frequency scalograms were further averaged across all electrodes. (3) From this time–frequency scalogram (averaged across electrodes), we determined individual  $\gamma$  frequencies as the frequency showing the maximum amplitude in a time window from 70 to 110 ms (early) and 200 to 450 ms (late  $\gamma$  activity) in the frequency range from 25 to 100 Hz. With a similar approach, we extended our analysis also to lower frequencies. In particular,  $\theta$  (4–7 Hz) activity was investigated in the time window from 250 to 600 ms,  $\alpha$  (8–12 Hz) responses were investigated from 80 to 250 ms, and  $\beta$  (13–20 Hz)-frequency band activity was investigated from 80 to 120 ms. (4) Statistical analyses were performed on mean amplitudes of these individual frequencies in the respective time windows of interest after channels were pooled into an anterior (electrodes FP1, FP2, F7, F8, F3, F4, Fz, FT9, FT10, FC5, FC6), a central (FC1, FC2, T7, T8, C3, C4, CZ, TP9, TP10), and a posterior (O1, O2, P3, P4, P7, P8, Pz, CP1, CP2, CP5, CP6) region of interest (ROI).

Repeated measures ANOVAs were computed for the factors Pattern (circular, parallel, random)  $\times$  Awareness (aware, unaware) for each ROI (anterior, central, posterior). Most previous studies on visual awareness investigated awareness on a trial-by-trial basis, contrasting trials in which a stimulus was perceived with trials in which the stimulus was not perceived. In our study, participants reported general awareness or unawareness of the different pattern structures after the experiment. Assuming that the participants

classified as “aware” were not aware of the global patterns from the very first trial of the experiment, we hypothesised that the magnitude of the electrophysiological effects should vary between early and late trials. Hence, we conducted analyses of pattern effects in aware participants separately for the first and the last third of trials. We decided to analyse the first and the last thirds because the time point when participants acquired awareness of the different pattern types can be assumed to be variable between participants. For this analysis, repeated measures ANOVAs with the factor Pattern (circular, parallel, random) were calculated for “aware” participants.

In order to provide detailed insights into the origin of the early evoked oscillatory effects, i.e. the question whether amplitude modulation vs. phase locking contributed to the signal, we analysed early phase locking and total (single trial) activity in the  $\gamma$ -frequency range as well. Statistical analyses were performed only for those comparisons that yielded significant results for early evoked  $\gamma$  activity. We found similar effects in early evoked activity, phase locking, and total activity, although effects on total activity was less pronounced. This suggests that both phase-locking and event-related amplitude dynamics in single trials contributed to the observed effects in our study. Hence, further comparisons were calculated for the early evoked  $\gamma$  response.

## Results

### *Behavioural data and post-experimental interview*

In the post-experimental interview, nine participants described having clearly identified a circular pattern structure and thus were classified as “aware” of the circular pattern. The remaining seven participants reported not having noticed any pattern differences at all. They were thus classified as “unaware” of the pattern structure. Noteworthy, a few of the “aware” participants reported having noticed a second global pattern (parallel) although they were not able to verbalise the structure type. For this reason, we decided not to further subdivide this group. We compared participants as “aware” and “unaware” of the circular pattern structure for all further analyses. Response times were analysed for valid trials only in the time interval 200 to 1200 ms after stimulus onset. Excluded data (response times exceeding time window or 2 standard deviations from mean) represented 3.78% of all trials. Mean response times were 582 ms (SD 103 ms). Participants’ correct responses were on average 84.4%. Analyses of response times revealed no differences neither between groups (awareness:  $F_{(1,14)}=1.21, p=0.29$ ) nor between patterns within groups (aware:  $F_{(2,16)}=0.26, p=0.73$ ; unaware:  $F_{(2,12)}=0.95, p=0.40$ ).

### *Electrophysiological responses*

#### *$\theta$ , $\alpha$ , and $\beta$ -frequency band activity*

Fig. 2 depicts the baseline-corrected Time $\times$ Frequency scalograms averaged across all experimental conditions for evoked activity, phase locking, and total activity for all frequency bands at posterior and anterior sensors. Topographical distributions are shown in Fig. 3. Inspection of lower frequency band showed a peak in the  $\theta$ -frequency range from 250 to 600 ms, the  $\alpha$ -frequency range from 80 to 250 ms, and the  $\beta$ -frequency range from 80 to 120 ms relative to stimulus onset. These peaks were observed in evoked and total activity and for the phase-locking factor. However, analyses of the  $\theta$ -frequency band yielded no significant

effects of awareness (all  $F_{(1,14)}<0.1$ ) nor a Pattern $\times$ Awareness interaction (all  $F_{(2,28)}<1.8$ ) for either ROI. Similar results were observed in the  $\beta$ -frequency band; neither an effect for Awareness ( $F_{(1,14)}<0.3$ ) nor a Pattern $\times$ Awareness interaction (all  $F_{(2,28)}<1.7$ ) for either ROI was revealed.

Evoked  $\alpha$  activity was enhanced in “unaware” compared to “aware” participants over anterior sensors. This enhancement resulted in a significant awareness effect ( $F_{(1,14)}=10.99, p=0.005, \eta^2=0.44$ ), which was also present for total  $\alpha$  activity ( $F_{(1,14)}=5.28, p=0.038, \eta^2=0.27$ ), and which resulted in a trend for  $\alpha$  phase locking ( $F_{(1,14)}=3.34, p=0.089, \eta^2=0.19$ ). No Pattern $\times$ Awareness interaction was observed for either ROI (all  $F_{(2,28)}<1$ ) confirming that frontal  $\alpha$  activity was similar for all pattern types.

#### *Early $\gamma$ -frequency band activity (70–110 ms)*

Planned comparisons based on a significant Pattern $\times$ Awareness interaction ( $F_{(2,28)}=4.46, p=0.038, \eta^2=0.24$ ) demonstrated that early evoked  $\gamma$  responses (70–110 ms) were modulated by pattern type in participants classified as “aware” at posterior sensors ( $F_{(2,16)}=10.12, p=0.002, \eta^2=0.56$ ), but not in participants classified as “unaware” ( $F_{(2,16)}<1$ ). “Aware” participants showed significantly larger amplitudes to circular as opposed to random ( $F_{(1,8)}=16.59, p=0.004, \eta^2=0.68$ ) and as opposed to parallel patterns ( $F_{(1,8)}=11.14, p=0.010, \eta^2=0.58$ ), while parallel and random patterns evoked similar responses ( $F_{(1,8)}=2.36, p=0.294, \eta^2=0.23$ ).

In order to provide detailed insights into the origin of the observed early evoked  $\gamma$  effects, we analysed phase locking and total activity in “aware” participants, as well. Note that the same individual peak frequencies were used for early phase locking and early total  $\gamma$  responses as for early evoked  $\gamma$  responses in order to allow for a direct comparison of the three analyses. We found similar effects in early phase locking and early total activity as for early evoked activity. This suggests that both phase-locking and event-related amplitude dynamics in single trials contributed to the observed evoked effects in the present study (see Fig. 2). In detail, early phase locking yielded pattern differences in “aware” participants ( $F_{(2,16)}=5.99, p=0.018, \eta^2=0.43$ ), which resulted from enhanced phase locking in response to circular as compared to random patterns ( $F_{(1,8)}=10.21, p=0.013, \eta^2=0.56$ ) and in response to circular as compared to parallel patterns ( $F_{(1,8)}=6.91, p=0.030, \eta^2=0.46$ ). Parallel and random patterns showed similar phase locking ( $F_{(1,8)}=1.85, p=0.211, \eta^2=0.19$ ). Early total activity also showed pattern differences in “aware” participants ( $F_{(2,16)}=4.25, p=0.038, \eta^2=0.35$ ). Circular as opposed to random patterns were enhanced as indicated by marginal significance ( $F_{(1,8)}=5.22, p=0.052, \eta^2=0.40$ ). Circular patterns induced larger amplitudes than parallel patterns ( $F_{(1,8)}=8.74, p=0.018, \eta^2=0.52$ ) while parallel pattern did not differ from random ones ( $F_{(1,8)}=0.50, p=0.499, \eta^2=0.06$ , see Fig. 2).

Interestingly, early evoked  $\gamma$  responses were generally enhanced in “aware” participants over central (awareness:  $F_{(1,14)}=6.05, p=0.028, \eta^2=0.30$ ) and over posterior sensors ( $F_{(1,14)}=6.71, p=0.021, \eta^2=0.24$ ). In a similar manner, phase locking was stronger in “aware” participants at central ( $F_{(1,14)}=5.41, p=0.036, \eta^2=0.28$ ) and posterior sensors ( $F_{(1,14)}=5.89, p=0.029, \eta^2=0.30$ ). Furthermore, early total activity was more pronounced in “aware” participants at posterior sensors ( $F_{(1,14)}=6.10, p=0.027, \eta^2=0.30$ ). This points towards a difference between the two groups in the activation of cortical networks underlying the processing of the employed patterns. In order to rule out that

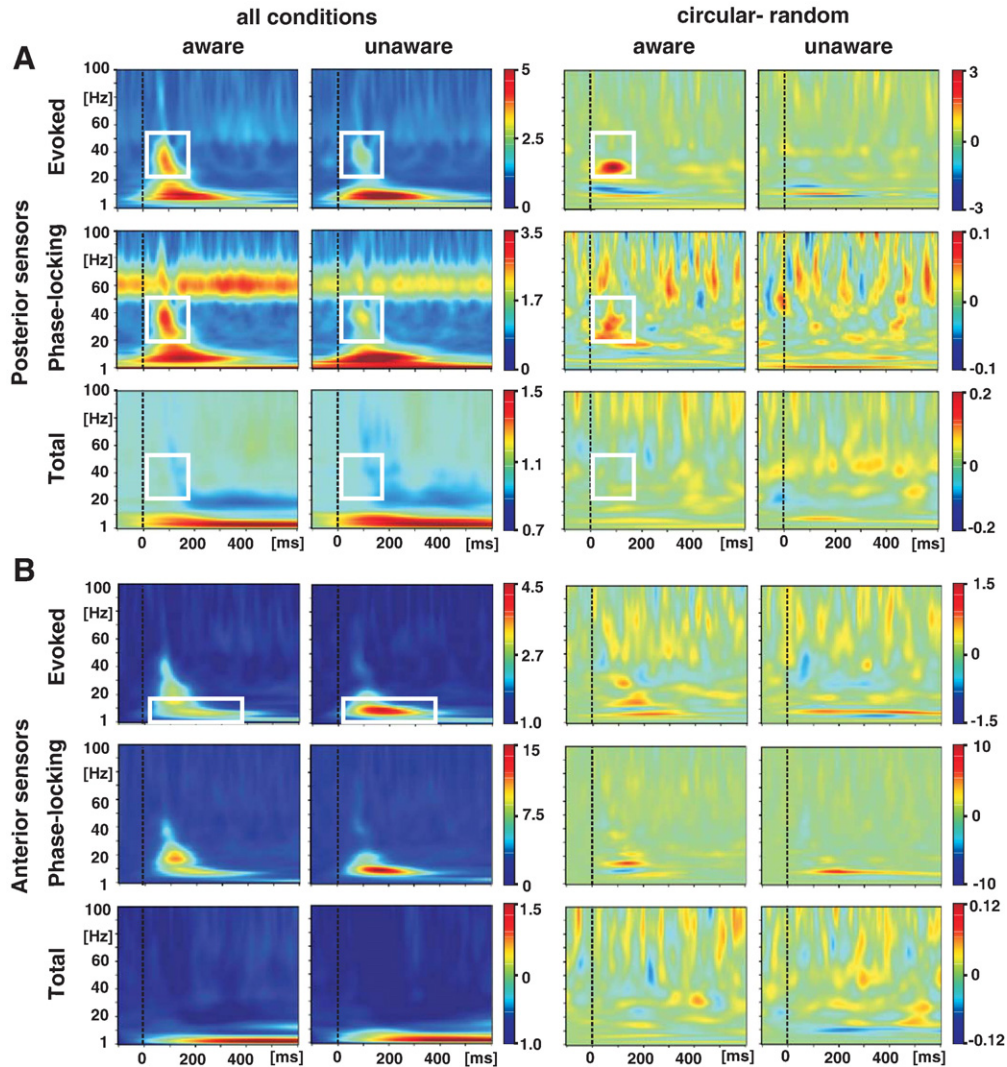


Fig. 2. Grand averaged Time  $\times$  Frequency (tf) scalograms for “aware” and “unaware” participants. (A) tf scalograms at posterior sensors for evoked activity (1st row), phase locking (2nd row), and total activity are depicted as averages across all experimental conditions (left two columns) and as the effect “circular patterns minus random patterns” (right two columns). Early  $\gamma$  activity was generally enhanced in “aware” participants. Moreover, circular patterns elicited significantly higher amplitudes in the  $\gamma$ -frequency band as compared to random patterns only in “aware” participants. (B) tf scalograms at anterior sensors show enhanced evoked  $\alpha$  activity in “unaware” participants. Note: Colour scales represent signal change relative to baseline. White rectangles do not mark time and frequency windows as used for statistical analyses but instead visualise areas with significant effects schematically.

pattern effects in the “unaware” group failed to reach statistical significance as a result of the reduced absolute response amplitudes in this group, we compared overall response amplitudes with the pattern effect. If pattern effects were proportional to absolute response amplitudes, this should manifest in correlation between strength of pattern effect (circular minus random) and absolute response amplitude (across all conditions), which was not the case in our study ( $r=0.252, p=0.347$ ; see Fig. 4).

The present study differed from previous ones through the fact that participants were left naive as to the different pattern types. Hence, we investigated whether pattern effects built up gradually during the course of the experiment by comparing early evoked  $\gamma$  responses in the first and in the last third of trials for the “aware” participants. The time course of early evoked  $\gamma$  activity is depicted in Fig. 5. This analysis revealed a pattern effect only in the last third over posterior sensors ( $F_{(1,14)}=4.56, p=0.048, \eta^2=0.36$ ). In

particular, “aware” participants showed significantly larger amplitudes to circular as opposed to random ( $F_{(1,8)}=5.65, p=0.045, \eta^2=0.41$ ) and as opposed to parallel patterns ( $F_{(1,8)}=7.17, p=0.028, \eta^2=0.47$ ) while parallel and random patterns evoked similar responses ( $F_{(1,8)}=1.71, p=0.227, \eta^2=0.18$ ). Hence, pattern differences in the last third of trials were similar to the above reported pattern effects across all trials.

#### Late $\gamma$ -frequency band activity (200–450 ms)

Late  $\gamma$  responses were determined by analysis of total activity in single trials. This response did not exhibit effects of pattern type in either group in either ROI (Pattern  $\times$  Awareness: all  $F_{(2,28)} < 0.5$ ). Moreover, late total  $\gamma$ -frequency band responses were equally pronounced for both groups of participants (awareness: all  $F_{(1,14)} < 0.1$ , Fig. 2). However, a comparison between the first and the last third of trials for “aware” participants revealed enhanced

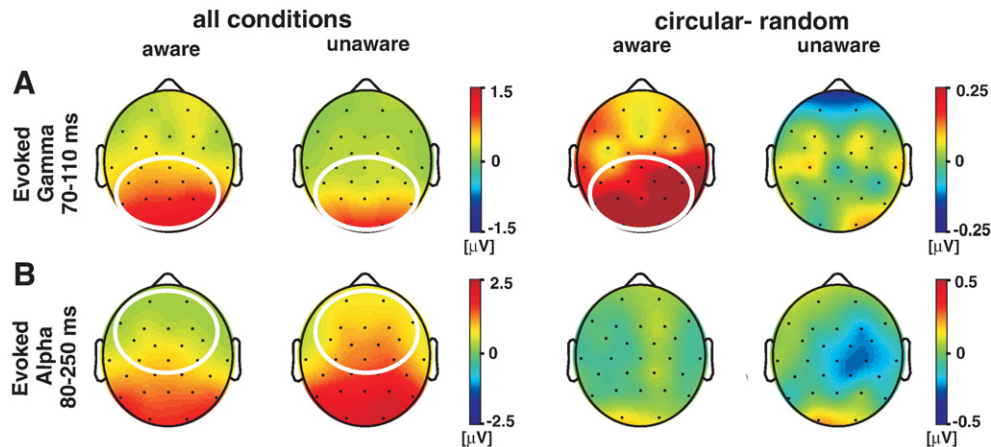


Fig. 3. Topographical distribution of  $\gamma$  and  $\alpha$  activity for “aware” and “unaware” participants. (A) Topographical distributions of evoked  $\gamma$  activity averaged across all experimental conditions (left two columns) and for the effect “circular patterns minus random patterns” (right two columns) from 70 to 110 ms relative to stimulus onset.  $\gamma$  activity across experimental conditions is distributed over postero-parietal sensors irrespective of the degree of awareness. However, the effect “circular patterns minus random patterns” shows a widespread postero-central distribution in “aware” participants. (B) Topographical distributions of evoked  $\alpha$  activity from 80 to 250 ms relative to stimulus onset. Evoked  $\alpha$  at frontal sensors was significantly enhanced in “unaware” participants irrespective of pattern type (left two columns). No significant differences were revealed between patterns (right two columns). Note: White circles do not mark electrode clusters as used for statistical analyses but instead visualise areas with significant effects schematically.

amplitudes over central sensors for circular patterns in the last third of trials. Although this pattern effect failed to reach statistical significance ( $F_{(2,16)}=3.2$ ,  $p=0.071$ ,  $\eta^2=0.286$ ), it showed a clear trend that is in line with previous findings (Tallon-Baudry et al., 1997).

#### Event-related potentials

Analyses of event-related potentials (ERPs) were reported previously (Ohla et al., 2005). Early ERPs, which are known to be sensitive to sensory processing, were not influenced by the degree of awareness. Instead previous analyses revealed enhanced N170 amplitudes in response to circular patterns for all participants (Ohla et al., 2005). This finding indicates that the global structure was processed at a sensory level in all participants. This processing, however, was insufficient for generating awareness of the pattern structure. These results thus underline that evoked  $\gamma$  activity is

more closely tied to awareness of the patterns than to merely sensory processing.

#### Discussion

In line with the assumption that  $\gamma$  activity is part of a signature of visual awareness in animals (Engel and Singer, 2001; Fries et al., 1997), we found an early modulation of  $\gamma$ -frequency band responses by pattern types only for those participants who reported having been aware of the different stimulus patterns. In this group, circular patterns evoked larger  $\gamma$  amplitudes than parallel and random patterns. Although we cannot precisely determine the time point when participants acquired awareness of the global patterns, it seems plausible to assume that they were not aware of the global patterns from the very beginning of the experiment (this assumption is supported by their statements in the postexperimental interview). If the differentiation of early evoked  $\gamma$  responses to the different pattern types were in fact related to subjective awareness of the global patterns, the electrophysiological effect should build up gradually in the course of the experiment. In fact, when early trials were compared to late trials, pattern effects were only found for late trials, after awareness of the global forms was acquired. Moreover, “aware” participants evoked larger  $\gamma$ -frequency band responses to all stimuli as compared to “unaware” participants. The results thus suggest that stimulus-locked  $\gamma$  activity represents a facet of the neural correlates of visual awareness and might moreover be modulated by attentional processes.

Coherence within and between the respective brain areas has been suggested as a prerequisite of effective stimulus processing (Fries, 2005; Fries et al., 1997). This claim is supported by studies on binocular rivalry in cats (Engel and Singer, 2001; Fries et al., 1997) and lead to the conclusion that the activation of visual neurons by a stimulus *per se*, as measured by firing rates, is not sufficient for the conscious perception of a stimulus. While perceived and unperceived stimuli did not differ with respect to firing rates in the study by Fries et al. (1997), only consciously

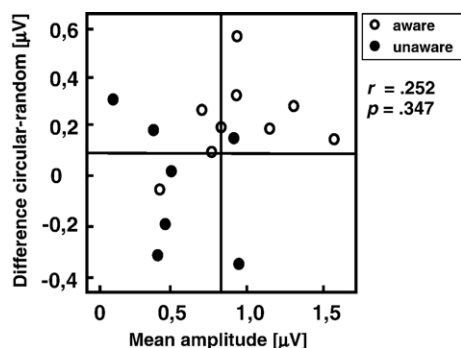


Fig. 4. Scatter plot for early evoked  $\gamma$  activity. Amplitudes of individual frequencies are averaged from 70 to 110 ms at posterior sensors for “aware” (white circles) and “unaware” (black circles) participants. A comparison between strength of pattern-effect (circular minus random) and mean response amplitude (across all conditions) revealed no significant correlation ( $r=.252$ ,  $p=.347$ ). Hence, pattern effects were not proportional to response amplitudes.

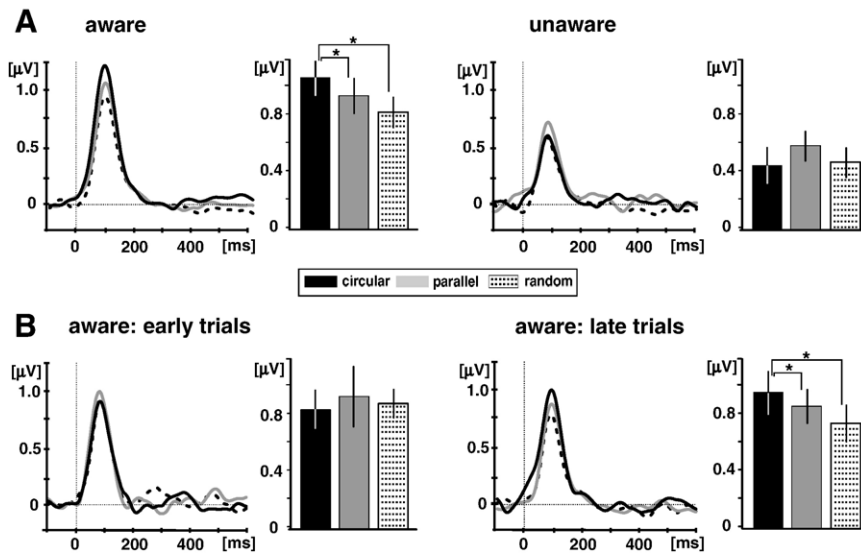


Fig. 5. Time courses of individual frequencies for early evoked  $\gamma$  activity at posterior sensors. (A) Time courses for “aware” and “unaware” participants. Early evoked  $\gamma$  activity was generally enhanced for “aware” compared to “unaware” participants. Bars show mean amplitudes in the time window 70–110 ms, error bars represent standard errors. In addition, circular patterns evoked higher early evoked  $\gamma$  activity in response to circular compared to parallel and random patterns for “aware” participants only. (B) Time courses for early trials (first third) and late trials (last third) in “aware” participants [ $n=9$ ]. Early evoked  $\gamma$  activity was significantly enhanced for circular patterns only in the last third of the experiment.

perceived stimuli were associated with synchronisation among the corresponding cell assemblies. In a similar vein, Crick and Koch (1990) hypothesised that synchronised activity in the  $\gamma$ -frequency range constitutes the neuronal correlate of visual awareness. Although synchronised activity in the  $\gamma$ -frequency range in response to visual stimulation has been found to occur in various brain regions, synchronisation in primary visual cortex (V1) has not been related to the perceptual state in binocular rivalry in awake monkeys (Gail et al., 2004). Support for the suggestion that extrastriate visual areas contribute to perceptual awareness comes from Leopold and Logothetis (1996) who reported that neuronal activity in monkey areas V1 and V2 did not vary with the monkey’s perception in a binocular rivalry experiment. In contrast, responses in areas V4, MT, MST, IT, and IST were strongly associated with the monkey’s perceptual state (Leopold and Logothetis, 1999, 1996). Thus, visual  $\gamma$ -frequency band responses from extrastriate visual areas are more likely to be associated with visual awareness than those originating in primary visual cortex. To ensure that the percept of the employed stimuli was predominantly achieved in extrastriate areas we used Glass patterns as there is evidence that the perception of the global structure in Glass patterns is dependent on processing at intermediate levels of the visual processing pathway. While early visual areas V1 and V2 process merely the local information contained in the single dots, the perception of the global pattern has been suggested to be achieved only after a further processing stage in area V4 (Wilson et al., 1997). Neuronal responses to structured Glass patterns can be easily compared to those of unstructured or random patterns since both pattern types are equal with respect to elementary visual features such as contrast or spatial frequency and thus allow to rule out confounds of stimulus properties. Hence, Glass patterns are ideal stimuli for the investigation of neuronal correlates of conscious perception.

Our results are in line with other studies, which reported enhanced  $\gamma$  activity due to attentional processing (Tiitinen et al., 1993; Fries et al., 1997; Herrmann and Knight, 2001; Debener et al.,

2003). In fact, from research on electrophysiology it is well known that attention plays a crucial role in visual perception since it can influence sensory coding (Luck and Hillyard, 1999), and moreover it improves perception of visual stimuli (Lu and Doshier, 1998). Similar findings from animal research support this notion. In extrastriate areas (e.g. V4), neurons’ responses to a preferred stimulus in their receptive fields are enhanced when the stimulus is attended (Moran and Desimone, 1985; Luck et al., 1997; Reynolds et al., 2000). Furthermore, synchronisation between neurons is enhanced (Fries et al., 2001; Bichot et al., 2005) by attention. It is well known that stronger synchronisation among assemblies results in larger amplitudes in scalp recorded EEG (Pfurtscheller and da Silva, 1999). Therefore, the increase in evoked  $\gamma$ -frequency band responses in “aware” participants can be interpreted as stronger underlying neuronal synchronisation. Hence, our findings of enhanced  $\gamma$  activity in “aware” participants might point to stronger attentional recruitment and neural synchronisation in this group of participants. We propose that the acquisition of awareness led “aware” participants to attend to the pattern structure as a second stimulus feature (even though it was not required by the task), in addition to attending to the patterns’ colour. Subsequently, attending to the different patterns supposedly facilitated their subjective perception of these patterns.

Stronger  $\alpha$  activity was found in participants who were classified as unaware of the global pattern structure. The traditional view of  $\alpha$  activity has interpreted this signal as an “idling” rhythm when the brain is at rest. A more active role has been assigned to  $\alpha$  activity by studies showing that  $\alpha$  activity can reflect the active inhibition of cortical areas, subserving the suppression of task irrelevant stimuli. For instance, Worden et al. (2000) found stronger  $\alpha$  activity over the hemisphere ipsilateral to the attended visual hemifield. A number of studies demonstrated that  $\alpha$  activity is related to behavioural performance in perceptual tasks. Ergenoglu et al. (2004) found that detection of a near-threshold visual stimulus was hampered by high amplitudes of  $\alpha$  activity. Hanslmayr et al.

(2005) demonstrated that good performance in a discrimination task is related to low  $\alpha$  amplitudes, but stronger  $\alpha$  phase locking. In a similar vein, Palva et al. (2005) found stronger  $\alpha$  phase locking to perceived as compared to unperceived somatosensory stimuli. It is important to note, however, that participants in the present study were perfectly aware of the stimuli as a whole, but some of them were unaware of the global pattern embedded in the stimuli. In contrast, the studies by Palva et al. (2005) and Hanslmayr et al. (2005) compared perception of a stimulus to a condition where the same stimulus was not perceived at all. It is conceivable that in the present study, participants classified as “unaware” of the global pattern structures devoted more resources for performing the colour discrimination task. Facilitation in the discrimination task (presumably reflected by enhanced  $\alpha$  phase locking) might have reduced the salience of the task irrelevant pattern structures. Although no statistically significant differences in overt behaviour were found between groups, “unaware” participants might have devoted more resources to the discrimination task in order to achieve a comparable level of performance. Additional investigations are needed to clarify the role and the interplay between early  $\gamma$  and  $\alpha$  oscillations for perceptual performance.

Although our results provide evidence for the critical contribution of early evoked  $\gamma$  activity to conscious perception, previous electrophysiological studies have suggested later induced oscillatory activity in the  $\gamma$ -frequency range as a possible neuronal correlate of perceptual awareness (Crick and Koch, 1990; Fries et al., 1997; Engel et al., 1999). This inconsistency might be due to the novel paradigm we used here. We left participants naive as to the purpose of the study and queried them after the experiment to report general awareness or unawareness, respectively. In contrast, most previous studies have compared neuronal responses in situations in which a stimulus was consciously perceived *per se* and situations in which no stimulus was perceived at all (e.g. dominant vs. non-dominant eye in binocular rivalry, Fries et al., 1997, or detected vs. undetected stimuli in signal detection experiments, Summerfield et al., 2002; Burgess and Ali, 2002; Schurger et al., 2006).

A different approach was taken in the study by Tallon-Baudry et al. (1997). Participants were presented with images of meaningless black and white blobs (neutral stimulus) and images with a hidden figure (a high contrast picture of a dalmatian dog). In the first half of this experiment, participants were not informed of the dog images. Here, participants were instructed to detect a particular meaningless pattern that served as a target stimulus. Prior to the second half of the experiment, participants were trained to perceive the image of the dalmatian dog. In the second half of the experiment, neutral stimuli were presented, as well as pictures with the image of a dog with its face turned rightward and a dog facing leftward, which now served as a target. The main findings were elevated late induced  $\gamma$  activity during the second half of the experiment as compared to the first half irrespective of stimulus condition. Moreover, stronger induced  $\gamma$  activity was observed for target stimuli (i.e. the meaningless target pattern in the first half and the dog picture facing leftward in the second half of the experiment) as compared to non-target stimuli (the meaningless non-target pattern in the first half and the meaningless pattern as well as the non-target dog in the second half). However, no difference was found between meaningless patterns (i.e. the neutral stimuli) and non-target dog pictures, even after participants were informed about these pictures.

In the present study, we investigated effects between patterns with a global structure and noise patterns, while this distinction

was totally task irrelevant for the participants. Thus, the comparison between participants that were aware or unaware of the pattern structures is not, at the same time, a comparison between different visual search strategies or stimuli with different task relevance. In sum, participants’ expectations and intentions in our design, which result from task instructions, differed substantially from those in previous studies. Moreover, the present experiment employed highly abstract visual stimuli, and the task was a simple colour discrimination task. This fact might account for the lack of effects on late induced  $\gamma$ -frequency band activity. Several authors have suggested that this brain response is related to a semantic representation of meaningful objects (Tallon-Baudry and Bertrand, 1999; Gruber et al., 2004). It should be noted, however, that when pattern effects were compared between early and late trials, also late induced  $\gamma$  activity showed a trend towards a pattern effect in late trials in aware participants. Future studies should confirm the present results by investigating  $\gamma$ -frequency band responses to Glass patterns on a trial-by-trial basis. By employing near-threshold Glass patterns in a detection task, trials in which a pattern was perceived could be compared to trials in which no pattern was perceived. Such an experimental design might even yield stronger effects of awareness, since the data from “aware” participants analysed in the present study (particularly in early trials) presumably included also trials, in which the participants had not acquired awareness yet. An advantage of the present analysis, however, is that effects of awareness were not confounded by detection of a task relevant stimulus.

In sum, we could identify an early EEG signal, which indicates whether or not a participant is having a certain visual experience. Being aware of the different pattern types seems to require an appropriate differentiation of early  $\gamma$  activity. This signal cannot be unambiguously be regarded as the neuronal substrate of visual experience, the “feeling” of seeing a global pattern. Instead, the electrophysiological differentiation between pattern types that was observed in “aware” participants only can be regarded as a correlate of a perceptual process, which in turn is a necessary prerequisite for subjective visual experience of the global pattern. Which role might enhanced early  $\gamma$  activity to global patterns play in the production of awareness of these percepts? According to Fries (2005), synchronisation of activity of neuronal assemblies increases the impact of information conveyed by these assemblies to upstream areas. Accordingly, we interpret the enhanced  $\gamma$  activity for global patterns in “aware” participants as a reflection of enhanced neuronal communication within and between neuronal assemblies.

## Acknowledgments

We are grateful to Markus A. Dahlem for invaluable discussions and technical assistance. We thank Kathie Ziehr for proofreading.

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