RESEARCH ARTICLE

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Human EEG responses to 1–100 Hz flicker: resonance phenomena in visual cortex and their potential correlation to cognitive phenomena

Abstract The individual properties of visual objects, like form or color, are represented in different areas in our visual cortex. In order to perceive one coherent object, its features have to be bound together. This was found to be achieved in cat and monkey brains by temporal correlation of the firing rates of neurons which code the same object. This firing rate is predominantly observed in the gamma frequency range (approx. 30–80 Hz, mainly around 40 Hz). In addition, it has been shown in humans that stimuli which flicker at gamma frequencies are processed faster by our brains than when they flicker at different frequencies. These effects could be due to neural oscillators, which preferably oscillate at certain frequencies, so-called resonance frequencies. It is also known that neurons in visual cortex respond to flickering stimuli at the frequency of the flickering light. If neural oscillators exist with resonance frequencies, they should respond more strongly to stimulation with their resonance frequency. We performed an experiment, where ten human subjects were presented flickering light at frequencies from 1 to 100 Hz in 1-Hz steps. The event-related potentials exhibited steady-state oscillations at all frequencies up to at least 90 Hz. Interestingly, the steady-state potentials exhibited clear resonance phenomena around 10, 20, 40 and 80 Hz. This could be a potential neural basis for gamma oscillations in binding experiments. The pattern of results resembles that of multiunit activity and local field potentials in cat visual cortex.

Keywords Alpha · EEG · Gamma · Flicker · Resonance · SSVEP · Steady-state potentials

Introduction

Oscillations in the electroencephalogram (EEG) are classified according to their relation to stimulation and can be spontaneous, evoked or induced (Başar-Eroglu et al. 1996). Spontaneous oscillations are not related to stimulation (also called background activity) while evoked oscillations appear after stimulation and are phase-locked to the stimulus. Induced oscillations also occur after stimulation but without phase-locking to the stimulus. Therefore, induced oscillations cannot be observed in averaged signals, since they cancel out due to their random phase relation to the stimulus.

The data presented here suggest a possible correlation between evoked/induced oscillations from cognitive experiments and oscillatory EEG activity which results from repetitive stimulation: so-called steady-state visual evoked potentials (SSVEPs).

Electrophysiological experiments have shown that neurons in human visual cortex synchronize their firing to the frequency of flickering light, leading to EEG responses which show the same frequency as the flickering stimulus – namely SSVEPs (Regan 1989; Silberstein 1995). This phenomenon is also called photic driving and is routinely used as an activation method in clinical EEG recordings (Takahashi 1993). SSVEPs can be evoked at weak stimulation intensities such as the monitor refresh flicker at frequencies up to at least 75 Hz when the flickering is no longer consciously perceived (Lyskov et al. 1998; Herrmann et al. 1999).[1]

Neurons in visual cortex are selectively responsive to certain features of stimuli, such as contours of specific orientation, color or motion. In order to perceive coherent objects which are composed of all these features, the brain needs to bind together the responses of the single neurons. This has been demonstrated to be done via syn-

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[1] It has been argued that the reason for not perceiving stimulus changes which are still processed by cortical neurons is due to a lack of cortical connections from frontal brain areas, where memory and executive functions are supposed to reside, to area V1 (Crick and Koch 1995).

chronization of the neural spikes in cat visual cortex (Gray et al. 1989). Especially spike discharge rates in the gamma frequency range (30–80 Hz, mainly around 40 Hz) have been found to represent such binding functions in animal brains (Engel et al. 1992). Experiments with humans were able to reproduce these findings showing that so-called induced gamma oscillations are present in the human EEG when the two parts of a moving bar are perceived as one coherent object (Müller et al. 1997). If frequencies in the gamma frequency range are responsible for feature binding in visual cortex, stimuli presented at those frequencies should be bound better than stimuli presented at other frequencies. Indeed, psychophysical experiments have recently shown that stimuli which flicker at a frequency in this frequency range lead to faster processing by the brain than stimuli which flicker at other frequencies (Elliott and Müller 1998). In that study, Kanizsa-like arrangements of L-shaped angles had to be detected among randomly arranged angles. Reaction times significantly decreased when target-relevant primes were preattentively flickering at a frequency of 40 Hz prior to the detection period. These behavioral differences were also reflected by latency differences of the evoked 40-Hz response to the stimuli (Elliott et al. 2000). Evoked and induced oscillations in the gamma frequency range have been found by many researchers and have been proposed to be responsible for visual binding (Tallon et al. 1995; Herrmann et al. 1999), Gestalt perception (Keil et al. 1999), attention (Tiitinen et al. 1993; Herrmann and Mecklinger 1999) and memory representations (Tallon-Baudry et al. 1998; Pulvermüller et al. 1999).

Since 40-Hz oscillations seem to play a key role in human perception, it seems plausible to assume a neuroanatomical reason for the constant appearance of this brain response in multiple functional roles. One possible reason for such a preference to a frequency is a resonance phenomenon in the brain, i.e., the brain responds more strongly to that frequency than to others. Such a resonance phenomenon is known to exist for frequencies in the alpha frequency range (approximately 8–12 Hz), which also has been associated with a variety of perceptual and cognitive functions ranging from primary sensory coding (Schürmann et al. 1997) to memory representations (Klimesch 1997). An overview is given by Başar et al. (1997).

The objective of this experiment is to test whether a similar resonance phenomenon exists for frequencies around 40 Hz in human visual cortex by driving the visual cortex at all frequencies from 1 to 100 Hz in 1-Hz steps.

Previous experiments, which nicely demonstrated SSVEPs in animal (Başar et al. 1998) and human brains (Schürmann and Başar 1994), have computed so-called amplitude-frequency characteristics. Such diagrams indicate how the amplitude of the SSVEP changes in response to the stimulation frequency. A more detailed analysis of the frequency content of signals was used in a recent animal study where recordings from cat visual cortex were analyzed with respect to which frequencies in the recording are evoked by which stimulation frequency (Rager and Singer 1998). This method is able to differentiate between response frequencies which are identical, harmonic, subharmonic or unrelated to the stimulation frequency. Therefore, this analysis method was used here to investigate the resonance phenomena of SSVEPs in the human cortex.

Another objective was to test the correlation of human and animal data with respect to oscillatory brain responses, since a recent article has requested that such comparisons shall be made for better comparability of the two (Juergens et al. 1999). Thus, we plot our results in the same fashion as Rager and Singer (1998) plotted their animal data and compare the observed phenomena in the human brain to their findings.

Materials and methods

Subjects

Ten subjects with a mean age of 24.5 years (ranging from 19 to 34 years, six female) took part in the experiment. All subjects had normal or corrected-to-normal vision. They showed no signs of neurological or psychiatric disorders and all gave written, informed consent. All subjects were explicitly informed that flicker stimulation might lead to seizures in epileptics and reported that neither they nor any members of their families had ever suffered from epilepsy.
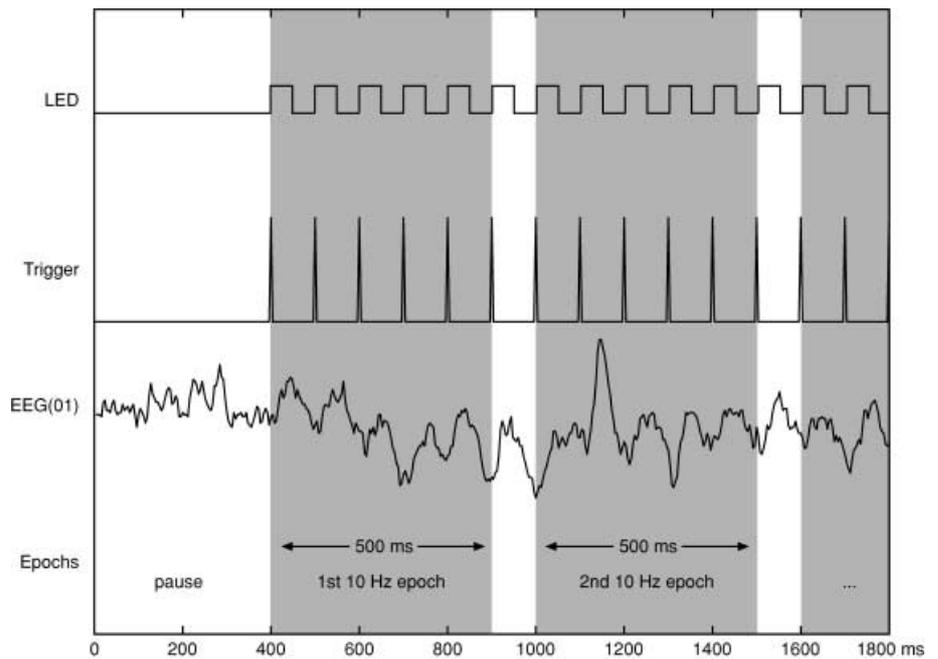
Stimuli

Special goggles were manufactured for this experiment with one light-emitting diode (LED) placed in front of each eyepiece. White LEDs with a light intensity of 3000 mcd (no. 153745, Conrad Electronic, 92240 Hirschau, Germany) were mounted in polished, concave metal reflectors. Thus, the full visual field was lit by the light of the two LEDs, i.e., we presented unstructured stimuli driving predominantly magnocellular (M) cells (Silberstein 1995). A frequency generator (Wavetek, 10 MHz Function generator, model 29) was used to drive the LEDs at all frequencies from 1 to 100 Hz in 1-Hz steps. Frequencies were pseudo-randomized and the same sequence of frequencies was presented to all subjects. Each stimulation frequency was presented for 30 s with a 5-s pause in between. Whenever the LEDs received a pulse from the frequency generator, a trigger impulse was transmitted to the EEG amplifier to record all stimulation events.

Data acquisition

The EEG was recorded with TMS amplifiers (Twente Medical Systems, Enschede, The Netherlands) using 19 tin electrodes mounted in an elastic cap. Electrodes were placed according to the international 10-20 system. The ground electrode was placed over the left mastoid and all electrodes were referenced to an additional reference electrode, also placed over the left mastoid (M1). Electrode impedance was kept below 5 kΩ. Horizontal and vertical EOG were registered with four additional electrodes. EEG amplitudes were sampled at 256 kHz with an analog, first-order, anti-aliasing RC low-pass filter at 5 kHz. Data were stored at 500 samples/s after digital downsampling and digital low-pass filtering at 135 Hz with a decimating filter (inside the hardware). Data were then digitally high- and low-pass filtered offline with a finite impulse response filter (FIR) at 0.05 and 100 Hz, respectively. Due to the filter settings, frequencies below 1 Hz and above 95 Hz may have been attenuated.

Fig. 1 Schematic of the procedure to extract 0.5-s stimulation epochs. Each 0.5-s epoch is extracted from the raw EEG data (e.g., electrode O1) where a light impulse (*LED*) starts. The beginning of every light impulse is indicated by a trigger

Data analysis

From the 30 s of each stimulation with one frequency, approximately 60 consecutive 0.5-s epochs were extracted from the EEG. Each epoch was extracted exactly at one of the trigger events where a single light stimulus started to ensure phase-locked averaging (cf. Fig. 1). All epochs were visually inspected for artifacts and were rejected if eye-movement artifacts or electrode drifts were visible. Baselines were computed in the 100-ms interval prior to the relevant event trigger for each single epoch and subtracted before computing the ERP averages.

Frequency spectra were computed for ERP averages of electrode O1 with the autoregressive method (AR, e.g., Lopes da Silva 1993). This method of estimating a frequency spectrum assumes that a spectrum can be generated by filtering white noise with zero mean and variance σ^2. Parameters a_i are estimated which set a virtual filter in such a manner that only the observed frequency components pass the filter.

The method is called autoregressive, since each digital EEG value can be predicted from the preceding values and the noise:

$$\text{eeg}(k) + \sum_{i=1}^{M} a_i \, \text{eeg}(k-i) = \text{noise}(k) \qquad (1)$$

M is the maximum number of frequency components in the spectra and was set to 20. Once these parameters have been estimated by a special algorithm, spectral power values can be computed at each frequency f (here, j is the imaginary number and ω is 2π times the frequency):

$$S(f) \frac{\sigma^2}{\left| 1 + \sum_{i=1}^{M} a_i \, e^{-jwi} \right|^2} \qquad (2)$$

Spectral values were multiplied by their frequency to correct for the $1/f$ characteristic of the typical frequency spectrum. The 100 frequency spectra were arranged in a two-dimensional plane and power values were coded in gray scales, i.e., one horizontally arranged spectrum was represented in gray scale for each stimulation frequency on the vertical axis (cf. Fig. 5). These spectral planes were averaged across all ten subjects.

Since the AR does not provide information on the phase angle of a frequency component, FFT spectra were computed to estimate the phase shift of an SSVEP relative to the stimulation and were used for some of the figures (where mentioned) for easy comparison with other studies.

Results

Subjects reported perceiving flickering light below and constant dim light above a frequency of about 30 Hz (flicker fusion frequency). In addition, most subjects reported form (stars or stripes) and color (blue, red or purple) illusions at frequencies around 10–15 Hz.

Event-related potentials

Figure 2 shows the SSVEP (top row) of one subject in response to stimulation frequencies of 10 (left), 20 (middle) and 30 Hz (right). In the bottom row, the corresponding frequency spectra (computed with an FFT) are displayed. For 10 Hz stimulation the SSVEP shows a clear 10-Hz and a harmonic 20-Hz response. At 20 Hz stimulation, only a 20-Hz response is visible in the SSVEP and at 30 Hz stimulation a 15-Hz subharmonic appears in addition to the 30-Hz response.

Figure 3 demonstrates the frequency selectiveness of the visual system of one subject for three adjacent frequencies. While the responses to 35 and 37 Hz stimulation lead to corresponding frequency peaks of about 17 μV^2, a stimulation frequency of 36 Hz leads to 27 μV^2.

A similar frequency selectivity can be observed for the 10-Hz SSVEP which was often evoked by flicker frequencies higher than 10 Hz. Figure 4 shows the SSVEP of one subject to frequencies of 79, 80 and 81 Hz. At 80 Hz a clear 10-Hz response was evoked which was not present at adjacent frequencies.

Fig. 2 SSVEPs of a single subject in response to 10 Hz (*left*), 20 Hz (*middle*) and 30 Hz (*right*) stimulation (*top row*) and the corresponding FFT frequency spectra (*bottom row*)
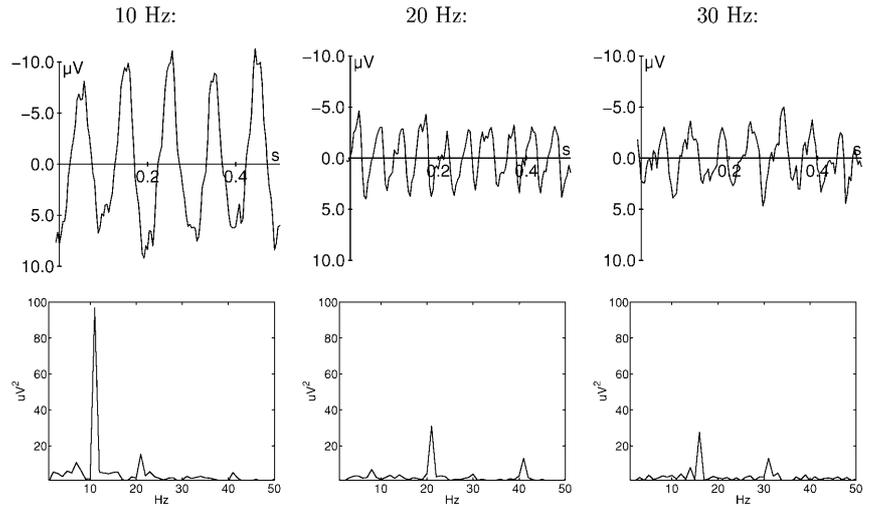
Fig. 3 SSVEPs of a single subject in response to 35 Hz (*left*), 36 Hz (*middle*) and 37 Hz (*right*) stimulation (*top row*). The corresponding FFT frequency spectra show an increase of power at 36 Hz for 36 Hz stimulation (*middle*) as compared to adjacent frequencies (*left and right*)
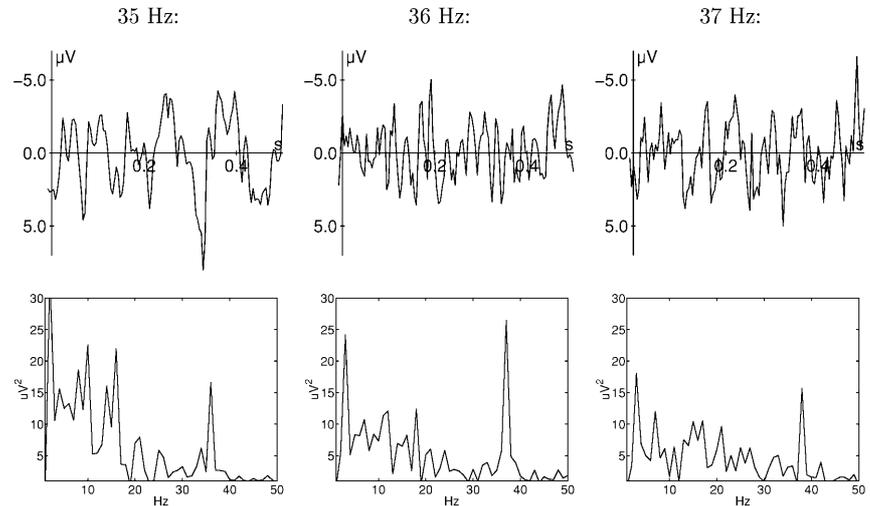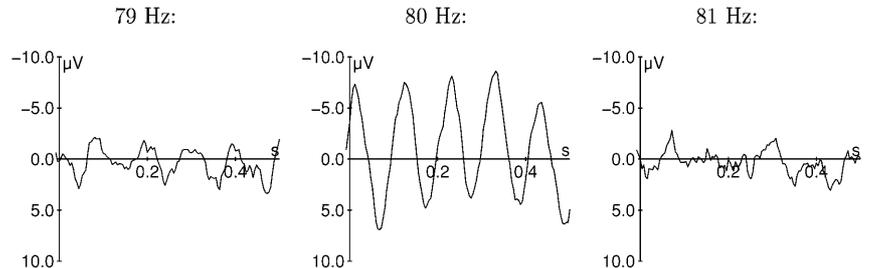
Fig. 4 SSVEPs in response to flicker frequencies 79 (*left*), 80 Hz (*middle*) and 81 Hz (*right*). The VEP shows clear 10-Hz oscillations at 80 Hz which are not as prominent for the adjacent frequencies

Frequency plane

Figure 5 shows the SSVEP response frequency as a function of the stimulation frequency. A clear fundamental can be seen as the diagonal which indicates that the visual cortex is driven by the flickering stimulus at precisely the stimulation frequency. In addition, a first and second harmonic are clearly visible and a third and even fourth harmonic can be marginally detected. This shows that response frequencies which are integer multiples of the stimulus frequency are also evoked by the flicker. Moreover, also subharmonic oscillations can be seen at the intersection with the 10-Hz alpha response. The alpha response is evoked not only by stimulation at and around 10 Hz, but also at higher frequencies which are possibly harmonics (compare with vertical 10-Hz line in Fig. 5). At 39 Hz stimulation frequency, a response in the SSVEP is seen at numerous frequencies which are all multiples of 13.5 Hz (cf. horizontal line at 39 Hz in Fig. 5). Here, the fundamental response frequency is shifted from 39 Hz to 40.5 Hz (3 × 13.5 Hz).

Fig. 5 Response frequency (*x-axis*) as a function of stimulation frequency (*y-axis*). The fundamental frequency (stimulus freq. = response freq.) can be seen as well as a first and second harmonic. Alpha (around 10 Hz) responds to many stimulation frequencies and preferably at intersections with the subharmonics. An enhanced response to 39 Hz stimulation can be observed
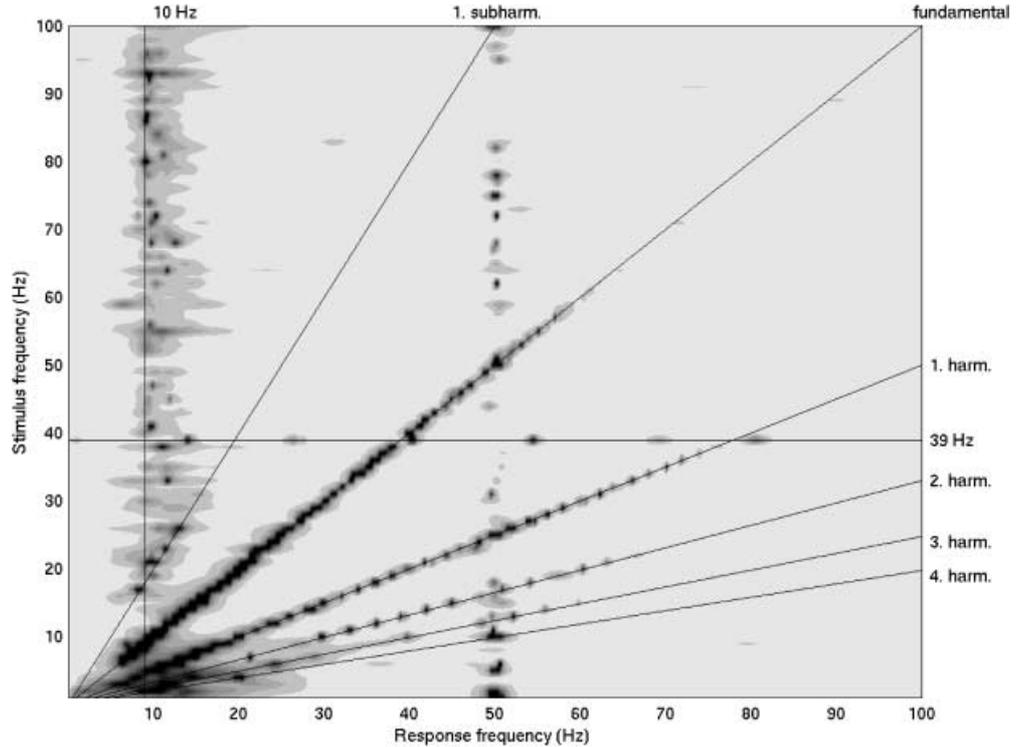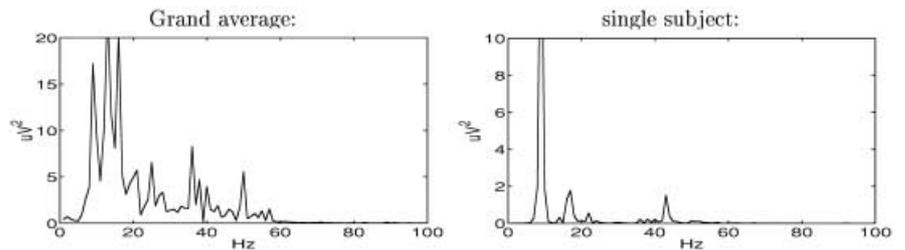

Fig. 6 Profile of the fundamental frequency for the average across all ten subjects (*left*) and for one single subject (*right*). Clear resonance peaks are visible around 10, 20 and 40 Hz

The profile along the fundamental frequency is shown in Fig. 6 for the average across all ten subjects (left) and for a single subject (right). The average exhibits strong resonance peaks around 10 Hz and weaker peaks in the 20- to 30- and 35- to 45-Hz range (the 50-Hz peak is due to the German line frequency). The single subject data show that each subject contributes only one of the spectral peaks per frequency range, i.e., one at 10, one at 16 and one at 42 Hz in the shown case.

Figure 7 shows SSVEP spectrum peaks at response frequencies 10, 20, 30, 40 and 50 Hz computed at the given frequency plus/minus 1 Hz from spectra of all stimulation frequencies (vertical profiles in Fig. 5). In each spectrum a peak is visible at the stimulation frequency. For higher frequencies, subharmonic peaks are also observed, e.g., a 10-Hz and a 15-Hz peak in response to the 30-Hz stimulation. The system mainly responds to the stimulation frequency and to frequencies which are subharmonic to the stimulation frequency.

Figure 8 shows the topographical distribution of the 10-Hz activity evoked by 10-Hz stimulation in a single subject. The map was computed for one positive peak in
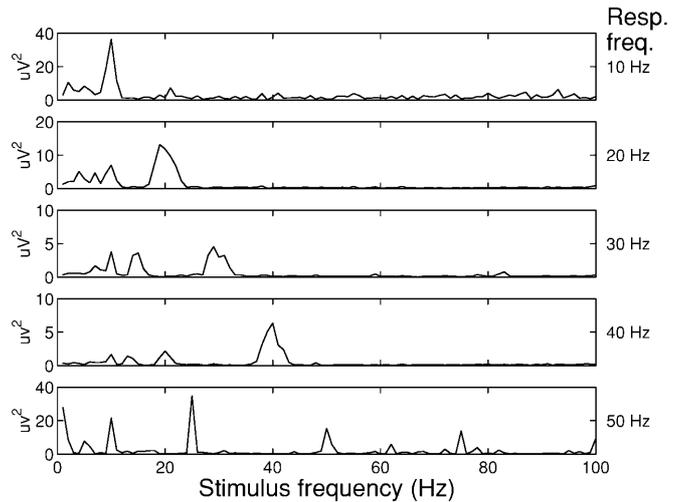

Fig. 7 Vertical profiles at certain response frequencies show that the system mainly responds to the stimulation frequency and subharmonic frequencies
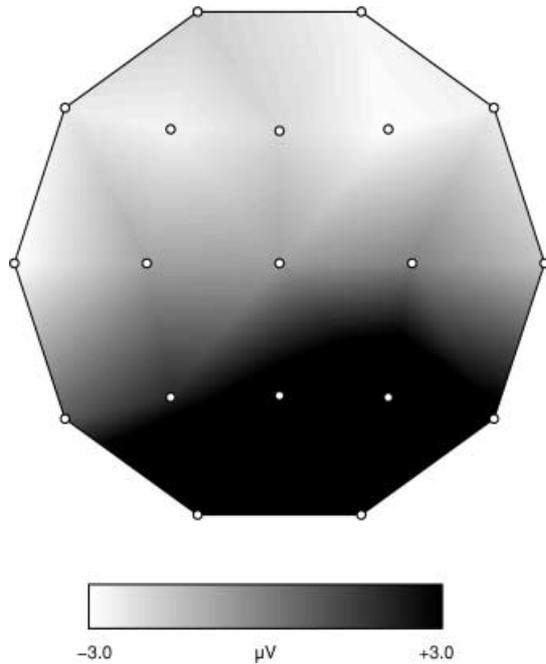
Fig. 8 Topographical distribution of the 10-Hz SSVEP of a typical subject. Occipital positivities and frontal negativities suggest an occipital source of the activity which projects to frontal regions

Fig. 9 Response frequency as a function of stimulation frequency for local field potentials of area 17 of cat visual cortex. Adapted from Rager and Singer (1998, Fig. 7) with permission of the corresponding author

the SSVEP and shows a positivity over occipital cortex with a simultaneous negativity over frontal cortex.

Discussion

The topographical distribution of the SSVEP shown in Fig. 8 is typical for occipital dipoles in visual cortex as they are assumed for primary visual ERP components, such as the P100 in response to checkerboard onset (Ossenblok and Spekreijse 1991). Therefore, it seems plausible to assume that the generators of the visual SSVEP also lie in visual cortex. This has also been found by functional magnetic resonance imaging (fMRI) experiments (Hillyard et al. 1997).

In a recent experiment, local field potentials (LFPs) and multiunit activity (MUA) were recorded from cat visual cortex during flicker stimulation from 2 to 50 Hz (Rager and Singer 1998). Our results are the first human SSVEPs which have been evaluated with the surface-plot method which was introduced for steady-state responses by Rager and Singer (1998). Our results demonstrate a high correlation of the cortical MUA and LFPs from cat visual cortex with human scalp EEG during flicker stimulation. The strong correlation is demonstrated by the marked similarity of Fig. 5 (our data) and Fig. 9 (cat data). Both recordings demonstrate that the visual cortex can be driven by external stimulation up to frequencies of at least 50 Hz. In addition, the brain oscillates at harmonic frequencies of the stimulation frequency. Juergens et al. (1999) have recently demanded that animal MUA and LFPs be correlated with human EEG
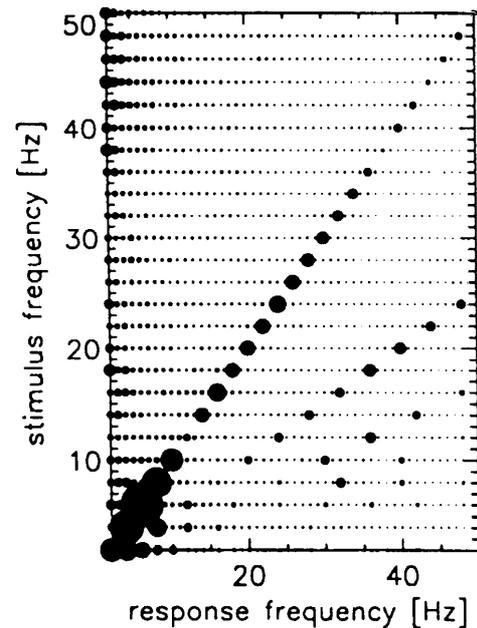
recordings to gain further insights into the similarities and differences of the two measures. Our results give rise to the assumption that oscillatory multiunit activity and local field potentials evoked by flickering light in cat visual cortex are closely related to the SSVEP recorded from the human scalp. In addition to the similarity with the cat data, our results also reveal a difference: the strong responsiveness of the alpha frequency range, especially where the subharmonic of the stimulation frequency intersects with the alpha band, was not found in the cat data. This may be due to the fact that the generators responsible for alpha oscillations are constituted of larger networks of neurons which are not captured when MUA or LFPs are recorded.

The SSVEPs in response to some frequencies show resonance phenomena indicating a selective frequency preference of the neural oscillators. Resonance phenomena occurred in the 10-, 20-, 40- and 80-Hz frequency range, i.e., human visual cortex responds to flickering stimuli at these frequencies more strongly than to stimuli flickering at adjacent frequencies, even though the stimuli are otherwise identical. Therefore, this resonance property may be the underlying phenomenon resulting in enhanced response characteristics when stimuli flicker at around 40 Hz, as demonstrated by Elliott and Müller (1998). This is especially probable, since those stimuli also resulted in EEG oscillations in the gamma frequency range (Elliott et al. 2000). At the same time, the resonance phenomena observed here may explain the predominance of 40-Hz rhythms in binding experiments that occur in human EEG (Tallon Baudry and Bertrand 1999; Keil et al. 1999), MEG (Herrmann and Mecklinger

2000) and animal MUA (Engel et al. 1992; Eckhorn 1994).

The axonal connections between the neurons of an oscillating ensemble have certain temporal characteristics which will propagate spikes at much the same delay after every spike discharge. This can lead to a preferred oscillation frequency and may be the neuroanatomical reason for 40-Hz oscillations even if the generators of evoked/induced and steady-state oscillations are not identical but share common feedback properties.

Our results demonstrate that the neural oscillators which underlie the observed SSVEP oscillations constitute a non-linearly coupled system. Harmonic oscillators show exactly one resonance peak in the frequency spectrum which is the systems resonance frequency. Taking into account that our results show harmonic as well as subharmonic resonance peaks in the spectral plane leads to the conclusion that the involved oscillators constitute a non-linearly coupled system. This interpretation goes in line with previous findings suggesting that the human alpha rhythm behaves in a non-linear fashion (Stam et al. 1999).

The observed hallucinations could be due to the oscillating SSVEP propagating across retinotopic areas of visual cortex. One area then is successively excited and inhibited, thus leading to hallucinations. This phenomenon is known from certain kinds of epilepsies and has been simulated in mathematical models (Tass 1995, 1997). Some of our subjects were retrospectively shown the hallucinations calculated by Tass (1995) and reported them to be identical to the ones observed. An alternative explanation might be that of the so-called Fechner colors. Fechner demonstrated that black and white images lead to color illusions when alternated at certain frequencies (Fechner 1938).

Last but not least, we find it notable that the SSVEP spectrum had clear 50-Hz peaks not only for 50 Hz stimulation frequency, but also for 1, 5, 10, 25, 75 and 100 Hz. Had the 50-Hz spectral peak been present at all stimulation frequencies to a similar extent, it would have just been an artifact of the German line frequency. However, the selective responsiveness to certain stimulation frequencies which are in harmonic relation to 50 Hz suggests that there is a clear interaction of the line frequency and brain oscillations.

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