Alternative perceptual states ‘apparent motion’ and ‘perceived simultaneity’ lead to differences of induced EEG rhythms


Department of Psychology, University Leipzig, Seeburgstr. 14-20, D-04103 Leipzig, Germany

Received 29 September 1999; accepted 17 June 2000

Abstract

An investigation of the cortical response (EEG) to periodically presented stimuli producing an ambiguity between long-range apparent motion and flicker is reported. ERPs to stimulus onsets differed slightly between the two percepts, in accordance with the results of Manning et al. (1988), Selmes et al. (1997). Induced rhythms exhibited a strong increase in induced beta and gamma powers at electrode positions T7 and T8 during the perception of apparent motion in two out of 10 participants. In addition, a small overall increase in alpha power at 12–13 Hz and a decrease in delta power below 3.5 Hz during perceived motion were found. The results indicate that a variety of different neural rhythms are involved in the perception of long-range apparent motion. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Apparent motion; Binding; Induced gamma band response; Alpha and delta band; Human EEG

1. Introduction

The integration of information of different origins into a single percept, often called binding, is one of the main focuses of current neurophysiological research. The suggestion that binding is mediated via the synchronous activity of different information-representing neurons (V. d. Maltsburg and Schneider, 1986) has found empirical support in studies of single-cell activities in the visual cortex of cats and monkeys (Eckhorn et al., 1988; Gray et al., 1989). The possibility of perceiving different stimuli as part of one whole (e.g. collinearly moving bars) led to increased synchronization of firing of the particular representing neurons. Eckhorn et al. (1988) found that visually
evoked synchronous firing in a frequency range of 35–85 Hz extended over different neuronal columns, areas and even hemispheres. The resulting oscillations were not stimulus locked.

On a much more global level of analysis, the evaluation of not necessarily stimulus-locked EEG activity in the gamma band revealed large-scale synchronous activity, so-called induced gamma band activity, which also is related to the integration of different parts of an object. For example Tallon-Baudry and Bertrand (1999) separated two major components of induced gamma after visual presentation of three pacman-like disks. A first burst of approximately 40 Hz at approximately 100 ms after stimulus-onset showed no difference between different stimulus arrangements, whereas a second burst of 30–60 Hz at approximately 280 ms after onset occurred when the pacman disks were arranged in a way that allowed the perception of an illusory (Kanizsa) or real triangle. The latter component could thus be seen as the result of a process that bound together different parts of an object and represented it as a whole. Herrmann et al. (1999), in contrast, with similar stimuli, did not observe changes in induced 40-Hz EEG activity depending on illusory contours. The existence of a different component of induced gamma which is associated with object representation in memory (Tallon-Baudry et al., 1998) demonstrates that induced gamma band oscillations may be involved in a wider spectrum of cognitive tasks (see also Tallon-Baudry and Bertrand, 2000; Müller et al., 2000).

There are two interpretations of the term ‘induced rhythm’ which differ by the oscillatory stimulus-locked content of the EEG signal. Letting \( \{x_i\}_{i=1,n} \) denote a set of stimulus-aligned EEG epochs and \( \bar{x} = \frac{1}{n} \sum_{i=1}^{n} x_i \) their average evoked response, then by the notion of induced power one may refer to the average power (AP) of \( \{x_i\}_{i=1,n} \) or of \( \{\bar{x}_i = x_i - \bar{x}\}_{i=1,n} \). We, throughout the whole article, like Tallon-Baudry and Bertrand (1999), refer to AP(\( \{x_i\} \)). The alternative AP(\( \{\bar{x}_i\} \)) is linked to it by the equation AP(\( \{\bar{x}_i\} \)) = AP(\( \{x_i\} \)) − power(\( \bar{x} \)). In the experiment by Herrmann et al. (1999), at approximately 40 Hz only the stimulus-locked power [i.e. power(\( \bar{x} \))] differed significantly for illusory vs. non-illusory contours.

The notion of binding is usually applied to situations where the different relevant pieces of information are simultaneously present. It is, however, possible to extend this term to the integration of information that is not concurrently available. A question which naturally arises is whether, in this case, synchronous oscillations also play a functional role in the formation of a common percept. The analysis of induced EEG rhythms during the perception of stimuli constituted of parts which are separated in time may provide an answer to this question.

In the present study, a display producing long-range apparent motion (LRAM) of the beta type (Kolers, 1972) was used as a very simple compound stimulus that extends not only in space but also in time. The applied periodically presented stimulus sequence is shown in Fig. 1. Basic determinants of the resulting percept are angular separation of the two disks (AS), exposure duration (ED) and interstimulus interval (ISI).

It is a well-known fact that apparent motion (AM) after ongoing inspection can give way to the perception of flicker and vice versa (Kolers, 1972). Consequently, the simultaneity threshold, the set
of parameters characterizing the transition from perceived motion to flicker, forms a broad band in the $ED \times ISI$ plane (Fig. 2a). It has been demonstrated, however, that under suitable conditions of measurement, the simultaneity threshold can take the form of a sharp border which can be determined with high accuracy (Geissler et al., 1999; Kompass and Geissler, 2000). The graph characterizing the transition between the two competing perceptual states then exhibits segments of locally constant ISI which are interpreted as manifestations of discrete timing mechanisms (Fig. 2b) with the ISI corresponding to a preferred period.

These mechanisms are assumed to be universal across different mental tasks and stimulus dimensions as well as with respect to the involved discrete periods. Universality is supported besides other empirical observations (Kompass, 1999) by the fact that the set of preferred ISI values in AM/flicker switching (Table 1) has large overlap with a set of critical periods of low sinusoidal tones determined by v. Békésy (1936) measuring auditory absolute thresholds with the method of limits. The existence of integer ratios of the preferred periods suggests that harmonically related brain rhythms may be an origin of emergence of the observed temporal structure. More specifically it may be asked whether such rhythms have a functional role in the generation of the motion percept. The observation that preferred ISIs span a wide range from 4 to 144 ms indicates that they should include a wide spectrum of frequencies from alpha to above gamma.

A study by Varela et al. (1981) provided evidence that the alpha rhythm is involved in the perception of AM. In their experiment, a simple stimulus sequence (left flash, ISI, right flash) led to increased perception of AM if it was initiated at the positive zero-crossing of a simultaneously monitored EEG alpha rhythm. These results led to the hypothesis that the integration of two flashes that may be separated in time by as much as 300 ms (stimulus onset asynchrony, SOA) is achieved by an interaction of different neural oscillations including alpha rhythms with periods

| Table 1 |
|-----------------|-------|-----|-----|-----|-----|-----|-----|-----|
| Preferred ISI threshold values and associated frequencies |
| Significantly preferred ISI-values (ms) | 4–5 | 9 | 18 | 22–23 | 27 | 36–37 | 44 | 54 | 107 | 144 |
| Corresponding frequencies (Hz) | 200–250 | 110 | 55 | 44 | 37 | 27 | 22 | 18 | 9 | 7 |
similar to temporal parameters of the stimuli as well as gamma oscillations.

The ambiguity between motion and flicker at the simultaneity threshold of LRAM allows for the investigation of the cortical response to both percepts under identical stimulus conditions. Previous studies by Manning et al. (1988), Selmes et al. (1997) demonstrated that it is possible to discriminate between the two perceptual states on the basis of flash-evoked potentials. The aim of the presented experiment was an exploration of possible ways to discriminate the EEG responses to perceived motion from those to the perception of flicker with various analysis methods. For that purpose ambiguous AM-stimuli were presented and flash-evoked ERPs and induced rhythms in a wide range of frequencies were determined and compared for either of the two possible percepts.

2. Method

2.1. Subjects

Ten students (four male) of psychology aged from 19 to 25 years participated in the experiment. They gave informed consent after the nature of the study had been explained to them. All had normal or corrected to normal vision.

2.2. Stimuli and procedure

The participants underwent one or two training sessions of 15 min and one EEG recording session of 15 min duration. The sessions consisted of eight (training) or 10 (recording) trials of 70 s ongoing periodically presented LRAM (as sketched in Fig. 1) separated by breaks of 10 s duration. Observers had to report their percepts by pressing one of two possible keys (right or left hand). The assignment of the right or left key to AM or flicker was changed for every second subject. Stimuli were white disks 0.96 cm in diameter against a dark background. They were presented on a 17"-computer monitor at a refresh-rate of 100 Hz with 1.1-m viewing distance. A small (3-mm) gray triangle 2 cm below the middle of the disks served as fixation point. ED and ISI were kept constant at 100 and 40 ms (resulting in a frequency of the flash alteration $f_0 = 3.57$ Hz) to allow for the averaging of single flash-evoked responses over the whole session. Compensation of individually differing preferences to perceived motion or flicker was achieved by the adaptive variation of the angular separation of both flashes during training sessions. The resulting distance during recording ranged from 3.2 to 8.1 cm ($1.6^\circ$–$4.2^\circ$ angular distance).

In the EEG recording session, participants were seated in a comfortable chair in an electrically and acoustically attenuated booth.

2.3. EEG recording and analysis

EEG was measured with Ag/AgCl electrodes from 25 scalp locations of the extended 10–20 system (Sharbrough et al., 1990) (FP1, FPZ, FP2, F7, F3, FZ, F4, F8, FC5, FC6, T7, C3, CZ, C4, T8, CP5, CP6, P7, P3, PZ, P4, P8, O1, OZ, and O2) and from the left and right mastoids (LM, RM). The horizontal and vertical EOGs were monitored with bipolar pairs of electrodes placed at the outer canthi of the left and the right eye and from above and below the right eye, respectively. The reference electrode was placed at the nose. EEG and EOG were digitized at 500 Hz (bandpass 0.05–100 Hz) in continuous mode.

For the computation of flash evoked ERPs the data were sampled down (4:1) and filtered offline with finite-impulse response filters (FIR, bandpass 0.5–20 Hz, 1001 points). Rejection was performed based on a S.D. criterion with a sliding window of 200 ms. On average, the records of 17% of the stimulus sequences were rejected. ERPs were computed by averaging the EEG responses for the two perceptual states, motion and flicker, separately. Epochs lasted from 100 ms before to 450 ms after the onset of the left flash.

Induced rhythms in the EEG activity were analyzed by performing a continuous wavelet transform based on the Morlet wavelet $\Psi(t) = e^{i2\pi t}e^{-t^2/2}$. The convolution of the scaled wavelet $\frac{1}{\sqrt{a}}\Psi\left(\frac{t}{a}\right)$ (a denoting the scale factor) with the EEG signal yields a new complex signal, the squared absolute value of which can be inter-
3. Results and discussion

3.1. Behavioral data

The durations of the phases of dominance of either percept were determined as asynchronies of alternative button presses by the observers. A box plot of the dominance phase durations (DPDs) of all subjects and both perceptual states of the EEG recording session is presented in Fig. 3. In eight of the 10 subjects, the median of DPDs of AM is greater than or equal to that of flicker. The smaller influence of the perceptual state on DPDs follows from its compensation by the adaptive variation of the angular distance of the alternating flashes. DPDs consequently vary by a factor of 3 between subjects and, as intended by the experimental procedure, only by a factor of 1.8 between AM and flicker. An ANOVA yielded a significant ($P < 0.01$) influence of subjects on log(DPD) whereas the influence of the perceptual state misses significance ($0.05 < P < 0.1$). The interaction of both factors is not significant.

3.2. Flash-evoked ERPs

Individual flash-evoked ERPs for three partici-
pants (S1, S3 and S6) and selected electrodes (FP1, FP2, F3, F4, P3, P4, O1, O2, T7 and T8) are shown in Fig. 4. The diagrams contain averages of 700–1200 single epochs for the two perceptual states: motion and flicker. Epochs were aligned relative to the onset of the left flash. At 100 ms, the left flash disappeared and at 140 ms, the right flash set on.

The selected curves demonstrate that the evoked responses for motion and flicker could be both quite similar (S6) and very different in amplitude and shape (S1, S3). One of the participants (S10) had extraordinarily large sinusoidal parieto-occipital ERPs. Both their simple shape and high amplitude (> 4 μV) suggest resonance of internal rhythms with the external flash-driving as a possible interpretation for this qualitatively different pattern. Amplitudes were higher for perceived motion than for flicker.

In order to compare flash-evoked responses with those reported by Selmes et al. (1997), grand-averaged evoked potentials were computed including data from all participants except S10 (Fig. 5).

At the onset of the left flash, the EEG responses at frontal to occipital positions exhibited an increasing negativity, whereas those in the study of Selmes et al. (1997) were positive-going. Diff-

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**Fig. 4. Selected individual flash-evoked ERPs.**
ferences between the ERPs of motion and flicker are bigger on the right hemisphere, in accordance with results reported by Manning et al. (1988), Selmes et al. (1997).

3.3. Induced rhythms

The distribution of the power of induced frequencies differed considerably between subjects.

To illustrate this, a selection of individual power characteristics for electrodes FP1, F3, P3, O3 and T7 is presented in Fig. 6. The restriction to left-sided electrodes is justified by the observation that the characteristics of induced power were similar for corresponding right and left electrode positions (e.g. F3 and F4).

While in general the power was a decreasing function of the frequency, there were deviations from this characteristic. Most frequently observed was an increase of power in a broad range of frequencies in the beta and gamma band in frontal or fronto-central electrode positions (five of the 10 participants, S3 and S6 in Fig. 6) and temporal electrode positions (four of 10 participants, S3 and S6 in Fig. 6; two other subjects only with AM, S1 in Fig. 6). Six observers had occipital to central increases in power at a frequency of approximately 10 Hz, which equals the third harmonic of the frequency of flash alteration $f_0$ (S1 and S3 in Fig. 6). Of course, the occurrence of alpha-activity could be due to a decrease in alertness of those subjects. In the case of S10, a peak of power at approximately $3f_0$ seemed surprising since ERPs for that subject exhibited a strong stimulus-locked second harmonic. Visual inspection of the raw EEG of S10 revealed generally enhanced alpha-activity with high correlation between different electrodes, which was not stimulus-locked and had a frequency mostly above $2f_0$. Apparently contradicting pictures of the ERP
and induced rhythm may have resulted from a tendency of alpha to synchronize with external driving only if the frequency equals $2f_0$. Apart from these observations, there was no further exploration of the EEG characteristics of S10. Because of the clear differences to the overall picture, participant S10 was excluded from the following analyses.

In relation to the high variability across subjects, differences of power between the two perceptual states of motion and flicker were rather small. They were assessed using non-parametric statistical methods, thus accounting for the fact that distributions of spectral power, in general, are not normal. An additional advantage of this approach is the possibility of combining rank based measures of perceptually induced power changes across subjects with different absolute characteristics (Fig. 6). From single epoch based rank values, the Wilcoxon statistics for the comparison power(AM) > power(flicker) was independently computed for every electrode, frequency and all participants except S10. For example, for S1 there were $n = 695$ accepted epochs with percept AM and $m = 340$ with flicker. The $n + m$ values of induced power (determined at the onset of the left flash) at electrode T7 and $f = 30$ Hz were rank ordered and the sum $w$ of the ranks for flicker determined. From $w$, the $z$-value

$$z = \frac{w - 1/2 - m(m + n + 1)/2}{\sqrt{mn(m + n + 1)/12}}$$

which is standard-normally distributed on the assumption of equality of power at both percepts. In this example, a $z$-value of 8.7 indicates that the power with AM is significantly higher than with flicker. Across-subjects combined $z$-values for selected electrodes and corresponding (two-tailed) $P$-levels are contained in Fig. 7. Positive values indicate higher power for AM.

Systematic changes of induced power during perception of motion include an increase in the alpha range at a frequency of 12–13 Hz and a decrease in the delta range below $f_0 = 3.5$ Hz across the whole scalp. Table 2 contains combined normalized ranksums for all electrodes at the frequencies 2.9 and 12 Hz, where the differences are greatest.

The fact, that the direction of changes in power remains the same for virtually all electrodes (exception: F8) leads to a strong validation of these observations. Combined $z$-values and two-tailed significance levels are $z = 10.4$, $P < 0.000001$ ($f = 12$ Hz) and $z = -11.7$, $P < 0.000001$ ($f = 2.9$ Hz).

Fig. 7 also contains an enhancement of induced beta and gamma rhythms at temporal electrode positions T7 and T8 during the perception of motion. A comparison of individual spectra revealed that this picture, in essence, is due to the characteristics of only two subjects (S1 and S4), which exhibited at these positions a very strong increase of induced power for perceived motion at frequencies above 20 Hz (Fig. 8 left).

Individual normalized Wilcoxon rank-sums ($z$-values) and $P$-levels for both subjects and electrode positions T7 and T8 for every frequency are presented in Fig. 8 right. The results show that the increases are highly significant (six or eight S.D., $P < 0.0001$).
Fig. 7. Combined normalized ranksums (all participants except S10) for non-parametric comparison of induced power. Positive values denote higher power during the perception of motion.

Taken together, the results confirm the hypothesis that perceptual processes arising during the inspection of two alternating flashes involve the occurrence of several rhythms in the brain. Besides rhythms in the alpha and gamma ranges, this applies even to slow oscillations in the delta band. Spontaneous alpha is normally reported to be suppressed during stimulus processing (see, however, Başar et al., 1997). In the induced power characteristics (Fig. 6), no such pattern is visible. The existence of maximum differences in alpha power across subjects at approximately 12 Hz, in contrast, points to a relation of this rhythm to stimulus processing. The fact that the differences for the two percepts, perceived movement and flickering, are small agrees with the assumption that only a small portion of oscillating neurons is involved in the immediate control of the specific

Table 2
Combined normalized ranksums (S1–S9) for all electrodes at 12 Hz and 2.9 Hz

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final perceptual structures (see Geissler and Kompass, 1999). The occurrence of strong perceptually induced variations of power in the beta/gamma bands in only two out of 10 subjects does not suffice to pinpoint a precise function in stimulus processing. However, a common significant difference in this range indicates at least that beside alpha faster rhythms may play a genuine role in stimulus processing.

In general, the results seem to indicate that the idea of expanding the problem of binding to sequential stimuli represents a promising rationale for future research. Of course, in subsequent investigations, alternatives to a direct functional involvement of the observed oscillatory components also have to be taken into consideration. A second issue of concern is strong individual differences whose origins remain obscure. To resolve these issues, detailed analyses of differences in response to stimulation with varying rhythms are suggested.

Acknowledgements

Supported by German research organization DFG, grant Gei 678/5-2

References


