

Subsecond changes of global brain state in illusory multistable motion perception

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Summary. This study explored transient changes in EEG microstates and spatial Omega complexity associated with changes in multistable perception. 21-channel EEG was recorded from 13 healthy subjects viewing an alternating dot pattern that induced illusory motion with ambiguous direction. Baseline epochs with stable motion direction were compared to epochs immediately preceding stimuli that were perceived with changed motion direction ('reference stimuli'). About 750 ms before reference stimuli, Omega complexity decreased as compared to baseline, and two of four classes of EEG microstates changed their probability of occurrence. About 300 ms before reference stimuli, Omega complexity increased and the previous deviations of EEG microstates were reversed. Given earlier results on Omega complexity and microstates, these sub-second EEG changes might parallel longer-lasting fluctuations in vigilance. Assumedly, the discontinuities of illusory motion thus occur during sub-second dips in arousal, and the following reconstruction of the illusion coincides with a state of relative over-arousal.

Keywords: Multistable perception, EEG, complexity, illusory motion.

Introduction

The study of visual multistable pattern and of binocular rivalry has inspired generations of scientists in the field of neuropsychology. These two experimental conditions involve related brain mechanisms (Leopold and Logothetis, 1999), are excellent objects to study the brain's perceptive strategies, and have

allowed fundamental insights in the mechanisms of perception and cognition (Eagleman, 2001).

The subjective perception of ambiguous stimuli is often remarkably stable. This stability indicates the existence of externally and internally driven processes that bias the subject in interpreting the ambiguous information. Multistable phenomena can be manipulated by altering the stimulus' properties, i.e. symmetry, closure, element proximity, brightness, contrast and spatial frequency content. Furthermore, the rate of perceptual transitions, i.e. switching from one to the other possible percept of a stimulus is influenced by factors such as semantic context and recognizability (Leopold and Logothetis, 1999). The rate of the transitions also varies across subjects, depending on intelligence, personality, psychiatric diseases and intake of stimulating substances (Walker, 1978; Pettigrew and Miller, 1998).

Neurophysiological methods have given further insight into the understanding of how the brain is handling ambiguous stimuli. Single cell recordings in monkeys during binocular rivalry provided no evidence for inhibition at the subcortical level in the geniculo-striate system (Lehky and Maunsell, 1996). However, a distributed activity during binocular rivalry was observed in the extrastriate cortex despite an unchanged retinal input; this activation included namely areas of the inferior temporal cortex and the superior temporal cortex (Sheinberg and Logothetis, 1997; Leopold et al., 2002; Blake and Logothetis, 2002). More recently, EEG and MEG studies have revealed a decrease of EEG alpha activity preceding perceptual reversals (Müller et al., 1999; Isoglu-Alkac et al., 2000; Struber and Herrmann, 2002). Additionally, changes of EEG gamma activity were found during perceptual transitions (Basar Eroglu et al., 1996; Tallon-Baudry and Bertrand, 1999; Keil et al., 2001). Functional magnetic resonance imaging (fMRI) of the human cortex showed greater activation in extrastriate (Kleinschmidt et al., 1998; Sterzer et al., 2002) and frontoparietal regions of the right hemisphere in binocular rivalry. When viewing ambiguous figures, increased fMRI activity was found bilaterally in ventro-occipital, parietal and some frontal areas (Blake and Logothetis, 2002). On the other hand, deactivation of the BOLD signal was found in primary visual cortex and thalamus in binocular rivalry (Blake and Logothetis, 2002) and multistable perception (Kleinschmidt et al., 1998). The latter gave evidence that changes of vigilance would affect visual attention and thus facilitate perceptual transitions.

Thus, although the conclusions drawn from the fMRI studies converge with the above outlined single cell, EEG and MEG studies about the location of the involved brain regions, knowledge about the sequence of events that drive the brain from one to another possible interpretation of the stimulus still is incomplete. For the investigation of the temporal evolution of these events, both the stimulus material and/or the type of analysis employed in the discussed studies are not well suited since they do not resolve time well. On the other hand, stroboscopic alternative motion (SAM) protocol (Schiller, 1933) provides discrete time points at which perceptual transitions may be evoked and thus, opens the possibility for a temporally fine-grained examination of the brain states preceding and following the perceptual transitions (see also Struber and

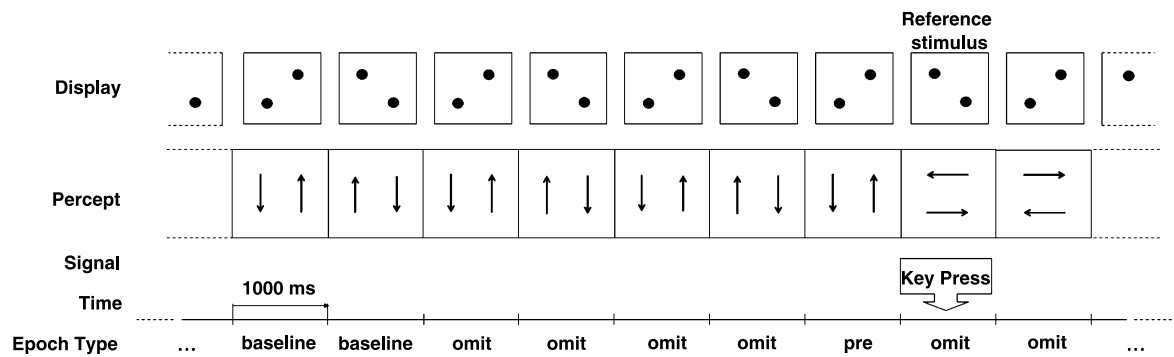


Fig. 1. Extraction of event-related EEG epochs (example): Time is running from left to right. The uppermost row shows the stimuli, each pair of dots was shown for 1000 ms (symbolized by a square). The row below shows one of the possible directions of subjective illusory motion perception. The time line at the bottom of the figure shows the subject's signaling of a perceptual transition and the corresponding identification of the immediately preceding stimulus as reference stimulus, and of the analysis epoch types as "baseline epoch" or "pre epoch" or as epochs to be omitted from analysis (5 s before the *pre* epoch, and 5 sec after a reference stimulus)

Herrmann, 2002). In its simplest form, SAM consists of two pairs of dots shown in alternation (Fig. 1). These stimuli, although static in their positions, evoke mutually exclusive patterns of illusory motion from one pair of dots to the other. Typically, this is perceived as movement in horizontal or vertical direction, but may also include left or right rotations. These motion patterns have considerable stability, and new motion directions, the so-called perceptual transitions, occur only occasionally and are seemingly unpredictable for the subject.

From the point of view of analysis strategies, the measures of EEG power spectra or the changes of fMRI-BOLD signals employed in many earlier studies account for state changes in the range of seconds. In the present study we wanted to refine the knowledge about the temporal evolution of events that lead to a perceptual transition. This requires that the functional brain state must be described with a time resolution in the sub-second range. In EEG, a millisecond time resolution is a-priori available because the momentary brain state is reflected directly by the momentary spatial configuration (topography) of the brain electric field. Changes of momentary EEG topography must be caused by changes of the active neural elements and thus imply changes of brain state. In previous work, these changes of EEG topography have repeatedly been shown to be discontinuous and to be separated by quasi-stable sub-second periods (Lehmann et al., 1987). Furthermore, the observed topographies tend to re-occur and can be clustered into a small number of topographic classes (Pascual-Marqui et al., 1995; Koenig et al., 1999, 2002). By applying a spatial clustering procedure, EEG data can thus be efficiently represented as a temporal sequence of re-occurring stable topographies with certain durations in time. These periods of stable topography have been called microstates and have been suggested to represent basic steps of information processing (Lehmann et al., 1987, 1998; Brandeis and Lehmann, 1989). In a series of studies, microstates

have indeed been shown to correlate with changes in cognitive mode, i.e. with momentary content of thought (Lehmann et al., 1998), psychopathology (Koenig et al., 1999; Strelets et al., 2003) or development (Koenig et al., 2002). Therefore, microstates appear well suited for the present study since they assess brain states as a function of time with millisecond resolution.

Another measure that can assess the transient variations of the brain functional state is Omega complexity (Wackermann, 1996). Omega complexity is based on the linear decomposition of multi-channel EEG into its principal, orthogonal (i.e., uncorrelated) spatial components; the entropy of the distribution of the relative contributions of these components to the total power (variance) then defines Omega complexity. When most of the variance of the data in a given analysis period can be explained by a single principal component, most of the active neurons, irrespective of their location and orientation, are synchronously active and collapse into a global functional brain state that is characterized by low Omega values. When the variance of the data is spread across many spatial principal components, many sets of neural assemblies operate in an uncorrelated way, indicating more complex brain spatio-temporal dynamics that yields higher Omega values. Technically speaking, Omega gives a lower-bound estimate of the number of uncorrelated processes in the brain. Due to its spatial nature, and contrary to other complexity measures used in EEG, Omega complexity can be assessed in short, sub-second time-windows. Omega complexity is thus local in time and global in space, whereas other complexity measures employed (Grassberger and Procaccia, 1983) are usually single channel time series analyses that are global in time, but local in space. Omega complexity therefore offers a unique possibility to study short lasting fluctuations in the degree of organization of the ongoing brain functional dynamics, which may be closely related to the capacity to maintain or change the direction of multistable illusory motion.

The aim of the present study was to investigate EEG epochs preceding perceptual transitions using microstates and Omega complexity, thereby assessing brain state on a global level and preserving the time-resolution in the sub-second range.

Material and methods

Subjects

The present, novel analysis approaches are applied to a dataset that was used earlier for spectral EEG power analysis during multistable motion perception (Müller et al., 1999). 13 subjects (3 females, 10 males; age mean 28.5, range 23–37 years) were recruited among staff members of the Department of Psychiatry of the University of Würzburg, Germany. All subjects had normal or corrected-to-normal vision, and were right handed as assessed by the Edinburgh handedness inventory (Oldfield, 1971). None of the subjects reported a history of major medical, neurological or psychiatric disorders or of psychotropic medication. All subjects gave their informed consent to the study. Approval for the study was obtained from the local Ethics Committee.

Stimulation

During the experimental session, subjects were comfortably seated in a dimly lit, acoustically shielded room. A chin rest was used to minimize head movements. The stimuli were presented on

a computer screen 120 cm in front of the subject's eyes, with a fixation point in the center of the screen to reduce eye movements. The stimuli consisted of two diagonal pairs of black dots with 2 cm diameter located in the corners of a rectangle with 13 cm width and 14 cm height and shown on a white background (Fig. 1). The pairs alternated with a frequency of 1 Hz without inter-stimulus interval. The used parameters were previously found to be optimal to obtain a reasonable frequency of perceptual transitions (Müller et al., 1999). The subjects were instructed to press a computer mouse key with their right hand whenever they perceived a change in motion. No further information was given.

EEG recording

During stimulus presentation, the EEG was recorded in 21 channels using GRASS gold cup electrodes attached to the scalp according to the International 10/20-system. For the detection of eye movements, three additional electrodes were placed at the outer canthi of both eyes and below the right eye. As recording reference, linked mastoids with compensating resistors of 10 kOhm each were used. Electrode impedances were kept below 5 kOhm. The EEG was amplified using a 32-channel DC-amplifier (Brain-Star), filtered at 0.5 to 70 Hz bandpass and digitized at 256 Hz. A separate channel recorded the moments of stimulus presentation and the subject's mouse key signal. The recordings took place in two sessions of 15 min. each, separated by a 5-min. break.

Data preprocessing

The continuous EEG was recomputed to average reference, and bipolar derivations for eye movements were constructed (horizontal eye movement: left versus right canthus; vertical eye movement: below right eye versus Fp1). The entire data was then scanned for artifacts using both, an automatic rejection procedure (maximal amplitude of eye movements exceeding 15 μ V as well as maximal voltage difference between successive sampling points more than 30 μ V to detect muscle artifacts), and visual inspection. The data were digitally bandpassed at 2–20 Hz. From the artifact-free periods, the markers indicating the moments of stimulus presentation were used to select 1-second epochs for further analysis. Stimuli followed by a key press were called reference stimuli. To remain compatible with the previous analysis (Müller et al., 1999) reference stimuli with reaction times below 150 ms were excluded from further computation.

Two types of epochs were identified for further analyses: (1) '*baseline* epochs', i.e. epochs that were separated by at least 5 seconds from any reference stimulus, and (2) '*pre* epochs', i.e. those epochs that immediately preceded reference stimuli. One subject was excluded from further analysis because of an insufficient number of artifact free *pre* epochs ($n = 3$). The remaining subjects had on the average 40 *pre* epochs (S.D. = 21, Range 10–144) and 274 (S.D. = 167, Range 35–591) *baseline* epochs.

Microstate analysis

The microstate analysis followed the standard procedure used in earlier work (Koenig et al., 2001): Global Field Power (GFP, Lehmann and Skrandies, 1980), a measure that quantifies the potential variance across all electrodes, was computed in each epoch and at each point in time. Topographies at momentary maxima of the GFP were selected for further analysis. As in previous work (Koenig et al., 1999, 2002), four optimally fitted microstate class topographies were computed across all epochs for each subject using a modified version of the K-mean clustering algorithm (Pascual-Marqui et al., 1995, program available at www.puk.unibe.ch/tk2/tk.htm). This number of classes has previously been found to be optimal using a cross validation criterion, and was maintained for compatibility with earlier findings. Across all subjects, the four classes accounted on the average for 74.7 (S.D. = 2.9) percent of the variance. Grand mean microstate class topographies across subjects were computed using a permutation algorithm that maximized the common variance over subjects and yielded a common labeling (class I to IV) for the individual microstate class topographies (Koenig et al., 1999). The EEG topographies of each epoch and each subject were then assigned to one of the individual microstate classes. Finally, within each subject and separately for *baseline* and *pre* epochs, the reference stimulus-related

probability of each microstate class was estimated for each moment in time (e.g., if at 300 ms post stimulus, 45 out of 100 epochs showed class III, the probability of class III at 300 ms was 0.45). In this way, for each of the four microstate classes and for *baseline* epochs and *pre* epochs, a time series of stimulus-locked microstate class probability was obtained. In order to compare the results with previous findings on microstates, a correlation matrix was computed relating the microstate topographies obtained here with those of previous studies on eyes-closed EEG (Koenig et al., 2002).

Omega complexity

Omega complexity is a measure of spatial synchronization of the brain's electrical activity and gives a lower-bound estimate of the number of uncorrelated activities in the brain. Omega attains a value from 1 to the number of electrodes: the higher the value of Omega, the lower the degree of synchronization between spatially distributed cortical areas and vice versa. Such computation of synchronization obviously requires the evaluation of the development of system state over some minimum time. For the continuous assessment of the time-varying Omega complexity we chose to use an analysis window of 64 time points (0.25 s) that was shifted time point-by-time point over the entire EEG recording (Stancak and Wackermann, 1998). Using the Omega complexity results of the previously defined *baseline* epochs and *pre* epochs, the values were log transformed and averaged within subjects, yielding a time series of stimulus locked, average Omega complexity for *baseline* epochs and *pre* epochs.

Time series statistics

All statistical analyses were based on normalized (z-transformed) individual differences between the obtained time series of *pre* and *baseline* epoch results. They were done across subjects and separately for Omega complexity and for each of the four microstate classes. Since there was no a-priori hypothesis about the nature of the differences between *pre* and *baseline* periods, the statistical assessment of differences was based on an analysis of differences over the entire analysis time (global level analysis) using a multivariate randomization test (a); given that there were significant differences in the global level analysis, those differences were further explored using moment for moment paired univariate t-tests (b).

- (a) Randomization test: The mean *pre* and *baseline* time series across subjects were computed. The difference between these two mean time series was assessed by the Euclidian distance using all pairs of values. Then, within each subject, the time-series were randomly re-assigned to *pre* and *baseline* condition, mean *pre* and *baseline* time series across subjects were recomputed and the difference was newly assessed. When this random shuffling is repeated a large number of times (we used 5000), one obtains a data-driven estimate of the distribution of the difference between the mean *pre* and the mean *baseline* transition probabilities assuming the null-hypothesis. The probability of the difference based on the observed assignments assuming the null-hypothesis is then determined by the rank of the observed differences among the differences obtained by randomization (Pitman, 1937; Manly, 1997; Strik et al., 1998).
- (b) In those time-series where the randomization test indicated significant differences, t-values were computed time instant by time instant. An interpretation of the t-values in terms of exact statistical probabilities was however omitted to avoid problems of multiple testing in temporally associated samples.

Results

The analysis of the key press records showed that across subjects, there was an average interval of 18.69 sec (SD = 28.80 sec) between successive perceptual transitions. The mean delay from the onset of the reference stimulus to the key press was 414 ms (SD = 251 ms). A histogram of the distribution of all key presses referred to the reference stimulus is shown in Fig. 2.

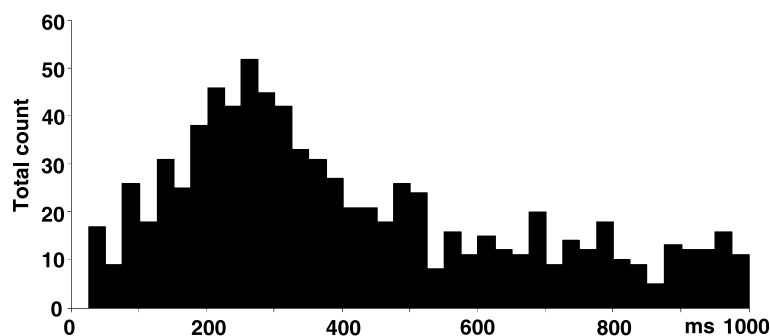


Fig. 2. Distribution of the key press signals of all subjects as function of time from reference stimulus onset (key signals earlier than 25 ms were not recorded due to technical reasons). The number of key signals increased continuously from stimulus onset to about 300 ms post-stimulus, whereafter it decreased again and reached an apparent baseline level at about 550 ms

The microstate topographies as identified by the clustering procedure are shown in Fig. 3: Microstates of class I had a left frontal to right parietal orientation of the brain electric axis, class II was oriented from anterior central to bilateral occipital, class III symmetrically from anterior to posterior and class IV from right frontal to left parietal. Three of the four microstate classes (II, III, and IV) closely resembled classes previously observed in eyes-closed EEG (classes D, C and A in Koenig et al., 2002), with more than 80% of the variance shared between the corresponding pairs of classes (Fig. 3).

The time courses of the mean microstate probabilities of the four classes of microstates and the time course of Omega complexity together with the time-varying effects of *baseline* vs. *pre* condition are shown in Fig. 4. In the global level analysis, the randomization test yielded significant effects of condition for microstate class I ($p < .02$), microstate class III ($p < .03$), and Omega complexity ($p < .001$).

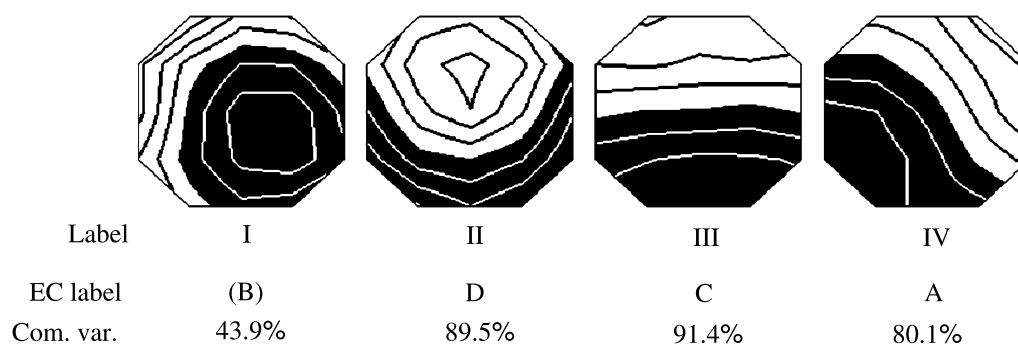


Fig. 3. Amplitude-normalized equipotential-line topographies of the four extracted microstate classes (Labels I–IV). Map areas of opposite polarity are arbitrarily coded in black and white. Left ear is left, nose is up. Below each class map, the corresponding eyes-closed (EC) microstate class (EC labels A–D from Koenig et al., 2002) is given, together with the percent variance (Com. var.) that microstate classes I–IV have in common with the best-corresponding EC classes

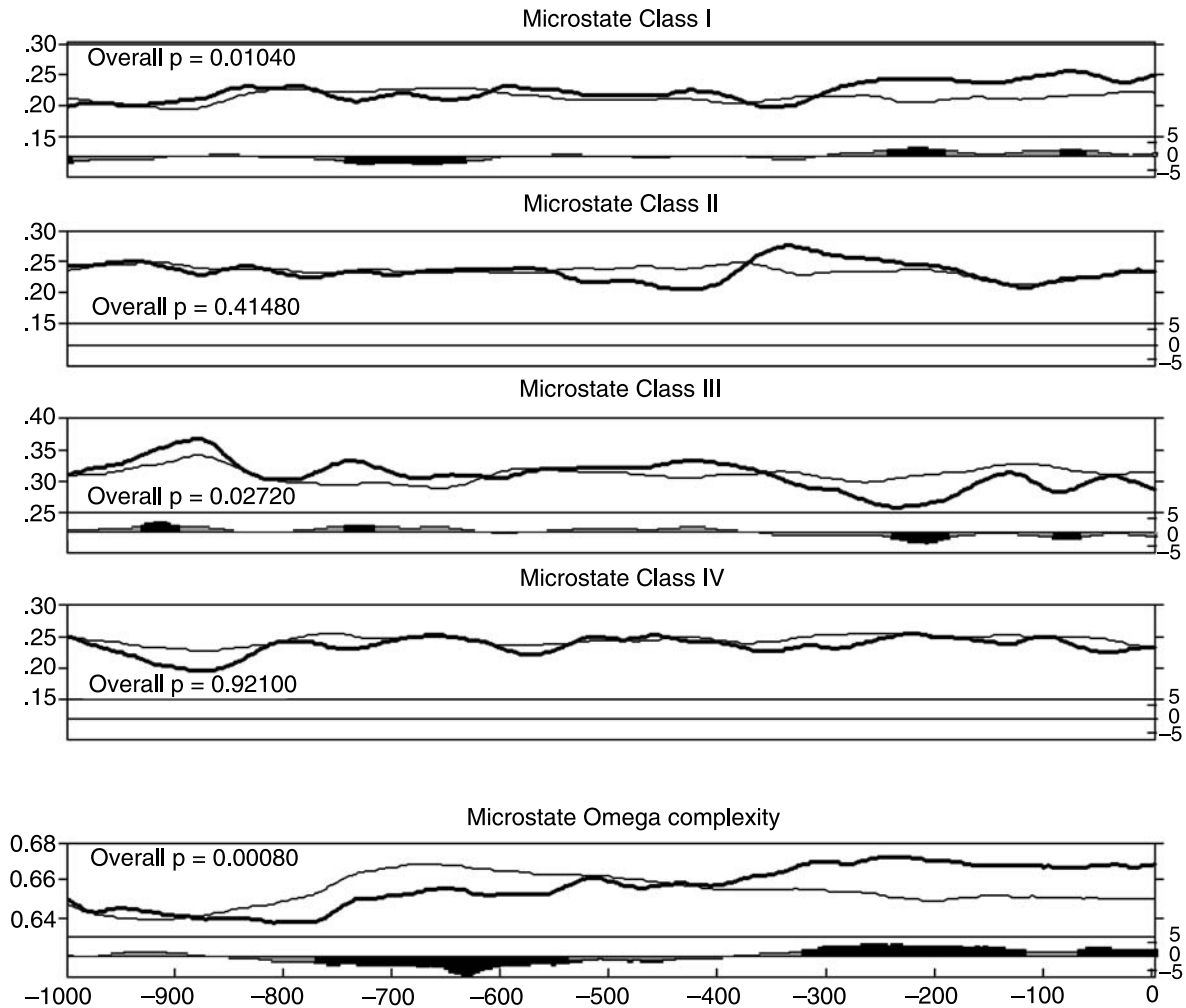


Fig. 4. Time course of probability of microstate class occurrences (classes I–IV, upper 4 graphs) and normalized Omega complexity (bottom graph). The upper part of each graph shows the time course of *pre* epochs (heavy line) and *baseline* epochs (thin line). The p-value of the global level analysis is displayed in each graph. Where this statistics was significant at $p < 0.05$ (microstate classes I and III, and Omega Complexity), the t-values of the mean difference between the two conditions (*baseline* minus *pre*) are shown below the time courses; dark areas indicate periods where the t-value yielded an uncorrected value below $p = 0.05$

Accordingly, the effects of condition in the time courses of microstate class I, III and Omega complexity were thus further examined utilizing moment by moment paired t-tests. In an early period from about 750 to 550 ms preceding the reference stimulus, the *pre* epochs were characterized by relative lack of class I microstates, excess of class III microstates, and decreased Omega complexity compared to *baseline* epochs. In a later period from about beginning about 300 ms before the reference stimulus, the opposite was observed, namely an excess of class I microstates, lack of class III microstates and increased Omega complexity in the *pre* epochs compared to *baseline* epochs.

Discussion

The present results showed that in defined, sub-second time periods preceding the reference stimulus, the brain electric fields exhibited specific changes of microstate probabilities and Omega complexity. In our experiment, the content of visual awareness changed while the stimulus characteristics were constant. This allows to attribute the observed effects to the neural events that implement perception independently from those that relate to the basic stimulus characteristics (Eagleman, 2001).

The subjective experience of a perceptual transition was preceded by a series of distinct, sub-second brain-electric events that deviated from the normally observed baseline patterns: In a relatively early phase, starting about 250 ms after the last stimulus and preceding the reference stimulus by about 750 ms, a relative excess of microstates of class III and a lack of microstates of class I was observed. This was accompanied by a decrease of Omega complexity. In a second phase starting about 300 ms before the reference stimulus, these deviations were reversed, i.e., there was a relative lack of class III, an excess of class I microstates, and Omega complexity increased. These deviations were in the range of about 10% of the normal signal amplitudes.

The observed results fit naturally into the framework of state-dependent information processing, where it is assumed that the momentary state of the brain is the fate of the incoming information (Eich, 1980; Koukkou and Lehmann, 1983; Maunsell, 1995; Hock et al., 1997). The global brain state reflects variations in internally controlled physiological states (excitation, relaxation, sleep stages; e.g. (Williams et al., 1966; Kiskey et al., 2001)), the developmental state (e.g., Gathercole, 1998) or induced states (alcohol, drugs; e.g., Spitzer et al., 1996). State dependency has also been shown on the microstate level (Kondakor et al., 1997b).

So what is the functional significance of the states that were involved in the perceptual transitions? Microstate class III has 91% of variance in common with a microstate class that has been identified in eyes-closed resting EEG; this class had been labeled class C and was the predominant microstate class in healthy adult subjects recorded during eyes closed relaxation (Koenig et al., 2002). The topography of microstate class I has not been observed in eyes-closed resting EEG (maximum of common variance with the eyes-closed microstate classes is 43.9%). While class III may therefore indicate a more relaxed, idling state, class I may be typical for a more active and alert state and may in addition be related to visual input. The changes observed in Omega complexity point in the same direction: Omega complexity has been shown to decrease progressively in the sequence of sleep stages 1 to 4 (Szelenberger et al., 1996), and increased Omega complexity in eyes open compared to eyes closed EEG was reported (Kondakor et al., 1997a). Omega complexity has also been shown to increase with age in the first two decades of life (Stam et al., 2000). Given this context, and given the existing literature, it seems that the first phase of the deviations that is characterized by low-Omega complexity and resting type microstates corresponds to a sub-second decrease of vigilance that is sufficient to discontinue the existing illusory motion (Struber and Herrmann,

2002). Given that the key press peaks at about 250 ms after the reference stimulus, and given that the reaction time to an alteration of unambiguous stimuli is about 550 ms (Struber and Herrmann, 2002), the construction of the new percept is likely to precede the reference stimulus by at about 300 ms. This coincides with a period where the EEG shows a reduction of states known from eyes-closed conditions, with an increase of states apparently related to eyes-open, and with an increase of EEG complexity; all this can be interpreted as a recruitment of vision-related brain resources and is indicative of the importance of the chaotic dynamics for a new perception (Freeman, 1994). With lower time resolution in the second range, the hypothesis has been raised earlier that changes in multistable perception are related to a decrease of vigilance, based both on the observation of a slowed EEG power spectral distribution (Müller et al., 1999), or on fMRI-detected decrease of thalamic activity that was followed by an activation in visual association and motion cortices after the perceptual transition (Kleinschmidt et al., 1998; Müller et al., 2002).

The argument that a perceptual change is initiated by a micro-fluctuation in vigilance also fits well with the observation that decreases of vigilance such as drowsiness and onset of sleep are typically related to a loosening of associations and decreased conscious cognitive control (Foulkes and Vogel, 1965; Lehmann et al., 1995), whereas over-aroused states such as anger or fear typically induce rigid and inflexible, “tunnel-vision” type, cognitive modes (Beversdorf et al., 1999). The interesting observation in the present results is that there appear to be micro-fluctuations of global brain state on a sub-second timescale that are associated with changes in perceptual strategies that parallel, both in function and in brain-electric signature, the vigilance fluctuations seen on larger time scales. These micro-fluctuations of brain state seem to have latency dependent effects on the ongoing perception and cognition and may be a functional mechanism for adaptive switches in perceptual and cognitive mode.

References

- Basar Eroglu C, Struber D, Kruse P, Basar E, Stadler M (1996) Frontal gamma-band enhancement during multistable visual perception. *Int J Psychophysiol* 1–2: 113–125
- Beversdorf DQ, Hughes JD, Steinberg BA, Lewis LD, Heilman KM (1999) Noradrenergic modulation of cognitive flexibility in problem solving. *Neuroreport* 13: 2763–2767
- Blake R, Logothetis NK (2002) Visual competition. *Nat Rev Neurosci* 1: 13–21
- Brandeis D, Lehmann D (1989) Segments of event-related potential map series reveal landscape changes with visual attention and subjective contours. *Electroencephalogr Clin Neurophysiol* 6: 507–519
- Eagleman DM (2001) Visual illusions and neurobiology. *Nat Rev Neurosci* 12: 920–926
- Eich JE (1980) The cue-dependent nature of state-dependent retrieval. *Mem Cognit* 2: 157–173
- Foulkes D, Vogel G (1965) Mental activity at sleep onset. *J Abnorm Psychol* 70: 231–243
- Freeman WJ (1994) Role of chaotic dynamics in neural plasticity. *Prog Brain Res* 102: 319–333
- Gathercole SE (1998) The development of memory. *J Child Psychol Psychiatry* 1: 3–27
- Grassberger P, Procaccia I (1983) Measuring the strangeness of strange attractors. *Physica* 9: 189–208
- Hock HS, Kogan K, Espinoza JK (1997) Dynamic, state-dependent thresholds for the perception of single-element apparent motion: bistability from local cooperativity. *Percept Psychophys* 7: 1077–1088

- Isoglu-Alkac U, Basar-Eroglu C, Ademoglu A, Demiralp T, Miener M, Stadler M (2000) Alpha activity decreases during the perception of Necker cube reversals: an application of wavelet transform. *Biol Cybern* 4: 313–320
- Keil A, Gruber T, Muller MM (2001) Functional correlates of macroscopic high-frequency brain activity in the human visual system. *Neurosci Biobehav Rev* 6: 527–534
- Kisley MA, Olincy A, Freedman R (2001) The effect of state on sensory gating: comparison of waking, REM and non-REM sleep. *Clin Neurophysiol* 7: 1154–1165
- Kleinschmidt A, Buchel C, Zeki S, Frackowiak RS (1998) Human brain activity during spontaneously reversing perception of ambiguous figures. *Proc Roy Soc Lond B Biol Sci* 1413: 2427–2433
- Koenig T, Lehmann D, Merlo MC, Kochi K, Hell D, Koukkou M (1999) A deviant EEG brain microstate in acute, neuroleptic-naive schizophrenics at rest. *Eur Arch Psychiatry Clin Neurosci* 4: 205–211
- Koenig T, Prichep L, Lehmann D, Sosa PV, Braeker E, Kleinlogel H, Isenhardt R, John ER (2002) Millisecond by millisecond, year by year: normative EEG microstates and developmental stages. *Neuroimage* 1: 41–48
- Kondakor I, Brandeis D, Wackermann J, Kochi K, Koenig T, Frei E, Pascual-Marqui RD, Yagyu T, Lehmann D (1997a) Multichannel EEG fields during and without visual input: frequency domain model source locations and dimensional complexities. *Neurosci Lett* 1: 49–52
- Kondakor I, Lehmann D, Michel CM, Brandeis D, Kochi K, Koenig T (1997b) Prestimulus EEG microstates influence visual event-related potential microstates in field maps with 47 channels. *J Neural Transm* 104: 161–173
- Koukkou M, Lehmann D (1983) Dreaming: the functional state-shift hypothesis. A neuropsychophysiological model. *Br J Psychiatry* 142: 221–231
- Lehky SR, Maunsell JH (1996) No binocular rivalry in the LGN of alert macaque monkeys. *Vision Res* 9: 1225–1234
- Lehmann D, Skrandies W (1980) Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalogr Clin Neurophysiol* 48: 609–621
- Lehmann D, Ozaki H, Pal I (1987) EEG alpha map series: brain micro-states by space-oriented adaptive segmentation. *Electroencephalogr Clin Neurophysiol* 3: 271–288
- Lehmann D, Grass P, Meier B (1995) Spontaneous conscious covert cognition states and brain electric spectral states in canonical correlations. *Int J Psychophysiol* 1: 41–52
- Lehmann D, Strik WK, Henggeler B, Koenig T, Koukkou M (1998) Brain electric microstates and momentary conscious mind states as building blocks of spontaneous thinking. I. Visual imagery and abstract thoughts. *Int J Psychophysiol* 1: 1–11
- Leopold DA, Logothetis NK (1999) Multistable phenomena: changing views in perception. *Trends Cogn Sci* 7: 254–264
- Leopold DA, Wilke M, Maier A, Logothetis NK (2002) Stable perception of visually ambiguous patterns. *Nat Neurosci* 6: 605–609
- Manly FJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London
- Maunsell JH (1995) The brain's visual world: representation of visual targets in cerebral cortex. *Science* 267: 764–769
- Müller TJ, Federspiel A, Fallgatter AJ, Strik WK (1999) EEG signs of vigilance fluctuations preceding perceptual flips in multistable illusionary motion. *Neuroreport* 16: 3423–3427
- Müller TJ, Federspiel A, Lövblad K, Lehmann C, Dierks T, Strik WK (2002) Distributed brain activity during multistable events as obtained by simultaneous EEG and fMRI. *Eur Arch Psychiatry Clin Neurosci [Suppl]* 1: I/4
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 1: 97–113
- Pascual-Marqui RD, Michel CM, Lehmann D (1995) Segmentation of brain electrical activity into microstates: model estimation and validation. *IEEE Trans Biomed Eng* 7: 658–665
- Pettigrew JD, Miller SM (1998) A 'sticky' interhemispheric switch in bipolar disorder? *Proc Roy Soc Lond B Biol Sci* 1411: 2141–2148

- Pitman EJG (1937) Significance tests which may be applied to samples from any populations. *J R Statist Soc* 4 [Suppl]: 119–130
- Schiller PV (1933) Stroboskopische Alternativversuche. *Psychol Forsch* 17: 179–214
- Sheinberg DL, Logothetis NK (1997) The role of temporal cortical areas in perceptual organization. *Proc Natl Acad Sci USA* 7: 3408–3413
- Spitzer M, Thimm M, Hermle L, Holzmann P, Kovar KA, Heimann H, Gouzoulis-Mayfrank E, Kischka U, Schneider F (1996) Increased activation of indirect semantic associations under psilocybin. *Biol Psychiatry* 12: 1055–1057
- Stam CJ, Hessels-van der Leij EM, Meulstee J, Vliegen JH (2000) Changes in functional coupling between neural networks in the brain during maturation revealed by omega complexity. *Clin Electroencephalogr* 2: 104–108
- Stancak A, Wackermann J (1998) Spatial EEG synchronisation over sensorimotor hand areas in brisk and slow self-paced index finger movements. *Brain Topogr* 1: 23–31
- Sterzer P, Russ MO, Preibisch C, Kleinschmidt A (2002) Neural correlates of spontaneous direction reversals in ambiguous apparent visual motion. *Neuroimage* 4: 908–916
- Strelets V, Faber PL, Golikova J, Novototsky-Vlasov V, Koenig T, Gianotti LR, Gruzelier JH, Lehmann D (2003) Chronic schizophrenics with positive symptomatology have shortened EEG microstate durations. *Clin Neurophysiol* 11: 2043–2051
- Strik WK, Fallgatter AJ, Brandeis D, Pascual-Marqui RD (1998) Three-dimensional tomography of event-related potentials during response inhibition: evidence for phasic frontal lobe activation. *Electroencephalogr Clin Neurophysiol* 4: 406–413
- Struber D, Herrmann CS (2002) MEG alpha activity decrease reflects destabilization of multistable percepts. *Brain Res Cogn Brain Res* 3: 370–382
- Szelenberger W, Wackermann J, Skalski M, Niemcewicz S, Drojewski J (1996) Analysis of complexity of EEG during sleep. *Acta Neurobiol Exp (Wars)* 1: 165–169
- Tallon-Baudry C, Bertrand O (1999) Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn Sci* 4: 151–162
- Wackermann J (1996) Beyond mapping: estimating complexity of multichannel EEG recordings. *Acta Neurobiol Exp (Wars)* 1: 197–208
- Walker P (1978) Binocular rivalry: central and peripheral selective processes? *Psychol Bull* 85: 376–389
- Williams HL, Morlock HC Jr, Morlock JV (1966) Instrumental behavior during sleep. *Psychophysiology* 3: 208–216

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