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Oscillatory Processes in Multistable Perception: Dissociating Perceptual- from Motor Processes

Verfasser

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Abstract

Previous work from our research group has shown a number of distinct oscillatory EEG responses occurring during the observation of multistable patterns. These are in particular: (a) a slow positive wave in the delta band (0-4 Hz), peaking about 250 ms before a button press indicating a perceptual reversal, which was interpreted as the completion of the reversal process and/or the establishment of a new stable percept; (b) a decrease in alpha band power (8-12 Hz) starting at 1000 ms before perceptual reversals, interpreted as the destabilization of the current percept.

However, as subjects had to press a button in order to indicate reversals, a possible overlap with motor-related potentials could not be ruled out.

The present study investigated reversal-related delta and alpha band components independently from motor activity, by separating the button press from the reversal through a special experimental setup.

The results clearly show that the delta- and alpha band modulations do occur during a multistable pattern change even in absence of a motor response. Thus, following previous interpretations, they may be seen as part of the oscillatory mechanisms by which the brain disambiguates and processes visual input.

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I. Theoretical Background

Perception

As humans, we gain most of the information about our environment and the objects surrounding us by means of our visual perception. Doing so, we encounter a perfect stable, coherent world almost all of the time, in which every moment's features correspond to the moment before.

A huge number of scientific experiments in the last century and beyond have been devoted to the miracle of visual perception, and an ever increasing knowledge on its nature and organization has been obtained since then. One conclusion that virtually all studies have in common is that perception, whether it originates from the visual or any other sense, is not realized in a way of mapping an outer world onto an internal representation, but is rather an active process of constantly constructing and reconstructing a representation that is in line with the incoming sensory input (Maturana, 1987).

From this point of view, the stable and coherent organization of the world perceived by us may not primarily be due to a stable and coherent organization of the world itself, but rather due to the organizing principles of our cognitive system (Strüber & Stadler, 1999).

1.1. Multistable Perception

A very simple, yet striking way to experience this active, creational process is via the phenomenon of *multistable perception*. This refers to situations, where one invariant stimulus pattern is perceived alternately in at least two different, mutually exclusive ways (e.g. Kruse, 1995; see fig. 1).

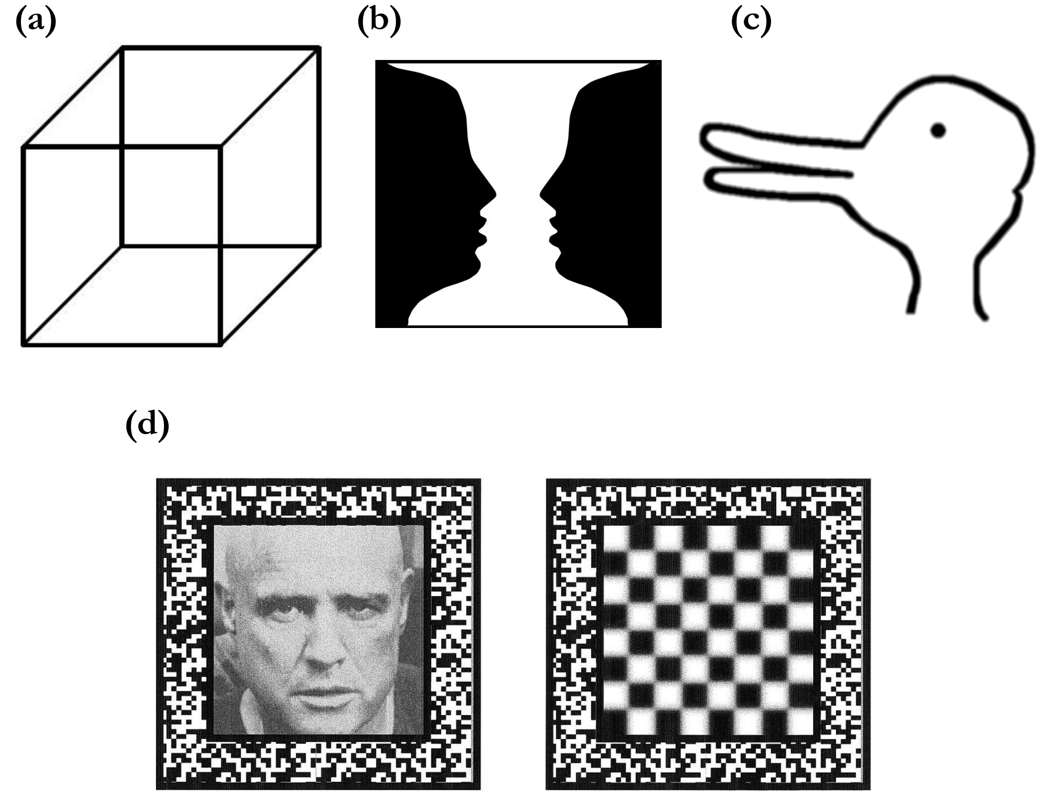

Fig. 1.: Different types of multistable stimuli. (a) The *Necker cube* can be perceived either pointing towards the upper right or towards the lower left side. (b) *Rubin's Vase* exemplifies figure-ground reversing stimuli. (c) The *duck/ rabbit illusion* is based on ambiguous semantic interpretability. (d) *Binocular rivalry* stimulus. When presented stereoscopically, only one of the two images is consciously perceived at a time.

Generally, two ways of inducing multistable perception can be distinguished (Leopold, 1999). *Ambiguous stimuli* (Fig. 1.,a-c) offer more than one possible meaningful interpretation to the observer, mostly by their special properties of depth, direction of motion, visibility or figure-ground configuration. In striving to disambiguate and to find the most simple, well ordered possible arrangement, our cognitive system consistently rearranges the relations between the elementary features of the stimulus, resulting in a continuous oscillation between the perceptual alternatives.

A different type of multistability is induced in the case of so called *binocular rivalry* (Fig. 1., d). Here, each eye is confronted with a different, conflicting image at the same time. Instead of fusing the two non matching inputs, the brain constantly switches the conscious percept from one eye's input to the others.

1.2. Characteristics of Multistability

In their ability to challenge our visual system to consistently come up with novel interpretations, the different forms of multistable perception all share an intriguing set of characteristics.

Most notably, the actual switching between possible perceptual alternatives is *inevitable* for as long as a person is watching an ambiguous pattern. However, a number of studies have found a significant influence of attention and voluntary control on the number of reversals (Lack, 1978). Switching rates turned out to vary up to three orders of magnitude between conditions where subjects were asked to slow down or to speed up the alternation process (Meredith, 1962).

Next, the different perceptual alternatives are always perceived *exclusively*. Even at the instant of switching, there is a discrete transition between one representation and the other. The phenomenological experience for most subjects is that at some point the observed pattern becomes blurry, and only an instant later a perfect stable new pattern emerges.

A lot of variability exists concerning the *temporal dynamics* of multistable perception. The duration of one percept or the other, the rate of switching at a given time, or changes in both parameters over longer periods of watching all vary substantially within- and between subjects (Kruse, 1995).

On stimulus side these dynamics are mostly defined by higher level, Gestalt properties such as symmetry, closure and proximity and in some cases by semantic content (Wertheimer, 1912; Strüber & Stadler 1999).

Concerning the subject watching, several studies have tried to correlate differences in switching rates with variables like intelligence or personality, however yielding quite contradictory results (Lindauer, 1971; Shiomi 1982; Haronian, 1966; Holt, 1974). However, more *state*-like parameters such as present mood, influence of pharmacological agents (e.g. coffee, nicotine) or even subliminal priming have been reported to significantly influence the dynamics of perception (George, 1936; Wilton, 1985).

Furthermore, quite distinct effects of learning have been shown in various multistable paradigms. While some naïve subjects have to be explicitly referred to the *ambiguous* nature of multistable patterns (Rock, 1992), the number of reversals exponentially increases with practice and culminates in a fairly stable plateau, as shown in figure 2. (Kruse, 1995).

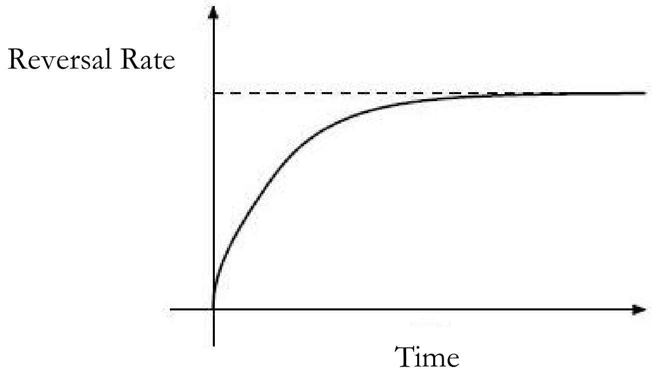

Fig. 2.: Learning curve, displaying the relationship between viewing time and reversal rates in *ambiguous* patterns (adapted from Kruse, 1995).

However, despite this usual increase in switching rates over time, the switching dynamics show a locally stochastic behavior. That is, in a sequence of perceptual reversals, the duration of one percept or the other is independent of the sequence's previous and subsequent dynamics (DeMarco, 1977).

1.3. What is it good for?

Leopold & Logothetis (1999) have proposed an interesting interpretation of the phenomenon of multistability. According to their hypothesis, perceptual reversals induced by ambiguous patterns may just be a particularly striking manifestation of an otherwise very common process. That is, a mechanism by which the brain purposely deconstructs and subsequently rebuilds its outer world representations, in order to increase the variance and thus informational content provided by the sensory input. From an evolutionary perspective, this might help orientation in a visually ambiguous environment, where a fast and correct evaluation of rather 'noisy' or subthreshold stimuli is crucial for surviving (figure 3.).

Building on electrophysiological, neuropsychological and imaging data (e.g. Sheinberg, 1997; Lumer et al., 1998; Ricci & Blundo 1990; see also chapter 3) this process is suggested to be realized in higher cognitive areas, such as fronto-parietal networks, acting upon downstream, earlier sensory cortices. Adding to this extrasensory localization are striking similarities between the already mentioned stochastic temporal dynamics of perceptual reversals and spontaneous behaviors, such as saccades in free-viewing situations or shifts in attention (Harris et al., 1988, Kustov and Robinson, 1996). This leads the authors to speculate that the mechanism underlying multistable perception may itself be a distinct form of behavior, executed by higher cognitive- upon early sensory areas in order to constantly reorganize sensory input and not to fall for a premature, disadvantageous interpretation. While present all the time, one may only become aware of those processes when confronted with highly ambiguous stimulus patterns.

Fig. 3.: Challenging visual sceneries. Continuous reorganization of the visual input increases the probability of spotting crucial objects within a noisy environment.

1.4. An Account from Systems Theory

An intriguing way of describing the behavior of the cognitive apparatus during multistable perception is by means of *systems theory* (e.g. Krieger, 1996). This interdisciplinary field of study deals with the behavior of complex, non-linear dynamic systems in various fields of natural and social sciences, such as physics, biology, psychology and sociology.

Following an account from Jäger (1996), a system may most generally be defined as a set of interdependent elements, corresponding relations describing their dependencies, and operations implemented on top of those relations. The state of the system at a given time can be described by a set of *n* parameters, which, all together, constitute the system's *n*-dimensional state space. As the system undergoes certain changes, like the performance of operations or the modification of relations between elements, the corresponding parameters change accordingly, resulting in a different localization of the system within its state space.

Most systems have a number of preferred, transient stable states called *attractors*, to which the system converges whenever possible. Being caught by an attractor, the system remains fairly stable, compensating small changes in its constituting elements or its environment. Only after the system itself or its environment is perturbed sufficiently, it might leave the attractor and undergo a phase of instability, until getting locked into another transient state of order.

Regarding the case of multistability, the different possible stable percepts induced by an ambiguous stimulus can be modeled as attractors, while the actual percept would be the systems state. Most of the time, the system is locked into a stable state, that is, our brain having successfully disambiguated the stimulus pattern. At certain points however, the state of the system may undergo a spontaneous change, as induced by a blink, a saccade or the evocation of a higher level semantic representation. This perturbation causes the present perceptual pattern to collapse and forces the brain to reevaluate the present stimulus, which is modeled by the system escaping the vicinity of the attractor and passing into a state of instability. Eventually, the system is locked onto another attractor, as the brain comes up with a different solution to the ambiguity (see figure 4.).

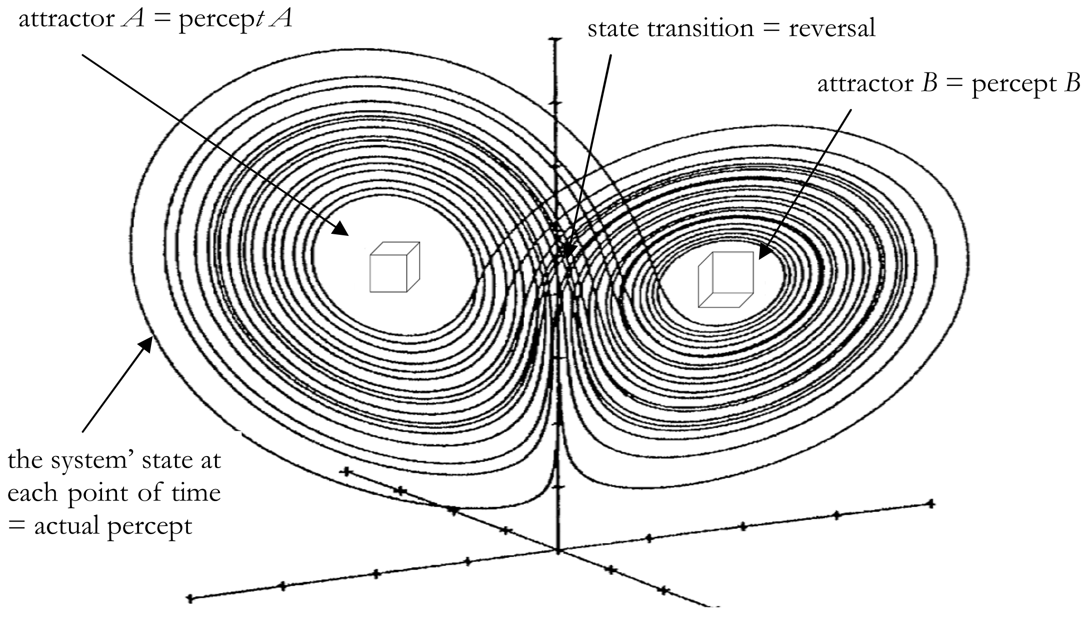

Fig. 4.: Attractor model of multistable perception. See text for details.

1.5. The Stroboscopic Alternate Motion

By the features reviewed above, multistable stimuli offer unique insights into the organizational principles of perception and the interpretative, active processes by which we construct our world. At the beginning of the last century, *Gestalt Psychologists* were among the first to apply multistable patterns in the study of visual perception (Köhler, 1940). One of the most sophisticated, yet simple stimuli they used, was the so called *stroboscopic alternate motion* (SAM) (figure 5.).

The principle of stroboscopic motion dates back to Wertheimer (1912), who described an experimental setup in which the fast successive presentation of two adjacent light flashes leads to the perception of a single flash moving from one spot to the other.

The SAM consists not only of two, but of four flashing light dots, aligned in a rectangular fashion. The timing of the dots appearance is realized in such a way, that the two diagonal pairs of dots always flash up alternately. By this stimulus configuration, the induced apparent motion can be either perceived as a horizontal- or a vertical one, in some cases even as a clock- or counterclockwise movement of the dots.

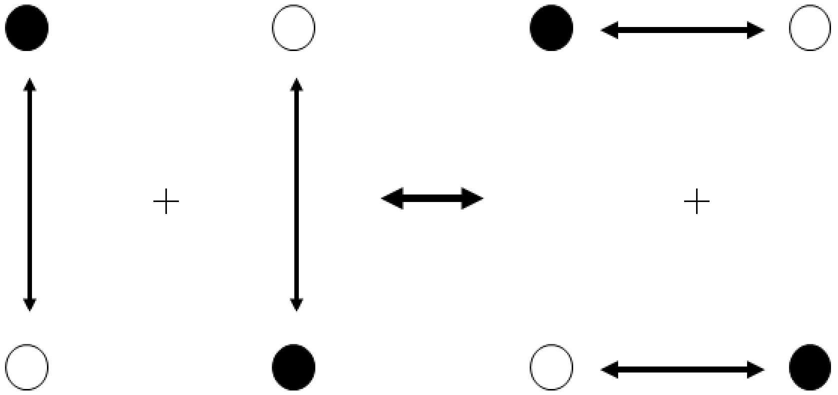

Fig. 5.: The Stroboscopic Alternate Motion (SAM). The SAM consists of two diagonal pairs of dots flashing up alternately, resulting in the perception of an either horizontal or vertical illusory movement

Thus, in addition to the phenomenon of apparent motion, this setup constitutes a dynamic multistable pattern, whose unique features make it an excellent tool for studying the organization of perception.

A first report of the SAM, along with a number of its psychophysiological features, came from v. Schiller in 1933. Since then, numerous notable works on this phenomenon have been published, such as on the implications of different spatial arrangements of the dots (Hoeth, 1968), on the contribution of local versus global stimulus features (Ramachandran & Anstis, 1986) or on the functional systems involved in the processing of the apparent motion (Kruse et al. 1986). More recent studies on the electrophysiological correlates of the SAM will be reviewed in chapter 3.

Brain Electric Activity

Within the 80 years of systematic electroencephalographic research since Hans Berger's seminal 1929 work (Berger, 1929), much knowledge has been gained on the electric activity of the brain, the significance of different *rhythms*, *evoked potentials* and transient network *oscillations*.

The following chapter aims to provide a brief introduction into the origin of the human electroencephalographic activity and the most common parameters describing it. The account given is by no means complete, but should serve as a guideline for the terms and concepts used in the subsequent sections. In addition, recent findings on the electrophysiological correlates of multistable activity are given, as well as a critical evaluation on the possible contribution of *motor potentials* to those correlates.

2.1. Neuronal Information Processing

Neurons can be considered as the basic building blocks of the nervous system, which communicate between each other by a cascade of electrical and chemical signals (Kandel, 2000).

Like virtually every other type of cell, each neuron has a negative electric charge, called the *resting potential.* Input from upstream cells by means of *post synaptic potentials* can shift the resting potential in both a more positive or more negative direction, resulting in either a depolarization or hyperpolarization of that particular cell. If the depolarization exceeds a certain threshold, the neuron eventually responds by generating the so called *action potential*. This potential is then travelling along the neuron's axon membrane, and the information it codes for is passed on to all of its downstream peers by means of chemical transmitters. At the target site, the transmitter again induces an either excitatory or inhibitory post synaptic potential, and the cycle begins anew (Kandel, 2000).

2.2. The Electroencephalogram (EEG)

In most common terms, electroencephalography is the measurement of electric potential fluctuations of the scalp (Niedermeyer, 2004). In research context, this is usually done by referencing the activity of a scalp-placed electrode to the activity of one located further away from cortical tissue, e.g. at the nose or the earlobes. The signal's underlying sources are, to the largest part, *extra cellular currents* produced by post synaptic potentials of cortical neurons aligned orthogonal to the face of the scull. As a single cell's activity is comparatively small and transient, the actual signal recorded from each electrode reflects the temporally and spatially integrated action of hundreds of thousands of neurons. Due to the largely synchronized activity within those neural populations, the EEG features a strong rhythmic character, which functionally corresponds to ongoing changes in the population's excitability. In this regard, negative deflections are usually interpreted as reflecting excitatory processes, and positive deflections as reflecting inhibitory processes (Niedermeyer, 2004).

As to classify different types of EEG readings, activity recorded from a subject at idle state is referred to as *spontaneous*, while the occurrence of a sensory or cognitive event results in *event related* activity. The latter can be further categorized as being *evoked* (showing, over a number of trials, a constant temporal relation to the preceded event) or *induced* (showing significant latency jitter, i.e. variance in the timepoint of its occurrence; Makeig et al., 2004). Spontaneous activity, long considered merely as background noise, is now widely regarded as a fundamental control parameter for the brains response to external and internal events (Başar, 2006).

2.3. A System of Rhythms

The EEG recorded from the scalp is, in fact, not originating from a single source within the brain, but a mixture of various signals produced by neural cell assemblies from all over the cortex (Niedermeyer, 2004).

Spectral analysis of the raw EEG data as well as single-cell and multi unit recordings in animals have suggested that neural networks operate preferably in a set of designated rhythms, commonly known as the *delta, theta, alpha, beta* and *gamma* frequency (e.g. Buzsáki, 2006; Sanei, 2007; table 1.). Using a digital filter, it is possible to decompose the originally recorded EEG signal into its constituting frequency components, and thus draw conclusions concerning the underlying neural- and corresponding cognitive processes (figure 6.).

Rhythm	Frequency range
Delta	below 4 Hz
Theta	4-8 Hz
Alpha	8-12 Hz
Beta	12-28 Hz
Gamma	above 28 Hz

Tab. 1.: Common frequency bands of the EEG.

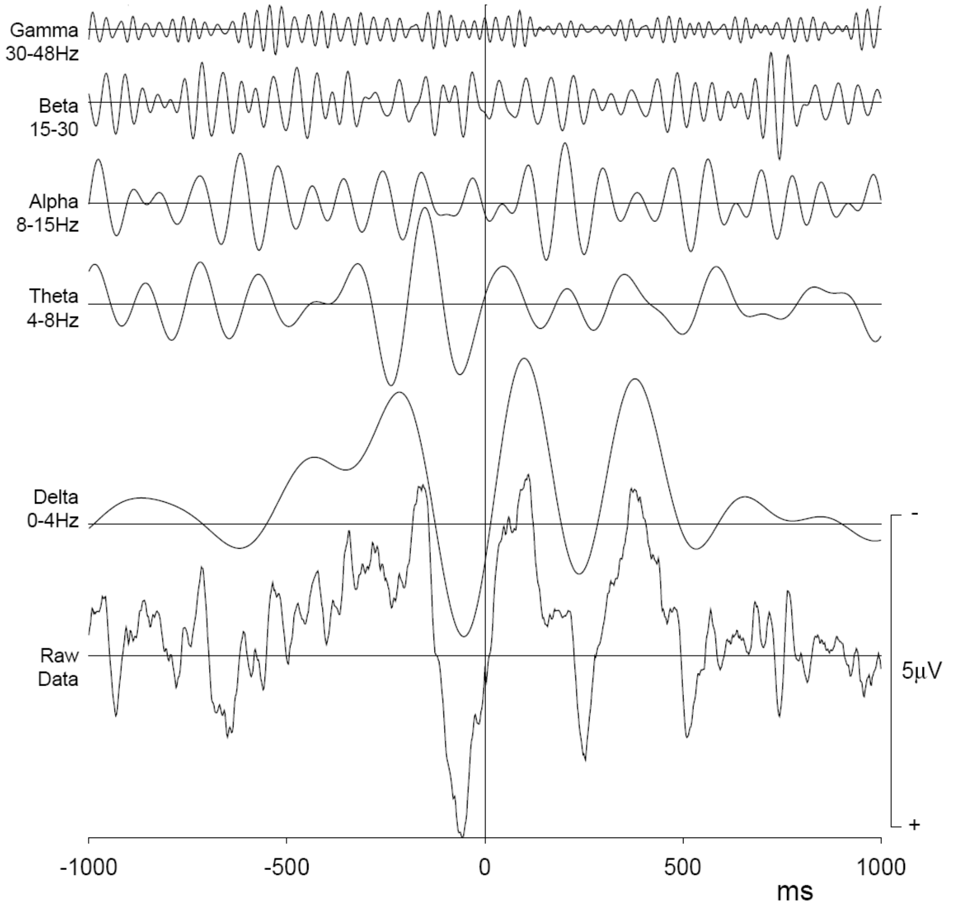

Fig. 6.: Example of filtered EEG data. Displayed is the raw signal (bottom) and its constituting waveforms in the five main frequency bands (above). Filtering was realized by means of an inverse Fourier-Transform (figure taken from Hoff, 2001).

A unifying theory considering this system of rhythms has been brought forward by Başar already in the mid 1970's (Başar, 1980; Başar et al., 2001; Başar, 2006). According to his view, cognitive processes are represented by temporally and spatially distributed oscillatory networks in the brain. Each cognitive process or subjective state correlates with a unique oscillatory pattern, defined by the *locations, frequencies, amplitudes* and *phases* of the participating neural networks and their activity, respectively. Thus, a given frequency band is corresponding not only to one distinct, but to a multitude of functions, depending on the characteristics of the above mentioned parameters.

Functionally, these oscillatory networks realize what Başar refers to as *transfer functions* (Başar, 1998, 1999). In physics, a transfer function describes the relation between the input and the output of a linear system, that is, the system's capacity to enhance or inhibit the transmission of its input. In case of the brain, this applies to the ability of a given network to modulate its excitability by shifting the resting potentials of its constituting neurons up and down in synchrony, thus either blocking or passing information to its downstream targets. Consequently, the brains immense computational power is proposed to be realized by the distinct superposition of several interrelated oscillatory networks, which communicate with each other via a system of rhythms.

As Başar has put it into metaphor, "*The oscillations in the different frequency bands are like the phonemes in languages. Superimposed oscillatory responses are the words. The selectively distributed parallel processing pathways are the syntax of the brain language. And the wholebrain-work that follows […] is the sentences and the discourse in the language of the brain*" (Başar, 2006).

2.4. Quantifying EEG Activity

Following, a short account on the most important parameters defining oscillatory EEG activity is given, with special respect to theoretical considerations made in the previous section (for a more detailed description, see e.g. Niedermeyer, 2004).

Frequency

The EEG signal's frequency (f) is the number of periodic cycles repeating within a one second time frame. Its SI (Système International d'unités) unit is hertz (Hz), with 1 Hz quantifying one complete cycle per second. Reciprocal to the signal's frequency is its period (T), which is the duration of one full cycle in a repeating series of events.

$$f = \frac{1}{T}$$

Amplitude

The deflection of the EEG waveform from baseline 0μV to its peaks and troughs is referred to as its amplitude. As the EEG is an electric signal, the amplitude's unit is volts (V), usually ranging between 1 and 30 μV.

Phase

At each time point, a wave's phase is its stage in oscillatory motion, that is, its displacement from an initial offset at *T=0*. The property of two or more waveforms to be in a constant relation to each other is designated as *phase coherence*. Phase information plays a crucial role in the process of linear averaging event-related EEG signals (Makeig et al., 2004). On average, only activity which exhibits a similar phase angle in each trial can be seen, while signal components whose phase angle is distributed stochastically over trials will cancel each other out to the largest part. The former case was above referred to as evoked activity, the latter as induced.

RMS Values

A way of calculating a signals mean amplitude value in a given time-window is by means of root mean square (RMS) values.

$$RMS = \sqrt{\frac{1}{N}\sum_{n=0}^{N-1} X_n^2}$$

By squaring the amplitude at each time point, phase information is removed and opposing potentials cannot cancel each other out anymore. Thus, this is an effective way of averaging induced, not time-locked, event-related activity with phase angles varying across trials.

Neurophysiological Correlates

3.1. Invasive Recording-, Imaging- and Lesion Studies

Based on its intriguing psychophysiological characteristics, the phenomenon of multistability has raised the question whether the underlying neural activity corresponds rather to the stable visual input, or to the actual experience of the observing subject.

Single-unit recordings in monkeys addressing this question have found distinct responses in different parts of the brain. While activity in early sensory areas correlates mostly with the retinal image, higher visual cortices modulate their activity according to the actual perception (Sheinberg & Logothetis, 1997; Logothetis, 1989). In most cases, this modulation is realized only by a transient response to a pattern reversal, not by a sustained change in activity (Sheinberg & Logothetis, 1997). In addition to activity in the visual system, human *functional magnetic resonance imaging* (fMRI) studies have found neural responses in extra-sensory areas usually concerned with higher cognitive processes, most notably the right parietal, frontal and prefrontal cortices (Lumer et al., 1998).

Ricci & Blundo (1990) reported from a series of studies with patients suffering from unilateral posterior- or frontal brain damage. While the ability to perceive multistable pattern reversions was unaffected by posterior lesions, it was severely impaired if not impossible by damage to the frontal lobe.

3.2. Bottom Up vs. Top Down

As already mentioned, the notion of the process of perception argued in the present thesis is the organization of sensory input in a meaningful, viable matter. Thus, of course, perception is relying on both sensory input and according organizational principles already existent in the brain. The data reviewed in the previous section support this view by strongly suggesting the involvement of higher cognitive areas in the processing of ambiguous stimuli (e.g. Ricci & Blundo, 1990; Lumer et al., 1998; Mathes et al., 2006). A common way of classifying different processing strategies in the brain[1] is by the notions of *Bottom Up* and *Top Down* (Eysenck, 2000).

Bottom Up refers to sensory driven, rather passive, low level processes in perception, which are primarily based on a stimulus' elementary features and can be located in early sensory areas. On the contrary, Top Down characterizes the active influence on perception exerted by higher level cognitive functions, such as attention, emotion or memory.

Early explanations for the phenomenon of multistability were clearly in favor of a Bottom Up account. Köhler (1940) argued that perception might switch from one alternative to another due to alternating satiation or exhaustion of the underlying neural populations. Whenever activity in one population drops beneath a certain threshold, the pattern collapses and the other network takes over. As empirical evidence, he referred to the already mentioned effect of switching rates increasing with viewing time. According to his view, this is caused by the exhausted network not being able to fully recover during the other networks dominance. As a result, its own active phase and with it the other population's recovery phase will be abbreviated, resulting in ever decreasing viewing times and thus increasing switching rates. Another study supporting this view comes from Long and Toppino (1994), who presented their subjects a disambiguated version of the Necker cube, clearly pointing into one direction. When, after some time, confronted with the original ambiguous pattern, the subject's perception immediately shifted to the opposite interpretation. Also, the already mentioned

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[1] in fact in any information-processing system;

inevitability of the perceptual reversals can be interpreted as a result from the Bottom Up origin of the phenomenon (Strüber & Stadler, 1999).

However, some other of the above reviewed characteristics, such as the limited voluntary control over switching rates, or the inability of some naive subjects to initially perceive pattern reversals have been ascribed to a significant influence of higher cognitive areas (Rock & Mitchener, 1992, Mathes et al., 2006). This account is also in line with the mentioned lesion studies, which highlight the importance of frontal processing in multistable perception (Ricci & Blundo, 1990).

A unifying view on the different processing strategies comes from Long and Toppino (2004). According to their hybrid model, initial processing of the various elementary features of an ambiguous pattern works in an automatic, sensory driven, thus Bottom Up fashion. This information is then passed on to intermediated cortical levels, where representations of all possible pattern configurations are built. Simultaneously, higher cognitive, extrasensory areas such as frontal and prefrontal cortices contribute by providing information on context, expectation, previous experience or task. The actual pattern reversals are mediated by the influence of both the early sensory and the higher cognitive areas to the existing intermediate level representations.

3.3. Electrophysiological Correlates of Multistable Perception

Electroencephalic recordings from subjects viewing ambiguous patterns were done by Wolfgang Köhler as early as in 1949 (Köhler & Held, 1949). Köhler chose this paradigm in order to test his *isomorphism* theorem, which proposed that for every psychological state there exists a specific, corresponding physiological state. With the advance of recording and analysis techniques, a number of distinct EEG components accompanying perceptual reversals have been described. Johnston et al. (1974) presented their subjects the digits ‘1’ and ‘3’, which could be either read as the number '13' or the letter 'B'. The resulting reoccurring change of meaning went along with a late, frontal evoked potential.

Using the Necker cube, Elbert et al. (1985) and O'Donnell et al. (1988) reported the occurrence of a centrally located positive wave during pattern reversals.

Başar-Eroğlu et al. (1993) were the first to use the SAM in order to study a dynamic model of multistable perception. Their work describes the so called *perceptual switching related positivity* (PSP), a distinct slow positive wave starting about 500ms before a perceptual reversal, as indicated by the subjects pressing a button. Its amplitude was strongest at right parietal- and smallest at left frontal locations, and spectral decomposition showed contributions mainly from the delta-, but also from the theta- and alpha band. By these features, as well as by its morphology, this component was compared to the *P300*, as typically elicited in oddball paradigms. Following the functional correlates usually assigned to the P300, such as context- or working memory update (Donchin, 1981), the PSP was interpreted as reflecting the completion of the reversal process and the establishment of a new stable percept.

In a follow-up study using the same design, Başar-Eroğlu et al. (1996) reported an increase in frontal gamma band activity during the actual reversal process as compared to periods where perception remained stable. In addition, comparisons between spontaneous activity and observation of the ambiguous pattern showed an overall increase in gamma power between 40% and 50%.

In trying to disentangle contributions from Bottom Up and Top Down processes to the EEG activity, Mathes et al. (2006) asked their subjects to either hold or speed-up the perceptual reversals during watching the Necker cube. Power in both delta- and gamma bands turned out to be increased during the hold-, while being decreased during the speed condition, as compared to the passive-watching condition respectively.

Reversal related responses in the alpha (8-12Hz) band were first reported by Isoglu-Alkaç et. al, who, in a similar paradigm, observed a significant alpha desynchronization (i.e. a reduction in amplitude size) in a time window of 440ms to 80ms before the button press compared to a time window 880ms to 440ms before the button press.

Changes in the alpha-band were further investigated in a *Magnetoencephalography* (MEG) study by Strüber & Hermann (2002). The authors found a slow and even decrease in alpha activity over posterior locations, starting about 1000 ms in advance of the reversal. Interestingly, in a control condition using a disambiguated version of the SAM, this decrease appeared abruptly and steep only 200 ms before the stimulus change. This different time course of MEG activity elicited by an *endogenous* compared to an *exogenous* pattern reversal was interpreted as reflecting Bottom Up processes as discussed in the previous chapter. While watching the ambiguous stimulus, alpha band activity in occipital networks continuously decreases until reaching a certain threshold, upon which the actual percept collapses and a new one arises. In contrast, during observation of the control-stimulus, the brain continuously processes the non-ambiguous input and rapidly updates its representation only when necessary.

Another work in this respect comes from Işoğlu-Alkaç & Strüber (2006), who divided alpha activity into three sub bands, namely lower-1 (6-8 Hz), lower-2 (8-10 Hz) and upper (10-12 Hz) alpha. In presenting their subjects the Necker cube continuously for a period of 60 minutes, they reported an activity decrease in both lower-1 and lower-2 bands in advance of reversals, the former being most prominent at posterior-, the latter at anterior sites. Following Strüber & Hermann (2002) this finding was assigned to Bottom Up processing. Additionally, lower-2 alpha activity varied as a function of overall experimental time, which was interpreted as reflecting Top Down, attentional processes. No modulation however was found in the upper band.

3.4. Contributions from Motor Activity

Multistable perception is a solely endogenous phenomenon, that is, it is accessible only to the subject experiencing it. When studying such a phenomenon from the third person view, science is depending on the account of the subject. Even more critical, in order to correctly tag the data corresponding to perceptual reversals during EEG recording, a real time response from the subject indicating such a reversal in essential.

In virtually all preceding works on multistable perception, this response was realized by means of a button press executed by the subject immediately after a pattern change. Consequently, the close temporal succession of the perceptual- and the motor processes strongly suggests an overlap of their underlying activity in the EEG record, and thus raises the question, to which degree the previously reported findings actually correspond to the pattern reversal and not to the subsequent button press.

As it has been known since the work of Kornhuber and Deecke (1965) movements are preceded by a number of distinct event related potentials in the EEG (figure 7.). About 1000 ms to 1500 ms prior to the movement, a slow rising negativity occurs symmetrically over the lateral precentral areas, termed the (*early*) *Bereitschaftspotential* (BP).

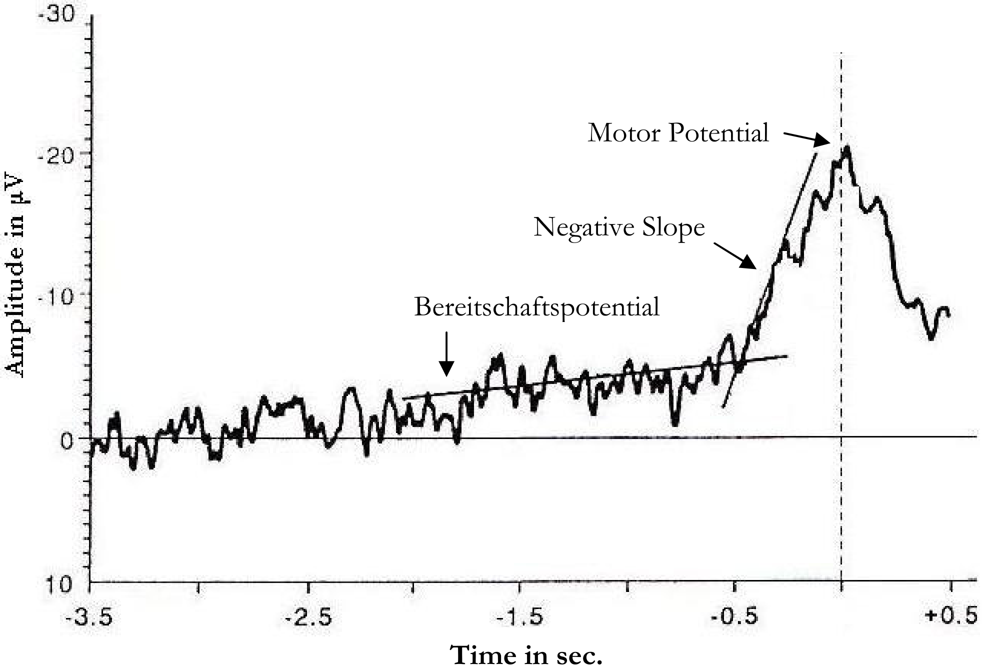


Fig. 7: Typical motor-related potential preceding a voluntary movement, recorded from location C1 (Stöhr et al. 1995). The gently rising Bereitschaftspotential is followed by the steep Negative Slope, which peaks in the Motor Potential.

This component fades into the *negative slope* (or *late* BP) some 500 ms before the action, consisting of a steeper negativity which is increased on the hemisphere contralateral to the movement. Finally, activity peaks in the *motor potential* just about 50 ms prior to the movement. This negativity is found on top of the late BP and is related directly to muscular activity.

However, this description holds true primarily for internally triggered, voluntary movements. If a movement is triggered by a regular external cue, the BP starts off significantly later and is reduced in amplitude (Papa et al., 1991). Responses to irregular, unpredictable cues show almost no preceding Bereitschafts-activity.

Additionally, there have been a large number of studies concerning the role of EEG oscillations prior to voluntary motor actions. Particular attention has been devoted to changes in the alpha-frequency range, which is referred to as *mu*-rhythm within the context of motor activity (Pfurtscheller & Aranibar, 1980; Pfurtscheller et al., 1997). Generally, a decrease in mu power can be observed about 1500 ms before movement onset in frontomedian and central cortices contralateral to the movement, later spreading to ipsilateral central sites.

Aim of the Study

One major shortcoming of virtually all previously conducted EEG experiments on multistable perception is the execution of a button press by the participating subjects immediately after each perceptual reversal. Although some kind of response is necessary to tag the occurrence of a pattern change within the EEG data, cortical processes inducing this motor action quite certainly add to the actual activity of interest, which is of perceptual nature.

Thus, the present study set out to dissociate the time point of the perceptual switch from the button press, in order to investigate the reversal related activity independently from motor components. With respect to the findings reviewed in the previous chapter, the presently known EEG correlates of perceptual reversals consist mainly of modulations in the delta, alpha and gamma band (see refs. Başar-Eroğlu et al., 1993; Strüber and Herrmann, 2002; Başar-Eroğlu et al., 1996 respectively).

However, most part of the response in the gamma band is an overall amplitude increase during the perception of multistable patterns as compared to spontaneous activity, which is most likely connected to focused attention (Başar-Eroğlu et al., 1996; Mathes et al., 2006). This response is present also during passive observation (i.e. no motor response) and thus not relevant to the present study. An investigation of the reported gamma increase during actual reversals as compared to stable perceptual periods (Başar-Eroğlu et al., 1996) was impeded by the applied task design and epoch lengths.

As furthermore the origin and functional relevance of early induced gamma band activity has been lately a matter of debate (Yuval-Greenberg et al., 2008), the present work confines on investigating responses in the delta and alpha bands only. Thus, the question underlying the present work is, if the reported responses in the delta and alpha band truly correspond to perceptual reversals, or if they are, at least to some degree, caused by the subsequent motor response. Put into more formal words, a preliminary hypothesis may read: *'The previously reported positivity in the delta band as well as the decrease in alpha band activity are actually corresponding to perceptual processes, and do occur over the course of pattern reversals even in the absence of motor responses'*

4.1. Hypotheses

As explained in more detail in the methods section, the motor response is separated from the perceptual change by 1500 ms, by means of a special experimental setup. Consequently, following the work of Başar-Eroğlu et al. (1993), İşoğlu-Alkaç et al. (2000) and Strüber & Hermann (2002), the PSP and the alpha activity decrease were expected to occur around 1500 ms prior to the button press. This *dissociated* condition was compared to a *standard* condition, resembling the design used in previous works. In the latter, with the button press being executed immediately after the pattern reversal, the PSP as well as the alpha decrease were expected to occur around the time point of the motor response. Thus, the following hypotheses were made:

1. Within the delta band, maximum positive potentials around 1500 ms prior to a button press should be stronger for the *dissociated* than for the *standard* condition.
2. Within the delta band, maximum positive potentials around the button press should be stronger for the *standard* compared to the *dissociated* condition.
3. Within the alpha band, minimum activity around 1500ms prior to a button press should be smaller for the *dissociated* than for the *standard* condition.
4. Within the alpha band, minimum activity around a button press should be smaller for the *standard* than for the *dissociated* condition.

II. Empirical Part

Methods

5.1. Subjects

21 healthy, right-handed undergraduate students participated in the study. Due to an insufficient number of artifact-free epochs (less than 20) six subjects had to be excluded from further analysis. An additional subject was excluded under the suspicion of not having understood the task properly, showing almost no evoked potentials in any condition. The remaining 8 female and 6 male subjects had a mean age of 22.8 years (SD 2.7), normal or corrected to normal vision and did not report any neurological disorders.

5.2. EEG Recording

EEG was recorded from F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1 and O2 locations according to the international 10-20 system (Jasper, 1958). Ag-AgCl electrodes were used and grass paste was applied between electrodes and the skin. The ground electrode was placed between locations Fz and Cz and linked earlobes served as reference. The signal was amplified and recorded by a 16 channel Nihon Kohden (EEG-4421 G) system with band limits between 0.1- 70 Hz (24 dB/ octave) and an additional notch filter at 50 Hz to take out noise from the line current. Data was digitized by means of a Data Translation digitizer (model DT21-EZ) at a 500 Hz sampling rate and stored on hard disk for off-line analysis. As the eye is a strong electric dipole, eye movements and blinks can produce severe artifacts in the EEG signal (Niedermeyer, 2004). In order to control for these artifacts, *electrooculographic data* (EOG) were additionally recorded from electrodes at the medial upper and lateral orbital rim of the right eye.

5.3. Stimuli

The stimuli and settings used in this study were reproduced according to earlier work from our lab (e.g. Başar-Eroğlu et al., 1993). The SAM was produced using the 'Presentation' software (vers. 10.0, NeuroBehavioral Systems), and displayed on a computer screen. The four dots were displayed white on a black background in a rectangular fashion, with a 5:8 vertical to horizontal distance ratio. At the subjects viewing distance of 150 cm, the horizontal dots distance of 2.4 cm lead to a viewing angle of 0.92, and the vertical dots distance of 3.8 cm to a viewing angle of 1.45. An additional white dot serving as a fixation point was displayed throughout the session in the center of the SAM. The dot's luminance and background contrast was kept at a comfortable level for the subjects to watch, while providing optimal conditions for the apparent motion and perceptual reversals to occur. The flashing frequency of the SAM was set to

2 Hz, with 165 ms displaying time for the dots followed by an inter-stimulus interval of 85 ms for each cycle. This timing works best to prevent the visual system from adapting to the stimulus, which would result in a decay of the apparent motion over time (Anstis et al., 1985).

In addition to the SAM, a disambiguated illusory movement pattern was used as a control stimulus. This so called *non-ambiguous* SAM resembled the original, *ambiguous* SAM in every aspect, except for a different time coupling of the dots, resulting in a either horizontal or vertical parallel movement (figure 8.).

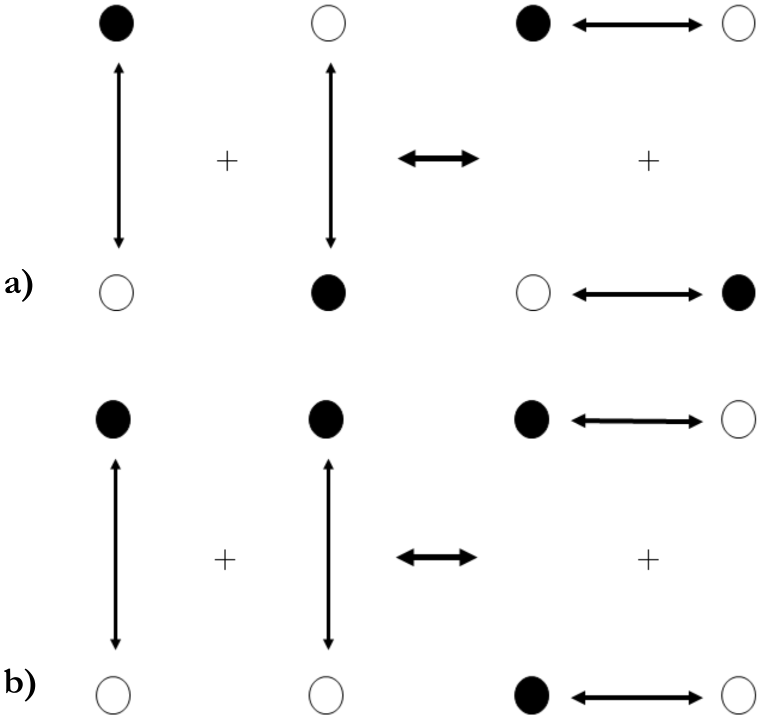
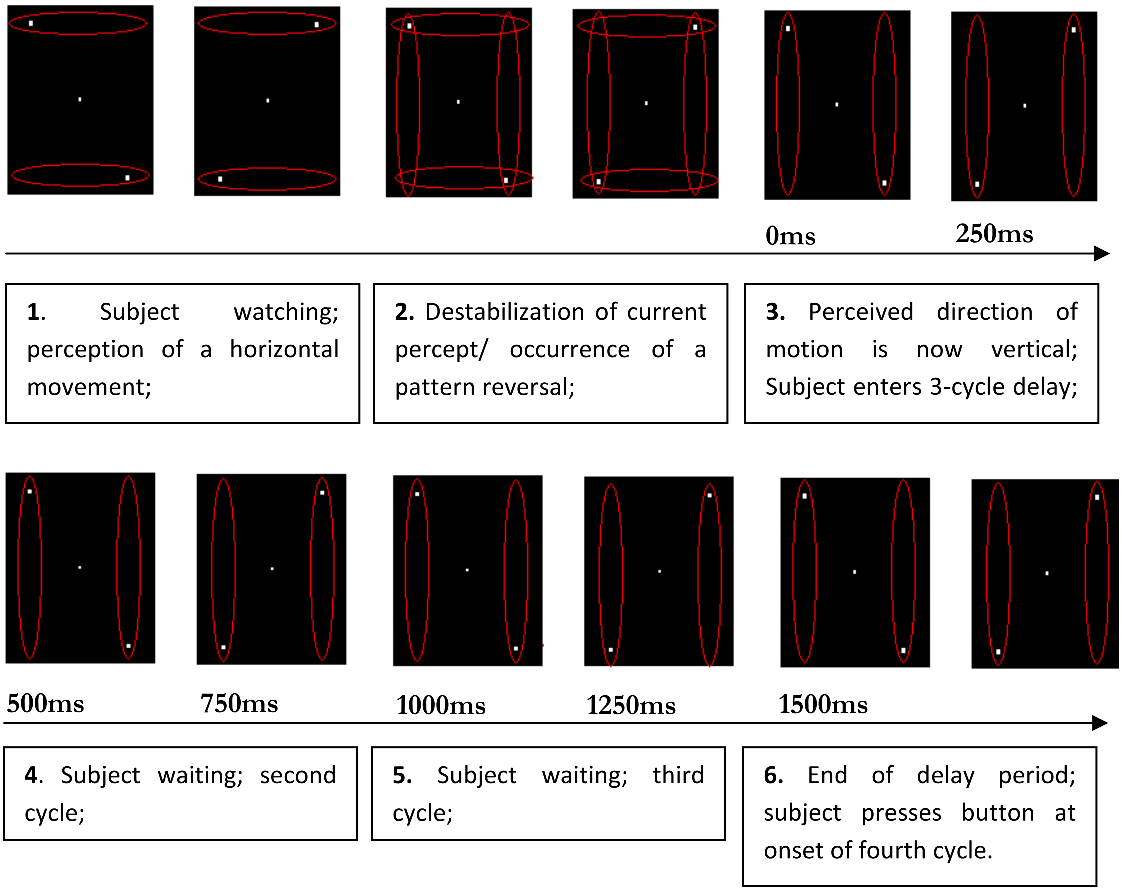


Fig. 8.: Stimuli used. a) *Ambiguous* stroboscopic motion. See for text details. **b) *Non-Ambiguous* stroboscopic motion** In a control condition, subjects were presented with a disambiguated version of the SAM, created by modifying the time-coupling of the dots.

5.4. Task

The experiment consisted of two main conditions, with each condition being performed once on the *ambiguous*- and once on the *non-ambiguous* stimulus (2x2 design). During the *standard* condition, subjects had to press a button immediately whenever a perceptual reversion occurred. This task resembles the one used in previous studies (Başar-Eroğlu et al., 1993; Başar-Eroğlu et al., 1996). During the *dissociated* condition (figure 9.), subjects were asked to delay the motor response for three movement cycles (i.e. a dot disappearing and the reappearing on the same spot) of the SAM.



1. Subject watching; perception of a horizontal movement;

2. Destabilization of current percept/ occurrence of a pattern reversal;

3. Perceived direction of motion is now vertical; Subject enters 3-cycle delay;

4. Subject waiting; second cycle;

5. Subject waiting; third cycle;

6. End of delay period; subject presses button at onset of fourth cycle.

Fig. 9.: Delayed button press during the ***dissociated*** **task;** each cycle consists of a 165 ms stimulus presentation followed by a 85 ms inter stimulus interval. Thus, the 3 cycle delay separates the button press from the time point of reversal by approx. 1500 ms, considering the various reaction times. The elliptic markers are for illustrational purpose only, and were not visible during the experiment.

As every cycle lasts 250 ms, this procedure separates the perceptual from the motor processes by 1500 ms.

The actual instruction given to the subjects was to pay attention to the lower left dot of the SAM (while still focusing on the fixation dot) and press the button simultaneously to the fourth flash-up of the dot after the perceptual reversal. Subjects were explicitly asked not to count the cycles, but to rely on their rhythmic feeling when awaiting the button press.

5.5. Conditions

In the beginning, a period of spontaneous activity was recorded, with the subjects having their eyes first closed and then opened for approx. two minutes each.

After that, the four experimental conditions followed:

1. *ambiguous/ standard*
2. *ambiguous/ dissociated*
3. *non-ambiguous/ standard*
4. *non-ambiguous/ dissociated*

The order of the conditions was pseudo- randomized for each subject, except for that (a) the *standard* and *dissociated* conditions always remained paired together, and (b) that the *ambiguous-dissociated* condition was never done at the beginning of a session. The first exception aimed to reduce the bias of effects occurring over the time course of the experiment, such as learning or fatigue, on the comparison between the two conditions. The second exception ensured that subjects had some amount of training on the task before working on the most complex of the conditions.

5.6. Setting

Prior to the actual recording, all subjects enrolled in a training session in order to get familiar with the task. It was ensured that all of them were able to perceive both alternatives of the SAM and knew exactly when to perform the delayed button press during the *dissociated* condition. Also, all subjects completed the Edinburgh Handdness Inventory (Oldfield, 1971) and a questionnaire on their current physical and mental health. During the recording, subjects sat in an electrically shielded, sound proof, dimly lit room.

5.7. Preprocessing

Offline, the data were further processed using the Matlab software (vers. 7.1, The MathWorks Inc.) including the EEGLab toolbox (vers. 6.02 beta, Delorme, A., Makeig, S., 2004). Epochs from 3000 ms before to 998 ms after the button press were extracted from the continuous data and subsequently scanned for eye, muscle and technical artifacts. Only epochs free of such were included for further analysis. After artifact rejection, the data was band-pass filtered within 0-4 Hz for the Delta band and 8-12 Hz for the Alpha band using a FFT (Fast Fourier-Transform) based filter. As epochs can differ slightly from each other in their baseline amplitude values (e.g. due to low frequency drifts), the mean amplitude value of each epoch was subtracted from every single data point of the same epoch as a baseline correction. However, no normalization procedure was applied in this study.

5.8. Missing Data

During the process of copying the continuous raw EEG data from the recorder to the lab server, two datasets[2] were accidentally deleted. For statistical analysis, values of those datasets were replaced by the remaining subjects' mean values for the particular condition.

Additionally, data recorded from channel Fz was corrupted in all subjects and excluded from further analysis.

5.9. Electrophysiological Analysis

A fundamental problem when studying endogenous phenomena like perceptual multistability is the weak time-locking between the cognitive processes and the motor response. The resulting strong latency jitter of the corresponding EEG components is, while present in the *standard* condition, even increased in the *dissociated* condition. This is due to the 1500 ms interval between the reversal and the button press. To account for that latency jitter, the occurrence of both perceptual and motor related activity was investigated at the level of single epochs.

5.9.1. Delta Band

As a first step, epochs were divided into two comparatively large time windows, mainly based on visual inspection. An *early* time window was defined as 2250 ms to 1000 ms before the button press, and a *late* time window was defined as 750 ms before to 350 ms after the button press. For the *standard* condition, both the reversal-related and motor-related activity was expected to occur within the *late* time window. In the *dissociated* condition, the experimental setup separated the perceptual- from the motor processes by approximately 1500 ms. This led to the

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[2] subject *06/CB*, *dissociated* condition/ *non-ambiguous* stimulus; subject *14/MC*, *dissociated* condition/ *ambiguous* stimulus

expectation of reversal-related processes to occur within the *early* time window, and motor-related processes within the *late* time window.

Next, the time points of the maximum positive deflections within both time windows were computed for parietal electrodes (P3, Pz, P4) on single sweep level. The parietal location was chosen, as this area of the cortex was previously found to feature the strongest PSP (Başar-Eroğlu et al., 1993). The median was computed over the three maximum deflections for both time windows and each epoch. Over those medians, another median was computed across epochs, resulting in a single measure for each subject, condition and time window. This measure served as a data-driven 'point of reference' for the delta response induced by the perceptual and/ or motor processes.

As a final step, mean values of the maximum positive amplitudes within -375 ms before to 375 ms after the 'point of reference' were computed over single epochs for each subject, condition, electrode and time window.

5.9.2. Alpha Band

Absolute alpha band activity was calculated by means of RMS values within a 500 ms time window. This measurement was chosen in order to capture the course of the total evoked and induced alpha activity (see section 2.4.). To illustrate the course of alpha activity, a RMS moving average was performed by shifting the RMS time window over the filtered data in 2 ms steps. Apart from that, analysis of the alpha band was done using a similar strategy as in delta band analysis.

In a first step, epochs were divided into two time windows, with an *early* time window defined as 2000 ms to 1000 ms before button press, and a *late* time window defined as -500 ms before to 500 ms after the button press. Within those two windows, the time point of minimum alpha power was computed at electrodes O1 and O2 on single sweep level for each subject and condition. This location was chosen, as previous studies found the strongest alpha power decrease at occipital electrodes (Strüber & Herrmann, 2002; Işoğlu-Alkaç & Strüber, 2006).

Next, median time points for each subject and condition over the time points of minimum alpha power within each epoch. Again, this data driven median time points served as 'points of reference' for the actual analysis.

As a final step, mean values of the minimum alpha power within -250 ms before to 250 ms after the 'point of reference' were computed over single epochs for each subject, condition, electrode and time window.

5.10. Statistical Analysis

Following suggestions from Mecklinger & Pfeifer (1996), electrodes were pooled together to *regions of interest* (ROI's) in order to avoid loss of statistical power when performing repeated measurement ANOVA's. Doing so, electrode sites F3 and F4 were merged to 'frontal', C3, Cz and C4 to 'central', P3, Pz and P4 to 'parietal', and O1 and O2 to 'occipital' locations. For statistical analysis, a repeated measurement 2x2x4 ANOVA was conducted for both the *ambiguous* and *non-ambiguous* stimulus and for both time points, using the factors *condition* (standard and dissociated) and *location* (frontal, central, parietal, occipital). For each ANOVA, Greenhouse-Geisser correction was applied when appropriate.

To further investigate topographical aspects of the EEG responses, post-hoc pairwise-comparisons were calculated between each ROI, using Bonferroni-corrected values.

Results

The following chapter presents the results of the experimental study. First, behavioral results are delineated, as well as data from the post-experimental questionnaire. Following, a descriptive account on the grand average EEG activity in both delta and alpha band is given. Finally, the results of the statistical analysis are given. Detailed statistical results are presented in tables 5.1. and 5.2. for the ANOVA's and in tables 5.3. to 5.6. for the pairwise comparisons at the end of the section.

6.1. Behavioral Data

During the *standard* condition, subjects had an average switching rate of 9.5 (SD = 5.6) reversals per minute. This value is slightly lower for the *dissociated* condition with 8.8 (SD = 4.4) reversals per minute. This difference was not significant [t(12) = 1.7, p = .116]. Reaction time was defined as the period between a perceptual reversal and the following button press. This measurement was only computed for the *non-ambiguous* condition, as no information on the time-point of reversal was available for the *ambiguous* condition. Mean reaction time was 516 ms for the *standard* condition and 1814 ms for the *dissociated* condition.

Accidental button presses, missing button presses after a reversal, and immediate, non-delayed button presses during the *dissociated* condition were all counted as errors. Again, these values could be only computed for the '*non-ambiguous* condition', where information on the occurrence of a reversal was available. Mean error rate was 4.1% for the *standard* condition and 15.1% for the *dissociated* condition.

Six out of the 14 subjects reported to have used silent counting to estimate the delay period at least at some point of the task. The remaining eight subjects managed to constrain on their rhythmic feeling.

6.2. Physiological Data

6.2.1. Delta Band

6.2.1.1. *Standard* Condition/*Ambiguous* Stimulus

Figure 10. shows delta band filtered grand averages (N=14) from the *standard* condition for all ten electrodes which are included in the analysis.

At most locations, a strong positive response can be seen at the time point of the button press. Posterior, at occipital and parietal locations, the response starts off between -750 ms and -500 ms before the button press and peaks almost exactly together with the motor response. Amplitudes reach 4 µV, being largest at parieto-occipital electrodes. At central sites, although still easy recognizable, the positivity is slightly reduced in amplitude.

Instead of a distinct single peak, central electrodes show a double peak with only little more than 2 µV. The frontal electrodes, particularly the left one, show the least distinct response, the positivity at the right site hardly reaches 2 µV.

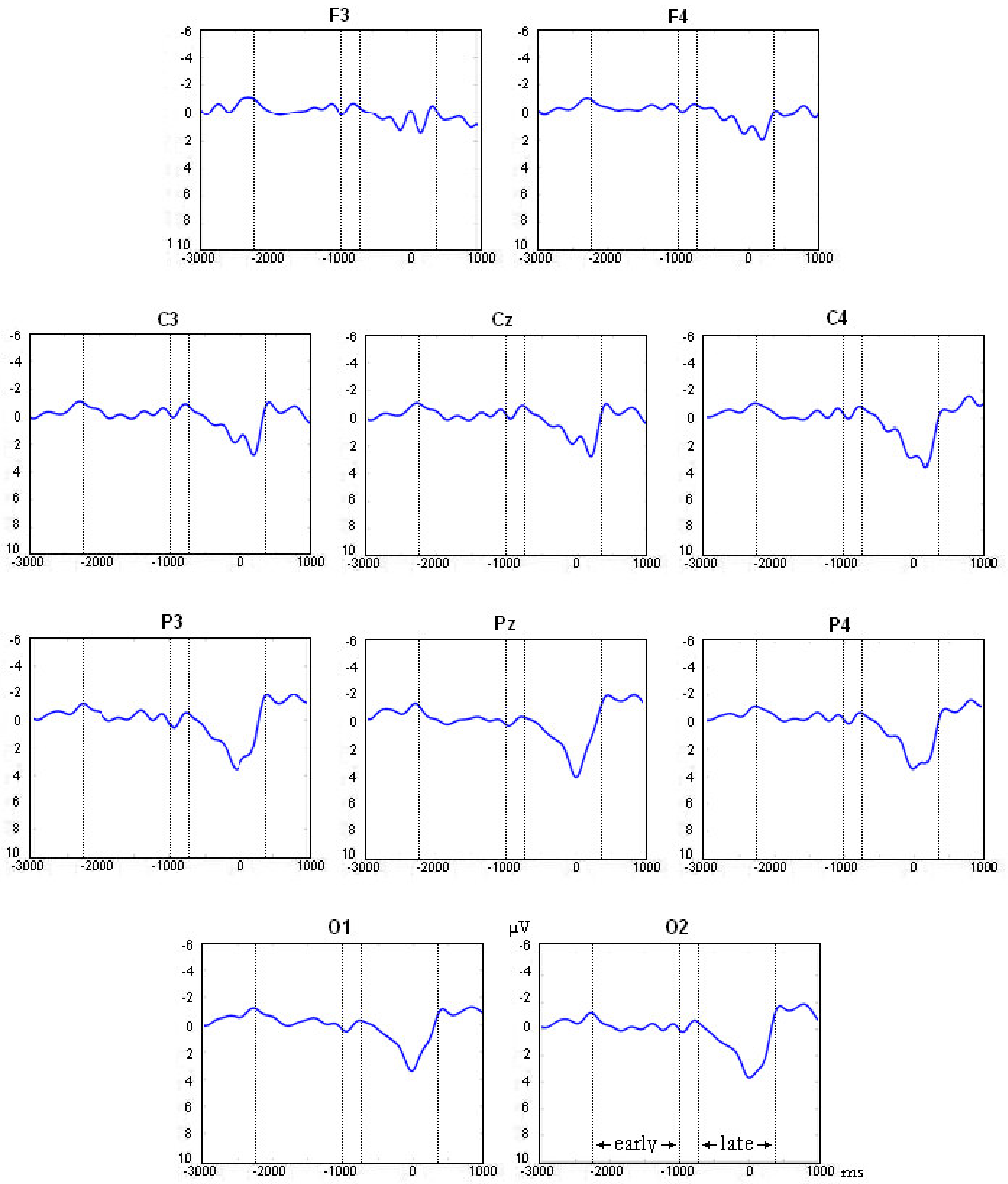

Fig. 10.: Delta band (0-4Hz) filtered **grand averages** (N=14) for the ***standard, ambiguous*** condition, for all electrodes included in the analysis. Vertical bars indicate early (-2250 to -1000 ms) and late (-750 to 350 ms) time windows. Abscissa: Amplitudes in µV; ordinate: time in ms; zero indicates the button press.

6.2.1.2. ***Dissociated*** **Condition/*****Ambiguous*** **Stimulus**

Similarly, figure 11. shows delta band filtered grand averages (N=13) from the *dissociated* condition for all ten electrodes included in the analysis.

In close temporal proximity to the button press, we can again find a positive wave at all electrodes. This one however differs from the one seen in the *standard* condition in some remarkable features. First, it is less pronounced at posterior locations, with amplitudes of less than 2 µV at occipital electrodes and its appearance is somewhat shifted to anterior regions, showing its maximum amplitude of almost 6 µV centrally at electrode Cz. The positivity's appearance at frontal sites, which is hardly recognizable in the *standard* condition, now features a distinct peak close to 4 µV. Considering its temporal characteristics, the wave starts off about -250 ms before the motor response at posterior-, and almost simultaneously with the motor response at anterior sites, in both cases peaking roughly 250 ms after the button press.

In the first half of the epoch another positivity stands out, which has not been featured in the *standard* condition. This positivity has a quite similar appearance at all locations, peaking thoroughly at -1500 ms before the button press. Its amplitude is comparatively low, with a maximum of 1.5 µV at the right occipital electrode and a minimum of 1 µV at the left frontal electrode.

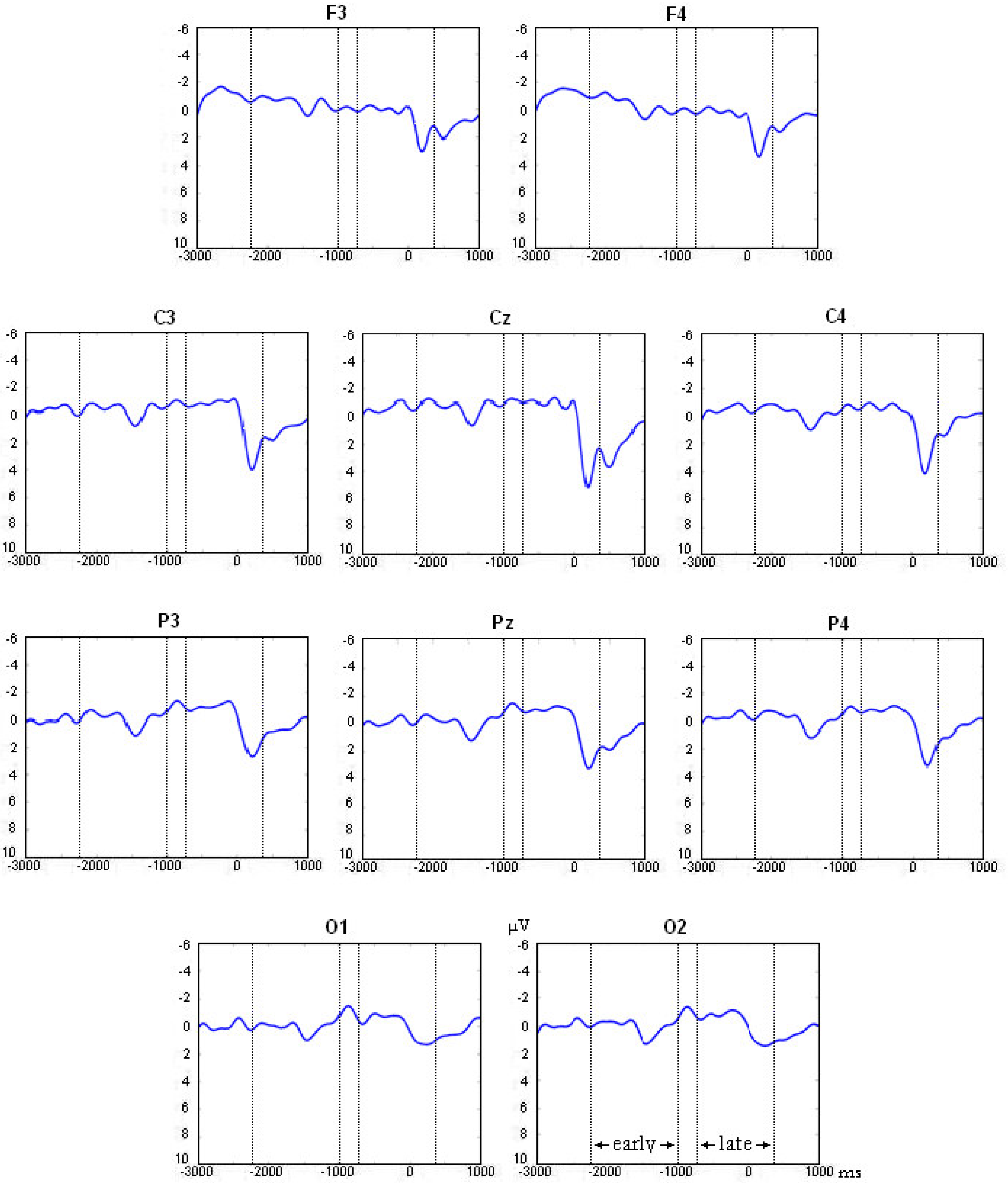

Fig. 11.: Delta band (0-4Hz) filtered **grand averages** (N=13) for the ***dissociated, ambiguous*** condition, for all electrodes included in the analysis. Vertical bars indicate early (-2250 to -1000 ms) and late (-750 to 350 ms) time windows. Abscissa: Amplitudes in µV; ordinate: time in ms; zero indicates the button press.

6.2.1.3 *Standard* Condition/ *Non-ambiguous* Stimulus

Figure 12. resembles the previous figures, here displaying data (N=14) for the *standard* condition from the *non-ambiguous* stimulus.

Again, the most prominent feature is a distinct positive wave, peaking almost simultaneously with the button press at all locations. However, notable differences to the one seen in the *ambiguous* condition are it's almost twice as large amplitude, its steeper rise and decrease and it's general narrower appearance. In addition the positivity here is followed by a negativity, which peaks around 500 ms after the button press reaching about -2 µV at all locations Considering the positivity, amplitudes are again larger posterior than anterior, with close to 8 µV at all occipital and parietal locations and a maximum of a little over 8 µV at electrode P3. At central sites, the positivity peaks at between 4 µV on the left and 5 µV on the right side, and is even more reduced at frontal sites with about 2 µV on each side.

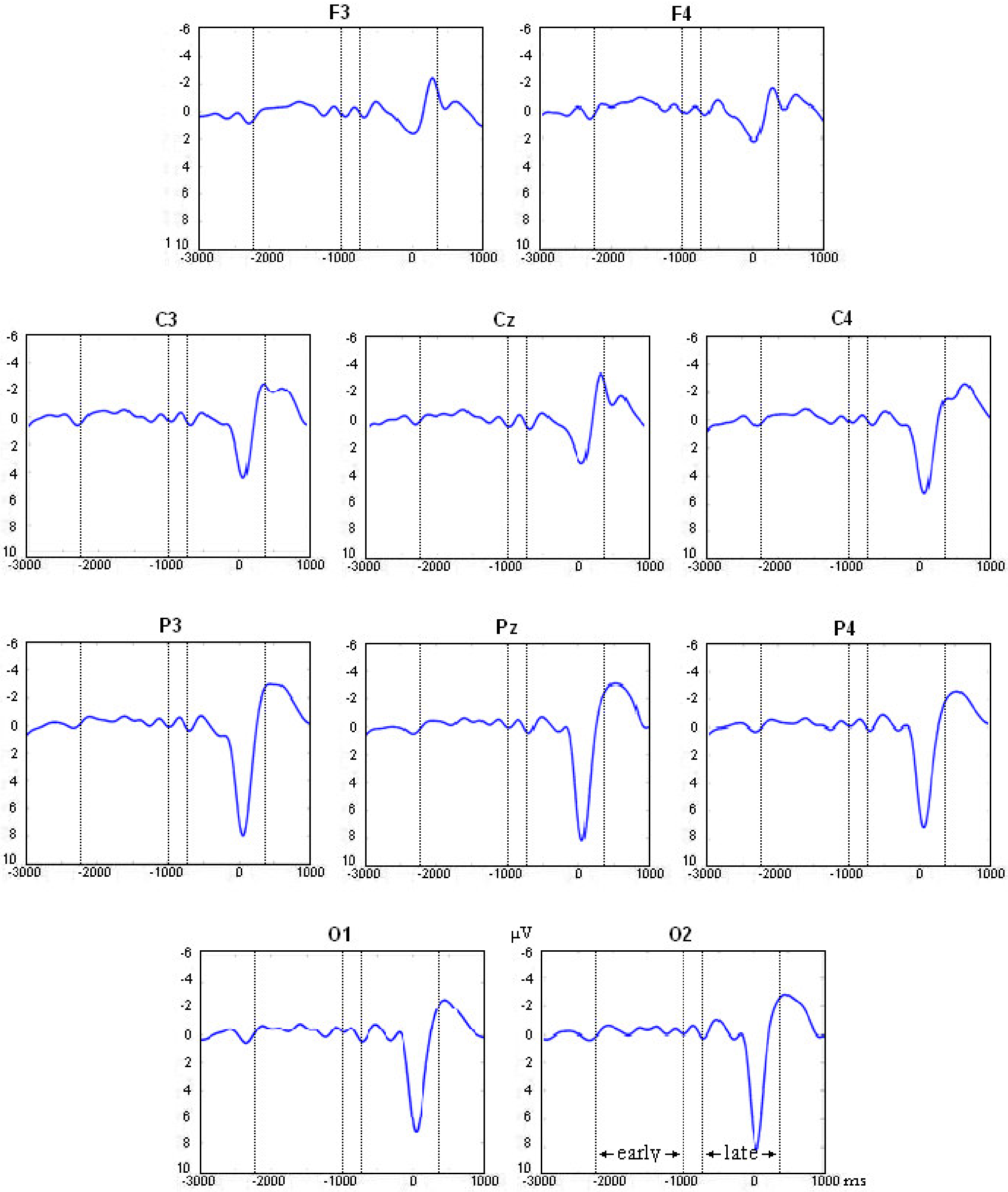

Fig. 12.: Delta band (0-4Hz) filtered **grand averages** (N=14) for the ***standard, non-ambiguous*** condition, for all electrodes included in the analysis. Vertical bars indicate early (-2250 to -1000 ms) and late (-750 to 350 ms) time windows. Abscissa: Amplitudes in µV; ordinate: time in ms; zero indicates the button press.

6.2.1.4. *Dissociated* Condition/ *Non-ambiguous* Stimulus

The final delta band results (N=13) for the *dissociated* condition from the *non-ambiguous* stimulus are presented in figure 13.

In line with the data from the *ambiguous* stimulus, two distinct positive waves can be observed. The first one is peaking just about -1500 ms before the button press, showing a similar morphology at all locations. This wave is slightly stronger at posterior than anterior locations, having the largest amplitude with 4.5 µV at electrode Pz and the smallest with 3 µV at electrode F3. A feature from the *standard non-ambiguous* condition reappearing here, which was not present within the activities for the *ambiguous* stimulus, is the distinct negative undershoot in succession to the positivity. It is peaking around -900 ms before the button press, having noticeable higher amplitudes on the left compared to the right hemisphere. The second positivity occurs in close succession to the button press, as seen within the *dissociated* condition for the *ambiguous* stimulus. It features the largest amplitudes at central locations, reaching a maximum of 7.5 µV at electrode Cz, and decreases in its amplitude size in both anterior and posterior directions. Just as in the *standard* condition, the delta responses for the *non-ambiguous* stimulus are noticeable stronger than those for the *ambiguous* stimulus, showing an up to as twice as large amplitude, particularly when considering the first positivity.

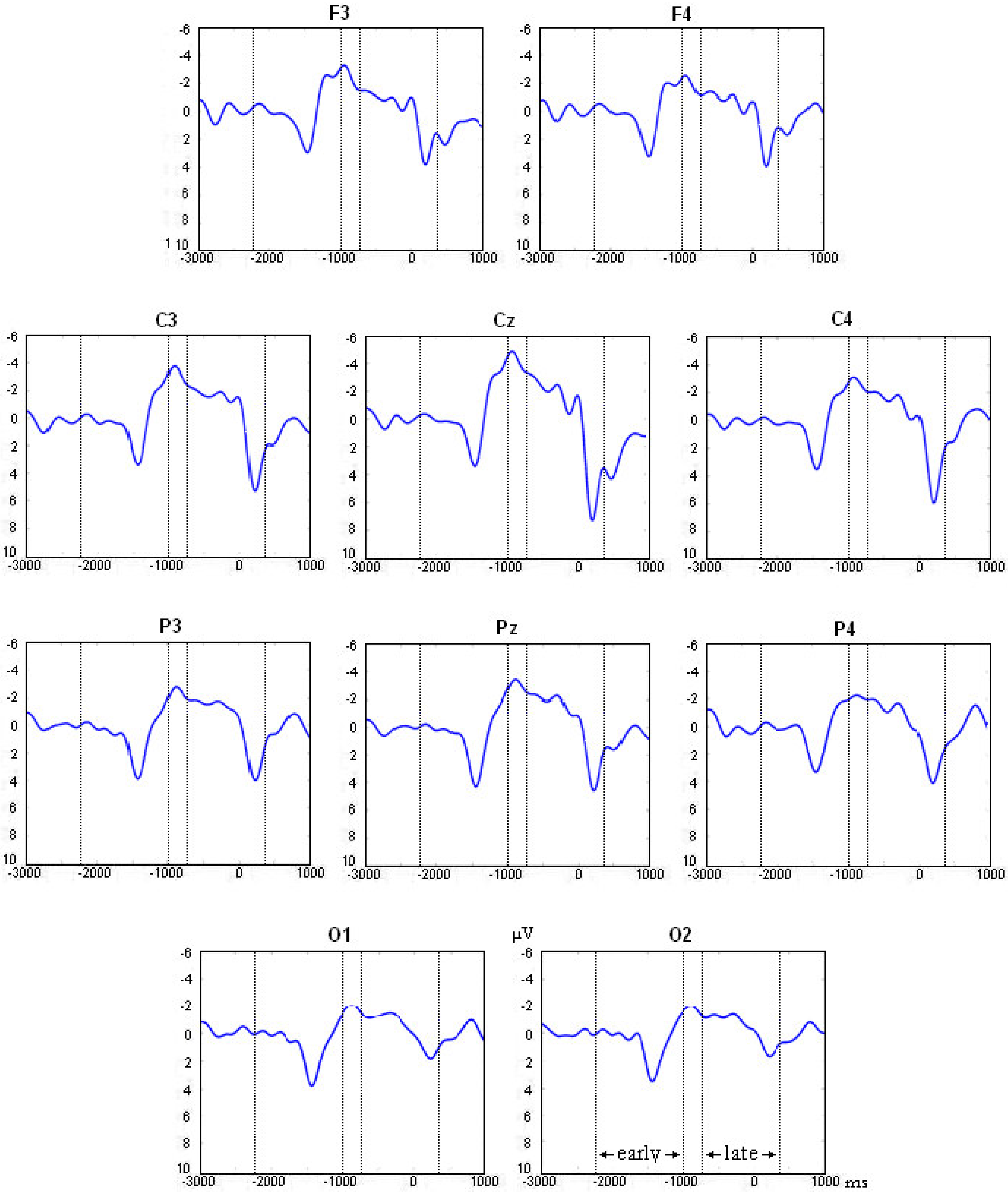

Fig. 13.: Delta band (0-4Hz) filtered **grand averages** (N=13) for the ***dissociated, non-ambiguous*** condition, for all electrodes included in the analysis. Vertical bars indicate early (-2250 to -1000 ms) and late (-750 to 350 ms) time windows. Abscissa: Amplitudes in µV; ordinate: time in ms; zero indicates the button press.

6.2.2. Alpha Band

Following are the results from the alpha band analysis. For displaying purposes, The time course of the absolute alpha response was plotted by means of a RMS moving average. In doing so, a 500 ms RMS averaging window was shifted through the data in steps of 2ms. Thus, each data point in the following plots corresponds to the RMS value within a 500 ms window.

6.2.2.1. *Standard* Condition/*Ambiguous* Stimulus

Figure 14 shows the grand average (N=14) alpha band time courses from the *standard/ ambiguous* condition for all 10 electrodes included in the analysis.
First, noticeable are the different baseline amplitude values at different locations. Amplitudes are highest at occipital electrodes starting off at 3.2 (left) and 3.3 µV (right), and steadily decrease in anterior direction, with between 2.8 and 3.1 µV at parietal, about 2.8 µV at central and about 2.4 µV at frontal locations.
Second, a distinct overall decrease in amplitude can be observed at most electrodes in the second part of the epoch. Beginning at about -500 ms before the button press, the decrease reaches its trough together with the motor response at occipital-, about 250 ms later at parietal- and about 500 ms later at central locations, being almost not existent at frontal electrodes.

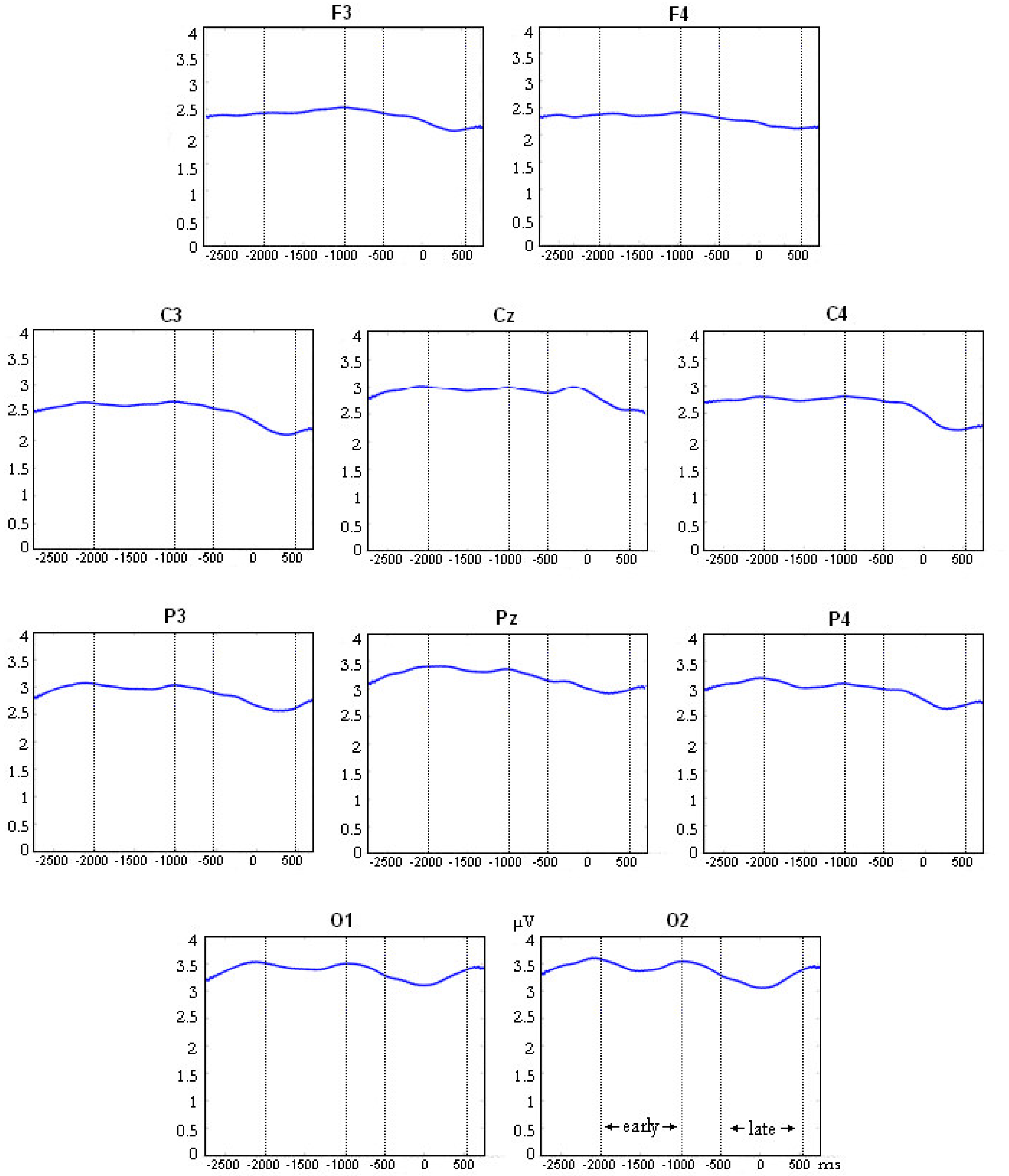

Fig. 14.: Alpha band (8-12Hz) **grand RMS moving average** (N=14) from the ***standard ambiguous*** condition for all electrodes included in the analysis. Vertical bars indicate early (-2000 to -1000 ms) and late (-500 to 500 ms) time windows. Abscissa: RMS values in μV; ordinate: time in ms; zero indicates the button press.

6.2.2.2 *Dissociated* Condition/ *Ambiguous* Stimulus

Grand average (N=13) alpha band amplitude courses from the *dissociated/ ambiguous* condition for all 10 electrodes included in the analysis are displayed in figure 15.

Again, we can see different baseline amplitude values at different locations, decreasing in size from posterior to anterior sites, overall being about 0.2 µV higher than in the *standard* condition.

Concerning the course of the RMS values, the overall picture of the alpha response is less consistent than in the *standard* condition. Occipital, a distinct decrease occurs in the first part of the epoch, starting at about -2000 ms and peaking at -1500 ms before the button press. This decrease, though not as strong, is still visible at parietal locations. Particularly at the right parietal electrode, a second decrease of the alpha response can be found, starting at about -500 ms before the button press and peaking roughly 250 ms after it. A similar picture is revealed at the right central electrode, with a slightly reduced first and increased second response. At the remaining central and frontal electrodes, no distinct modulation of RMS values can be observed.

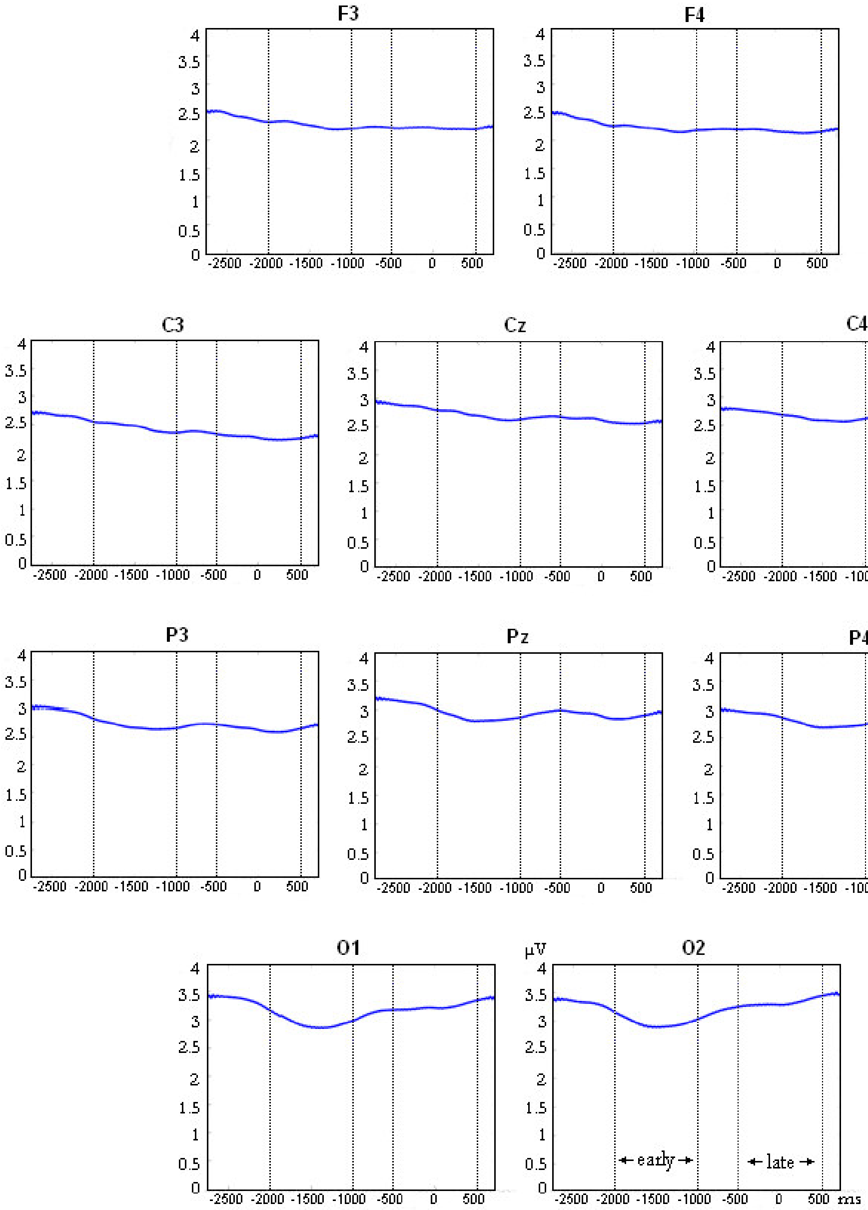

Fig. 15.: Alpha band (8-12Hz) **grand RMS moving average** (N=13) from the ***dissociated ambiguous*** condition for all electrodes included in the analysis. Vertical bars indicate early (-2000 to -1000 ms) and late (-500 to 500 ms) time windows. Abscissa: RMS values in µV; ordinate: time in ms; zero indicates the button press.

6.2.2.3. *Standard* Condition/ *Non-ambiguous* Stimulus

Figure 16 shows the grand average (N=14) alpha band amplitude courses from the *standard/ non-ambiguous* condition for all 10 electrodes included in the analysis. The results here resemble those from the *ambiguous* stimulus, but the amplitude decrease is a little more distinct in its appearance.

Again, the level of overall RMS values decreases from posterior to anterior, taking up values of roughly 3.4 µV occipital, 3.2 µV parietal, 2.8 µV central and 2.4 µV frontal. The second half of the epoch features a drop of RMS values clearly visible at all electrodes, beginning about -250 ms before the button press, reaching its trough simultaneously with the motor response occipital, about 250 ms later parietal, and 400 ms later central and frontal. Especially at anterior locations, this decrease is preceded by a slight increase in RMS values, being the most prominent at electrode Cz.

6.2.2.4. *Dissociated* Condition/ *Non-ambiguous* Stimulus

Grand average (N=13) alpha band amplitude courses from the *dissociated/ non-ambiguous* condition for all 10 electrodes included in the analysis are displayed in figure 17.

Like in the *standard* condition, results obtained here are quite similar to those from the *ambiguous* stimulus. Once more, the overall absolute amplitude values are higher at posterior than at anterior locations, in this case reaching about 3.7 µV occipitally, 3.4 µV parietally, 2.8 µV centrally and 2.4 µV frontally.

An early decrease in RMS value is clearly visible at occipital sites, starting off at -1700 ms on the left and at -2000 ms before the button press on the right, peaking at about -1250 ms. This response is less developed at left and midline parietal and central electrodes and almost none existent at right central and parietal as well as both frontal locations.

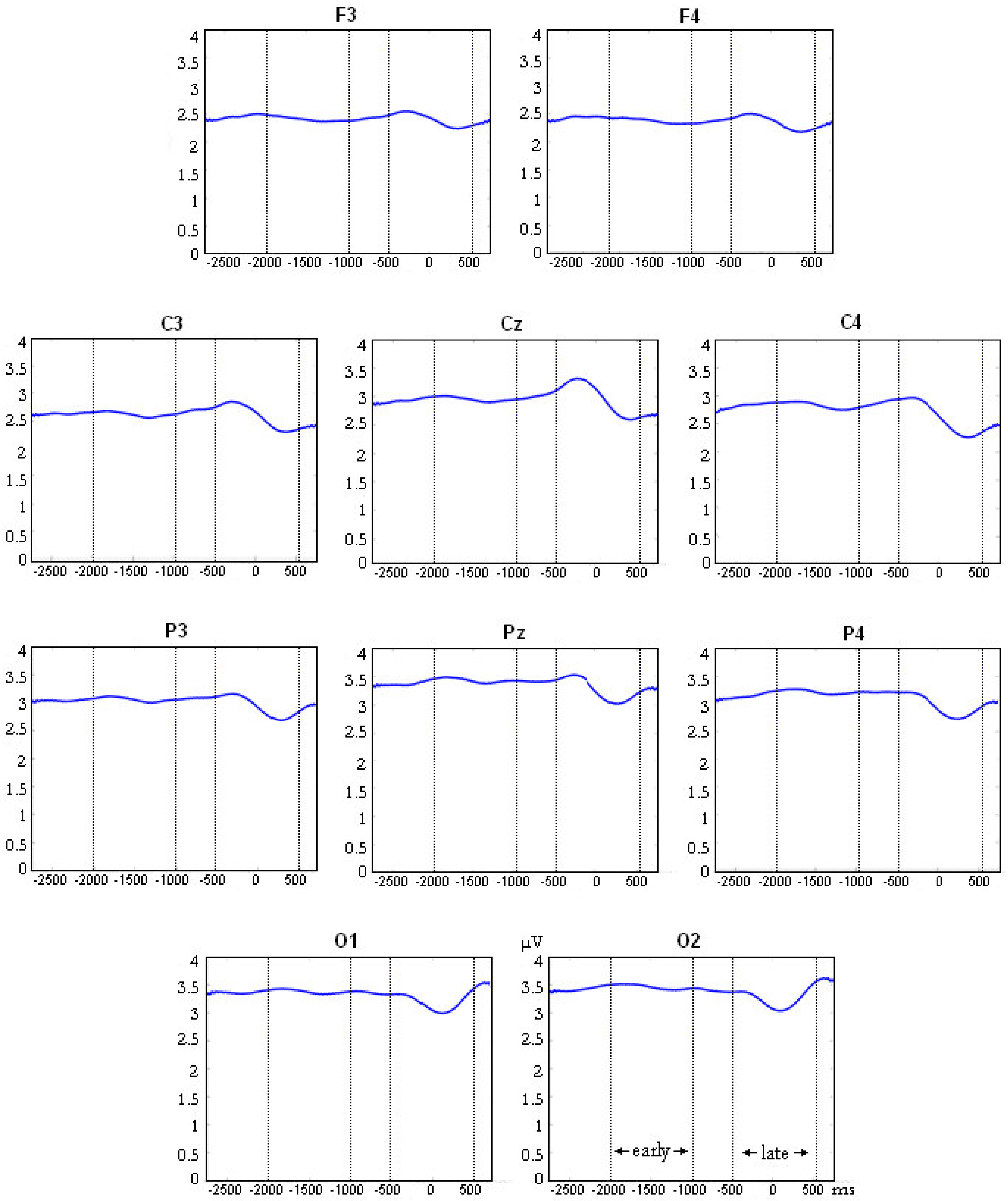

Fig. 16: Alpha band (8-12Hz) **grand RMS moving average** (N=14) from the ***standard*, non- *ambiguous*** condition for all electrodes included in the analysis. Vertical bars indicate early (-2000 to -1000 ms) and late (-500 to 500 ms) time windows. Abscissa: RMS values in μV; ordinate: time in ms; zero indicates the button press.

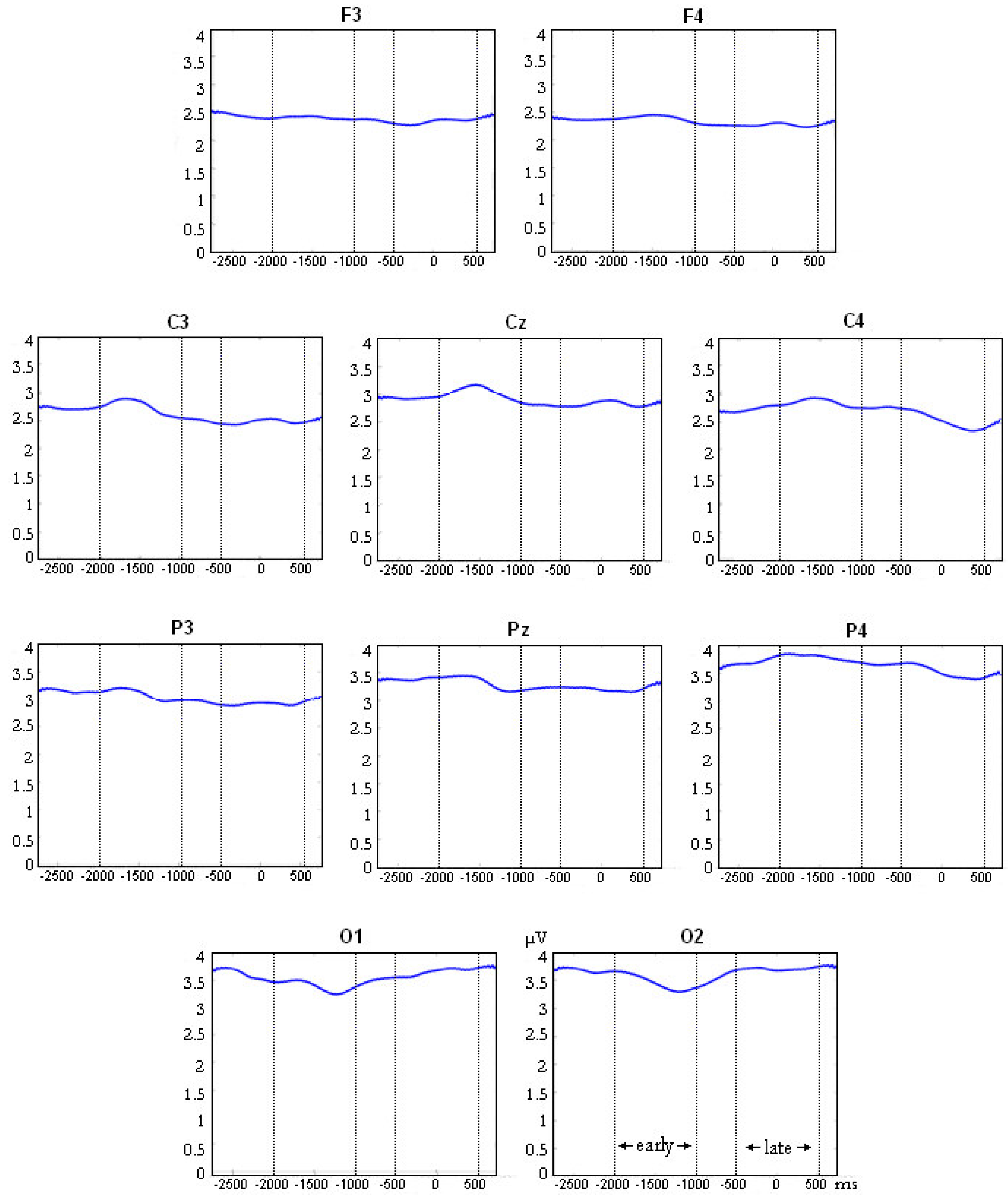

Fig. 17.: Alpha band (8-12Hz) **grand RMS moving average** (N=13) from the ***dissociated*, non- *ambiguous*** condition for all electrodes included in the analysis. Vertical bars indicate early (-2000 to -1000 ms) and late (-500 to 500 ms) time windows. Abscissa: RMS values in μV; ordinate: time in ms; zero indicates the button press.

6.2.3. Statistical Results

6.2.3.1. Delta Band/*Ambiguous* Stimulus

As seen in figure 18, within the *early* time window delta amplitudes are larger for the *dissociated* condition at all locations. This difference between conditions is significant as shown by the ANOVA, factor condition [F(1, 13)=6.8, P=0.023]. Amplitude size also differs between the ROI as indicated by the factor location [F(3, 39)=9.7, P=.000] as well as post hoc pairwise comparisons. In the *standard* condition, amplitudes are significantly smaller at frontal sites compared to all the other ROI's, while in the *dissociated* condition amplitudes are smaller at frontal as compared to central and parietal electrodes (see table 4 for details).

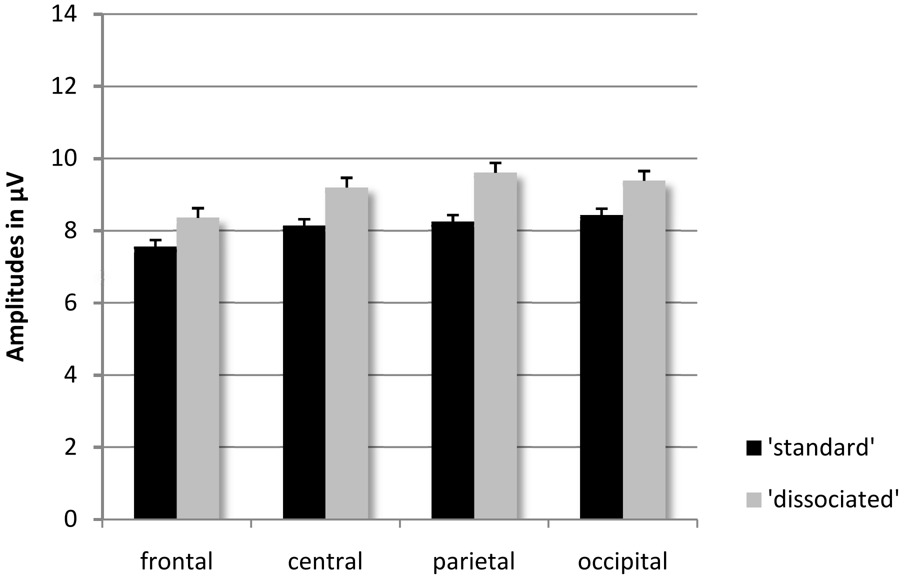

Fig. 18.: Maximum delta (0-4Hz) amplitudes within the ***early*** time window from the ***ambiguous*** stimulus. Abscissa: Amplitudes in µV; ordinate: recording site.

Within the *late* time window (figure 19), delta amplitudes are larger for the *standard* condition, as shown by the significant result for the factor condition

[F(1, 3)=10.3, P=.007]. Responses are smaller at frontal- compared to all other locations for the *standard* condition (factor location [F(3, 39)=9.2, P=.000]; pairwise comparisons, table 4.), and the localization of the response differs significantly between conditions (factor interaction [F(3, 39)=7.2, P=.001].

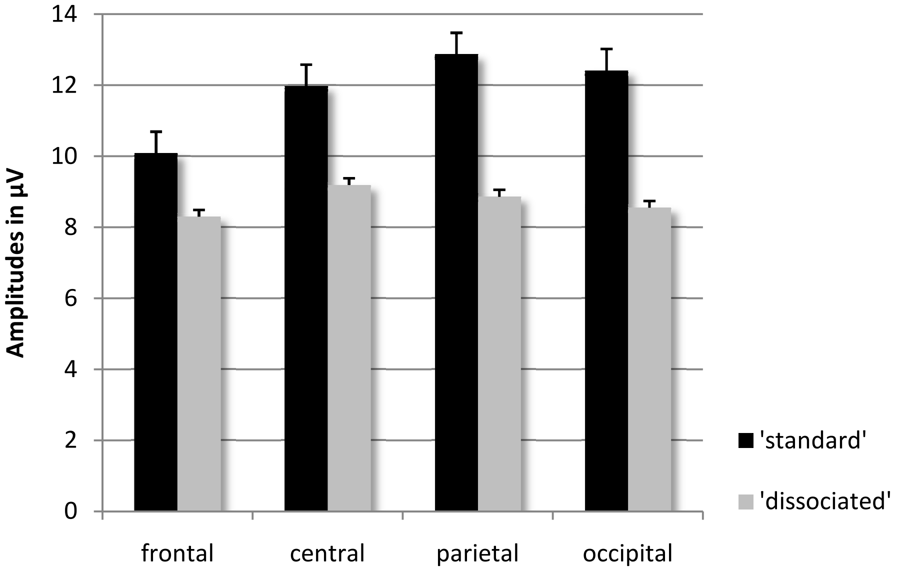

Fig. 19.: Maximum delta (0-4Hz) amplitudes within the ***late*** time window from the ***ambiguous*** stimulus. Abscissa: Amplitudes in µV; ordinate: recording site.

6.2.3.2. Delta Band/ *Non-ambiguous* Stimulus

Figure 20 displays the results for the *early* time window, showing a stronger delta response for the *dissociated* condition (factor condition [F(3, 39)=11.2, P=.000]). Amplitudes are smaller at frontal- than at central- and parietal electrodes for the *standard* condition, and smaller at frontal- than at all other electrodes for the *dissociated* condition (factor location [F(3, 39)=11.2, P=.000]; pairwise comparisons, table 5). Conditions also differ significantly regarding the topography of the response (factor interaction [F(3, 39)=5.2, P=.004]).

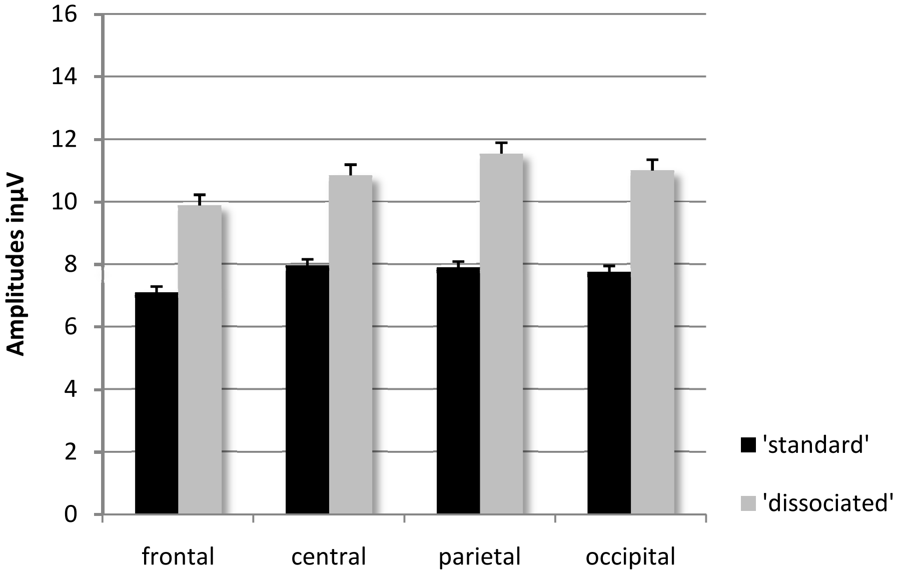

Fig. 20.: Maximum delta (0-4Hz) amplitudes within the ***early*** time window from the ***non-ambiguous*** stimulus. Abscissa: Amplitudes in µV; ordinate: recording site.

The *late* time window (figure 21) features larger delta amplitudes for the *standard* condition at all locations (factor condition [F(1, 3)=11, P=.006]). The *standard* condition shows the smallest response frontally, while the *dissociated* condition has smaller amplitudes at frontal compared to central and occipital electrodes, as shown by the factor location [F(3, 39)=14.7, P=.000] and the pairwise comparisons (table 5). Again, conditions differ in the localization of the response (factor interaction [F(3, 39)=22.5, P=.000]).

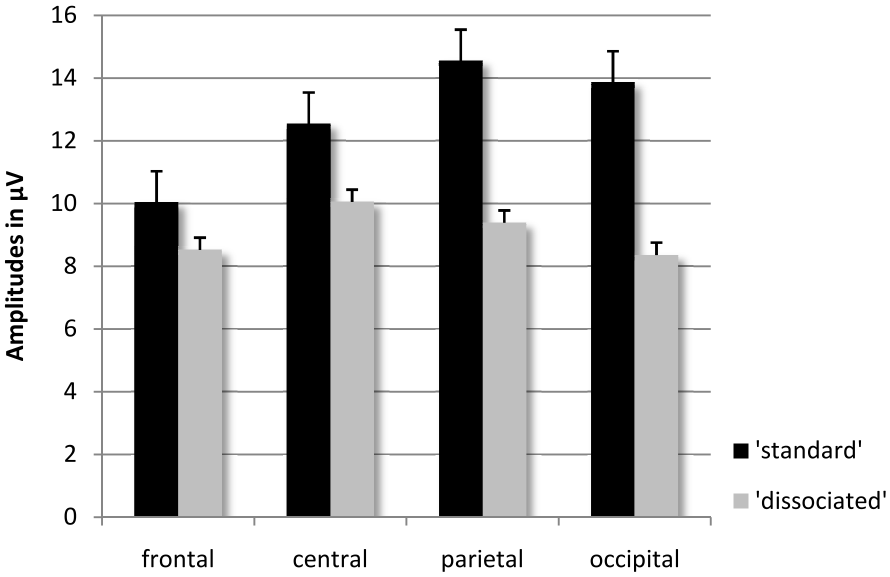

Fig. 21.: Maximum delta (0-4Hz) amplitudes within the ***late*** time window from the ***non-ambiguous*** stimulus. Abscissa: Amplitudes in µV; ordinate: recording site.

6.2.3.3. Alpha Band/ *Ambiguous* Stimulus

Figure 22 shows RMS values for the alpha band filtered data within the *early* time window. Amplitudes are lower in the *dissociated* condition (factor condition [F(1, 3)=6.8, P=.002]). In the *standard* condition, alpha activity is reduced at frontal and central sites as compared to parietal sites, whereas in the *dissociated* condition the activity is reduced at frontal as compared to parietal sites only (factor location. [F(3, 39)=6.7, P=.001]; pairwise comparisons, table 6)

The topography of the response differs between the conditions, as shown by a significant interaction effect [F(3, 39)=5.2, P=.004].

In the *late* time window (figure 23), RMS values in the *standard* condition are lower only occipitally, but higher at all other locations, although this effect did not reach statistical significance. Alpha activity was lower at frontal- than at central- and parietal electrodes for both conditions (factor location [F(3, 39)=2.7, P=.001]; pairwise comparisons, table 6)

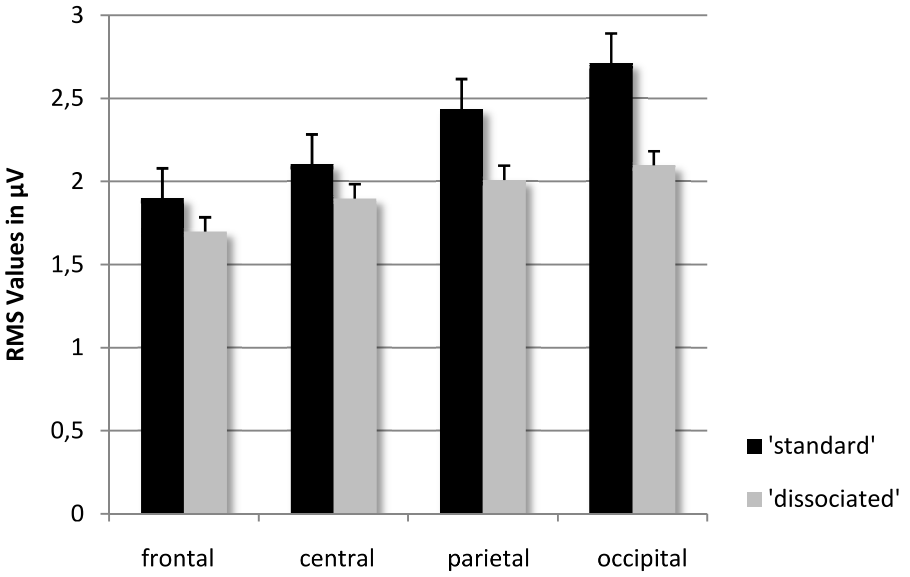

Fig. 22.: Minimum alpha (8-12Hz) RMS values within the ***early*** time window from the ***ambiguous*** stimulus. Abscissa: RMS values in µV; ordinate: recording site.

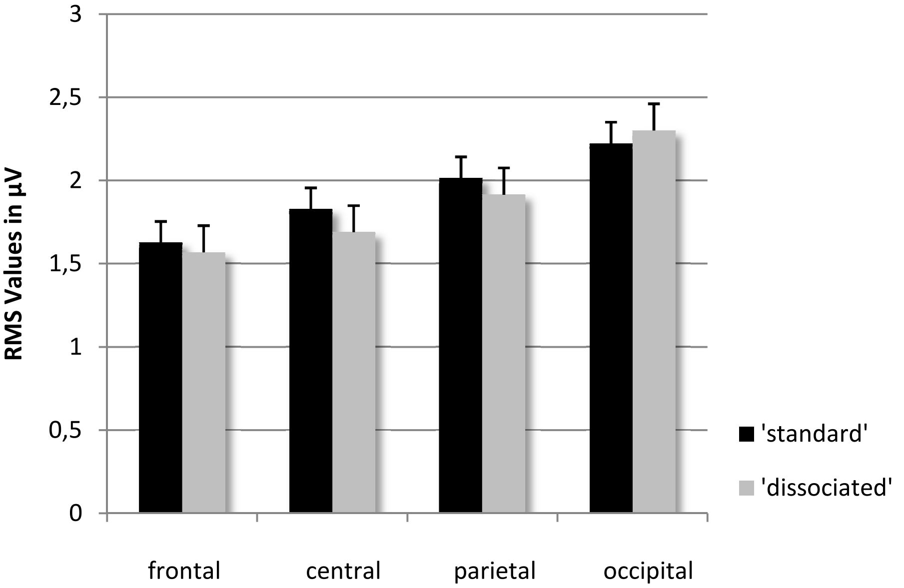

Fig. 23.: Minimum alpha (8-12Hz) RMS values within the ***late*** time window from the ***ambiguous*** stimulus. Abscissa: RMS values in µV; ordinate: recording site.

6.2.3.4. Alpha Band/ *Non-ambiguous* Stimulus

Very few differences exist between conditions within the *early* time window, and no significant effect was found for the factor condition (figure 24). Activity at frontal sites was reduced compared to all other locations, as shown by the factor location [F(3, 39)=9.8, P=.000] and pairwise comparisons (table 7).

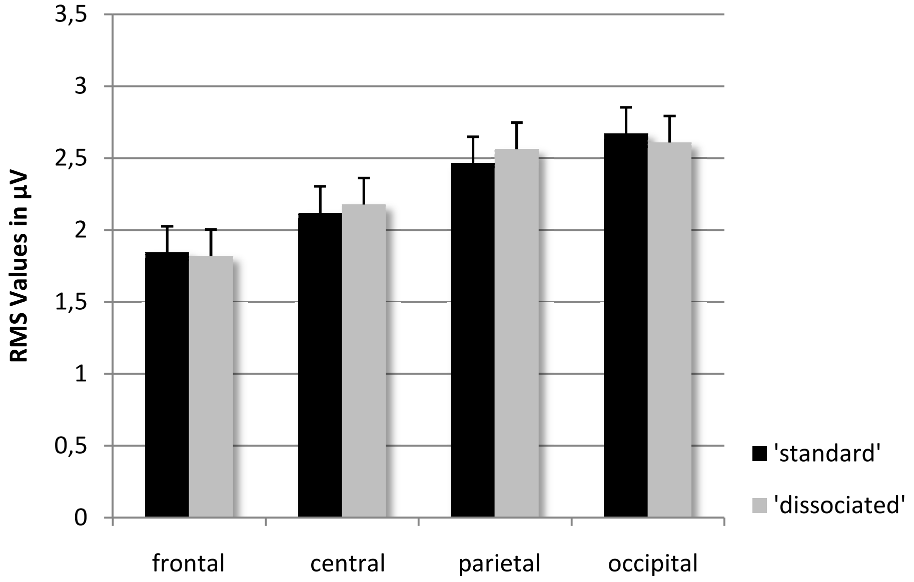

Fig. 24.: Minimum alpha (8-12Hz) RMS values within the ***early*** time window from the ***non-ambiguous*** stimulus. Abscissa: RMS values in µV; ordinate: recording site.

Within the *late* time window, the *standard* condition holds lower RMS values at all locations (figure 25), however this difference again did not reach statistical significance. Significantly lower amplitudes were found at frontal- compared to all other locations for the *standard*, and for frontal- compared to central- and parietal locations for the *dissociated* condition (factor location [F(3, 39)=8.6, P=.000]; pairwise comparisons, table 7).

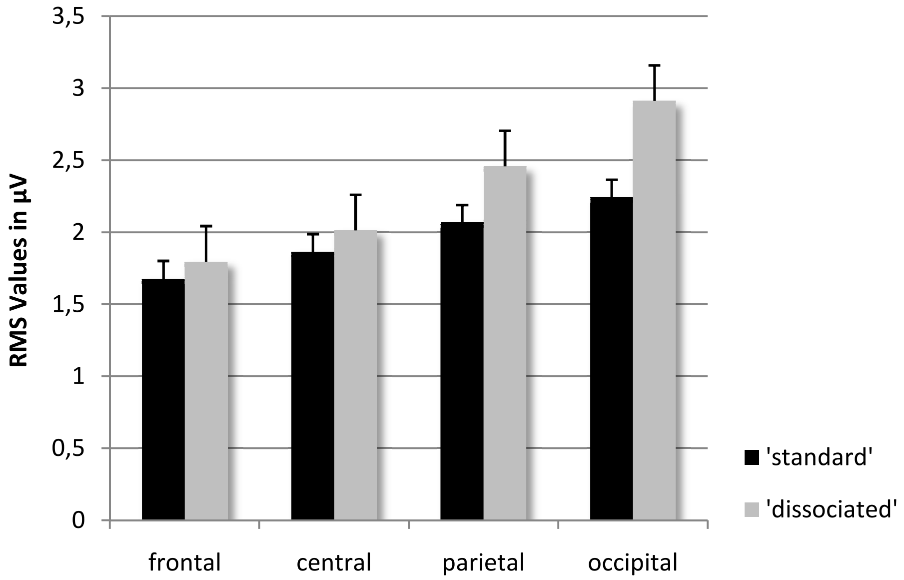

Fig. 25.: Minimum alpha (8-12Hz) RMS values within the ***late*** time window from the ***non-ambiguous*** stimulus. Abscissa: RMS values in µV; ordinate: recording site.

Time window/ stimulus	**Source**	**Sum of squares**	**dF**	**Error dF**	**Mean sum of squares**	**F**	**Sig.**
early/ ambiguous	condition	44.599	1	13	44.599	6.676	.023*
	location	18.660	3	39	6.220	9.675	.000*
	condition X location	1.536	3	39	.512	2.115	.114
late/ ambiguous	condition	190.224	1	13	190.224	10.283	.007*
	location	38.020	3	39	12.673	9.240	.000*
	condition X location	20.539	3	39	6.846	7.204	.001*
early/ non-ambiguous	condition	323.630	1	13	323.630	29.765	.000*
	location	35.913	3	39	11.971	11.152	.000*
	condition X location	12.215	3	39	4.072	5.208	.004*
late/ non-ambiguous	condition	315.286	1	13	315.286	10.982	.006*
	location	107.412	3	39	35.804	14.689	.000*
	condition X location	76.898	3	39	25.633	22.467	.000*

Tab. 2.: Statistical results from the ANOVA for the **Delta Band.** See text for details.

Time window/ stimulus	**Source**	**Sum of squares**	**dF**	**Error dF**	**Mean sum of squares**	**F**	**Sig.**
early/ ambiguous	condition	3.674	1	13	3.672	6.771	.002*
	location	5.815	3	39	1.938	6.662	.001*
	condition X location	.827	3	39	.276	5.186	.004*
late/ ambiguous	condition	.085	1	13	.085	.283	.604
	location	6.895	3	39	2.298	6.731	.001*
	condition X location	.186	3	39	.062	2.680	.060
early/ non-ambiguous	condition	.008	1	13	.008	.013	.912
	location	11.269	3	39	3.756	9.792	.000*
	condition X location	.112	3	39	.037	.431	.732
late/ non-ambiguous	condition	3.066	1	13	3.066	2.837	.116
	location	11.400	3	39	3.800	8.557	.000*
	condition X location	1.379	3	39	.460	3.295	.030*

Tab. 3.: Statistical results from the ANOVA for the **Alpha Band.** See text for details.

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.654	.116	.001*	-1.675	.352	.002*
	pariet.	-.750	.167	.004*	-2.499	.586	.006*
	occipit.	-.925	.261	.022*	-2.051	.612	.031*
centr.	**pariet.**	-9.617 E-02	.150	1.000	-.82	.345	.197
	occipit.	-.272	.179	1.000	-.376	.416	1.000
pariet.	**occipit.**	-.175	.185	1.000	.448	.202	.269

Standard/ Ambiguous

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-1.007	.255	.010*	-.983	.382	.139
	pariet.	-1.302	.374	.015*	-.498	.369	1.000
	occipit.	-.937	.361	.133	-7.651E-02	.432	1.000
centr.	**pariet.**	-.295	.213	1.000	.485	.257	.493
	occipit.	6.999E-02	.340	1.000	.907	.469	.450
pariet.	**occipit.**	.365	.194	.497	.422	.249	.672

Dissociated/ Ambiguous

Tab: 4.: Results for the **Delta Band** from the **pairwise comparisons** between **ROI's.**
Top: *Ambiguous* stimulus, *standard* condition; bottom: *ambiguous* stimulus, *dissociated* condition;

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.869	.150	.000*	-2.426	.339	.000*
	pariet.	-.705	.146	.001*	-4.275	.626	.000*
	occipit.	-.534	.227	.210	-3.557	.597	.000*
centr.	**pariet.**	.163	.121	1.000	-1.849	.410	.004*
	occipit.	.335	.221	.926	-1.131	.484	.217
pariet.	**occipit.**	.171	.198	1.000	.718	.275	.129

Standard/ Non-ambiguous

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-1.178	.239	.002*	-1.521	.314	.002*
	pariet.	-2.434	.610	.009*	-1.064	.477	.263
	occipit.	-1.460	.426	.027*	.532	.528	1.000
centr.	**pariet.**	-.1256	.553	.244	,457	.451	1.000
	occipit.	-.283	.380	1.000	2,044	.653	.048*
pariet.	**occipit.**	.973	.576	.689	1,587	.680	.218

Dissociated/Non-ambiguous

Tab. 5.: Results for the **Delta Band** from the **pairwise comparisons** between **ROI's.**
Top: *Non-ambiguous* stimulus, *standard* condition; bottom: *non-ambiguous* stimulus, *dissociated* condition;

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.204	.097	.338	-.201	.044	.003*
	pariet.	-.537	.103	.001*	-.388	.110	.022*
	occipit.	-.811	.289	.089	-.596	.252	.206
centr.	**pariet.**	-.333	.103	.039*	-.187	.085	.284
	occipit.	-.607	.275	.276	-.395	.233	.683
pariet.	**occipit.**	-.274	.201	1.000	-.208	.163	1.000

Standard/ Ambiguous

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.198	.074	.113	-.121	.029	.006*
	pariet.	-.311	.066	.002*	-.347	.097	.020*
	occipit.	-.398	.139	.079	-.732	.244	.062
centr.	**pariet.**	-.112	.059	.477	-.227	.076	.063*
	occipit.	-.199	.147	1.000	-.611	.220	.094
pariet.	**occipit.**	-8.680E-02	.101	1.000	-.348	.151	.146

Dissociated/ Ambiguous

Tab. 6.: Results for the **Alpha Band** from the **pairwise comparisons** between **ROI's.** Top: *Ambiguous* stimulus, *standard* condition; bottom: *ambiguous* stimulus, *dissociated* condition;

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.277	.081	.027*	-.187	.031	.000*
	pariet.	-.622	.149	.006*	-.388	.081	.002*
	occipit.	-.827	.232	.021*	-.563	.158	.021*
centr.	**pariet.**	-.345	.091	.014*	-.201	.56	.020*
	occipit.	-.550	.217	.149	-.376	.141	.116
pariet.	**occipit.**	-.205	.162	1.000	-.175	.098	.583

Standard/Non-Ambiguous

Region of interest		***early* time window**			***late* time window**		
(i)	**(j)**	Mean Diff.	Std. Error	Sig.	Mean Diff.	Std. Error	Sig.
front.	**centr.**	-.358	.055	.000*	-.216	.040	.001*
	pariet.	-.743	.152	.002*	-.661	.177	.015*
	occipit.	-.789	.254	.050*	-1.114	.392	.083
centr.	**pariet.**	-.385	.150	.143	-.445	.158	.088
	occipit.	-.431	.257	.707	-.898	.363	.167
pariet.	**occipit.**	-4.598E-02	.244	1.000	.453	.303	.955

Dissociated/ Non-ambiguous

Tab. 7.: Results for the **Alpha Band** from the **pairwise comparisons** between **ROI's.**
Top: *Non-ambiguous* stimulus, *standard* condition; bottom: *non-ambiguous* stimulus, *dissociated* condition;

Discussion

This section compromises the discussion of the experimental results presented above. Delta and alpha band are discussed separately, by comparing grand averages and statistical effects of the *standard*- with the *dissociated* condition for both time windows. Next is a summary of the results and implications of the study, especially regarding its original aims and goals.

The chapter is concluded by critical remarks on limitations within the present work and an outlook on possible future investigations.

7.1. Delta Band

7.1.1. *Early* Time Window

The delta response in the *early* time window is quite similar for the two stimuli, but differs largely between the two conditions.

In the grand average from the *standard* condition, there is hardly any response observable within both stimulus situations. This is in line with the hypotheses made, as the subjects were expected to experience no specific event, but a stable perceptual pattern during that time.

In the *dissociated* condition however, a distinct positive wave is occurring for the *ambiguous* and the *non-ambiguous* stimulus, peaking about 1500 ms before the button press. As the task separated the perceptual reversal from the motor response by about 1500 ms, this time point suggests a functional relationship to the former. The significantly larger amplitude at parietal- and central- compared the frontal ROI's with maximum activity parietally would also favor a perceptual- over a motor origin. These characteristics of appearance and localization of the response are furthermore in line with the initial report of the PSP as well as with more recent follow up studies (Başar-Eroğlu et al., 1993; Strüber & Herrmann, 2002; Mathes et al., 2006).

This difference in amplitude between the *standard* and the *dissociated* condition is also statistically significant, which is consistent with the hypothesis made. Moreover, the occurrence of an interaction effect between condition and location in the GLM adds to the notion of different cognitive processes taking place during the two conditions.

While timing and localization are similar for the responses to *ambiguous* and *non- ambiguous* stimuli, the amplitude is remarkably stronger for the latter. A reason for this may be a tighter time-locking between reversal, positivity and button press in the *non-ambiguous* condition, as its quicker, easier detectable pattern change quite likely results in less temporal variance of the delay period and in a more pronounced, distinct event-related potential. Yielding similar results, O'Donnell et al. (1988) as well as Başar-Eroğlu et al. (1993) have also taken into account a more functional interpretation. In analogy to interpretations of the P300 (e.g. Donchin, 1981), the larger amplitude in the *non-ambiguous* condition could be related to the easier discriminability of the external pattern change. Accordingly, the prolonged, smaller appearance of the positivity during the *ambiguous* condition may be due to increased processing requirements.

7.1.2. *Late* Time Window

The results from the *standard* condition essentially confirm the findings from earlier studies (Başar-Eroğlu et al., 1993; Strüber & Herrmann, 2002; Mathes et al., 2006).

For the *ambiguous* stimulus, the delta band features a distinct positive wave (i.e. the PSP) starting between -750 ms and -500 ms before- and peaking simultaneous with the button press. The posterior localization replicates the previous results, showing a maximum at parietal sites, as revealed by the grand averages and the pairwise comparisons. A very similar response considering timing and localization is found in the *non-ambiguous* condition, however showing up to twice as large amplitudes and a narrower, steeper appearance in the grand average. Like for the *early* time window, this fact again can be attributed to differences in latency jitter and task difficulty between the stimulus conditions.

The *dissociated* condition as well features a positive wave, however occurring somewhat later, peaking about 250 ms after the button press. An obvious difference to the *standard* condition is the localization of the response, as shown by a significant interaction between condition and location. In this respect, both grand averages and pairwise comparisons reveal a distinct shift from posterior towards anterior electrodes as compared to the *standard* condition. With central electrodes being located close to the motor cortex, this would be in line with an underlying motor- rather than perceptual process, as predicted by the hypothesis.

Like for the previously discussed responses, amplitudes are larger for the *ambiguous* than for the *non-ambiguous* stimulus. In this case however, the difference comes rather surprising, as the presumably motor-related positivity should essentially be the same in both conditions. A possible interpretation could again be drawn from the easier detectability of the *non-ambiguous* pattern change, which may lead to a pronounced positive response after successful completion of the task (i.e. the button press after the delay period).

7.1.3. Grand Averages

Figure 26 displays the overlapped delta band grand averages from the standard and dissociated conditions from electrode P4.

The shape of the delta positivity occurring around the button press of the standard condition suggests to reflect a summation of the ongoing perceptual and motor processes, both of which can be seen separately in the dissociated condition around -1500 ms and 250 ms, respectively. In fact, shifting the early (perceptual) component of the dissociated condition about 1500 ms to the right, and adding it up to the late (motor) component, will quite likely result in a waveform similar to the one occurring during the standard condition.

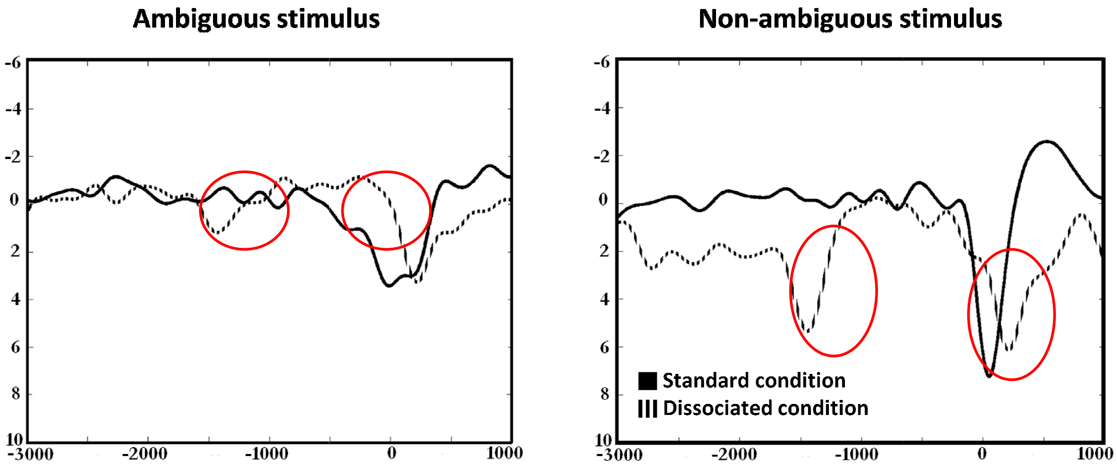

Fig. 26.: Overlapping delta band (0-4 Hz) **grand averages** (N=13) from the **standard- and dissociated condition** from electrode P4; Note how the shape of the early difference between conditions corresponds to the shape of the late differences. Abscissa: amplitudes in µV; ordinate: time in ms; zero indicates the button press.

7.2. Alpha Band

Resembling previously found results (Strüber & Herrmann, 2002; Işoğlu-Alkaç & Strüber, 2006), alpha activity by means of RMS values is modulated over the course of the epoch and decreases distinctly towards the occurrence of perceptual and motor processes. Both overall activity and the impact of the modulation are stronger at posterior- than anterior electrodes in all conditions.

7.2.1. *Early* Time Window

Similar to the delta band, the *early* time window in the alpha band features quite different responses for the two condition.

During the *standard* condition, alpha activity remains rather stable for both the *ambiguous* and the *non-ambiguous* task with smaller amplitudes at frontal- compared to the other electrodes. Again, this corresponds well to the hypothesis made, as no perceptual or motor processes were demanded, respectively elicited by the task.

In contrast, the *dissociated* condition features a distinct decrease in alpha band amplitudes which is most prominent at occipital electrodes. For the *ambiguous* task, this decrease starts off approximately 2500 ms before the button press and has an even, continuing appearance. In response to the *non-ambiguous* task, the decrease is occurring about 500 ms later in a more steep and abrupt fashion. Again, activity is smaller frontally compared to the posterior sites.

Following the report by Strüber & Herrmann (2002), occipital alpha could be interpreted as functionally connected to the maintenance of the current percept. The endogenously induced pattern change in the *ambiguous* condition may be preceded by a slow and even decay of the functional network underlying the current percept, as represented by the alpha decrease, which gives way to a perceptual reversal after reaching a certain threshold. In contrast, the occipital alpha network reacts merely passive to the exogenous pattern change of the *non-ambiguous* stimulus, therefore dropping steeply only short before the reversal. The latter case would be in line with a series of works by Klimesch and colleges, who reported a drop of alpha power over parieto-occipital areas preceding the processing of various kinds of sensory-semantic information (Klimesch et al., 1993, 1994, 1996, 1997).

Statistically, the *dissociated* condition features significantly lower alpha activity in response to the *ambiguous* stimulus than to the *standard* condition. Again, considering the experimental task and the grand average figures, this result can be interpreted as the occurrence of an alpha power decrease in the case of the *dissociated* condition, for which an underlying perceptual process is highly probable. This strongly supports the results found previously during the observation of multistable visual patterns (Strüber & Herrmann, 2002; Işoğlu-Alkaç & Strüber, 2006) and suggests a functional relationship between alpha activity decrease and the occurrence of a perceptual reversal.

Although a similar difference in responses between the *standard-* and *dissociated* condition is also visible in the grand average figure for the *non-ambiguous* stimulus, this modulation does not produce a statistically significant effect.
A likely reason for this is that the chosen time windows did not capture the different time-courses between the two conditions properly.
As shown by Strüber & Herrmann (2002), the steep and abrupt drop of alpha power during the non-ambiguous condition happens shortly before the button press, within about 250 ms. Given that the averaging window for the alpha band in the present study is as large as 500 ms, the effect of such a quick alpha response may be averaged out. Additionally, the ANOVA conducted included all four ROI's as groups. With the alpha response occurring almost exclusively at occipital sites, this statistical procedure may not be perfectly suited to detect significant differences between the conditions.

7.2.2. *Late* Time Window

In the *standard* condition, a decrease in alpha band activity can be observed at central-, parietal- and occipital electrodes during the *late* time window, again with smaller amplitudes at anterior- than posterior locations.
Similar to the response in the *early* time window as well as to the report by Strüber & Herrmann (2002), the appearance of the decrease is quite different for the *ambiguous-* compared to the *non-ambiguous* stimulus. While alpha activity in the former is reduced in a slow, continuing matter starting at about 1000 ms before the button press, it drops rather abruptly in the latter only about 200 ms prior to the response. Again, a perceptual interpretation, implying the notion of a slow decaying perceptual representation in one case and a quick adaptation to a changing stimulus in the other, as made in the previous section, is applicable. This interpretation fits particularly well with the part of the response located occiplitally.

However, as discussed in length in chapters 3 and 4, the *standard* condition features button-press related motor potentials occurring in close temporal succession to the reversal, putting a solely perceptual origin and interpretation of the alpha response in question. Numerous studies have also reported motor-related responses in the alpha band, which may contribute to the present findings (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989; Toro et al., 1994; Stancák and Pfurtscheller, 1996; Leocani et al., 1997). These works all described a localized decrease of alpha power over contralateral sensory-motor areas, starting as *early* as 2000 ms prior to voluntary movements. While the alpha decrease is quite evident over central electrodes in the present work, it is enhanced on ipsilateral sites and occurs much later, beginning between 500 ms and 250 ms before-, and peaking about 250 ms after the button press, thus arguing against a substantial influence of motor activity. Besides, as discussed in more detail in the *Limitations* section, this specific motor response may not be regarded as a voluntary, internally triggered movement, but as a response to an external, imperative trigger, with rather different neuronal- and electrophysiological correlates.

During the *dissociated* condition, an activity decrease towards to button press can be seen quite clearly at the right central and parietal electrodes for both stimulus tasks, however being almost non-existent at other locations.

Following the discussion of the delta positivity as well as of the alpha response during the *standard* condition, this decrease may be interpreted as a correlate of either the motor response or the completion of the delayed-response task.

Just as for the *standard* condition, time-course and localization of this alpha band response are not in line with previous reported movement-related correlates. Pfurtscheller and Lopes DaSilva (1999) discuss a widespread power decreases in the lower alpha frequency range (7-10 Hz) as a response to almost any kind of task, reflecting cognitive demands or attentional processes. However, those characteristics again do not match the late, right centro-parietal occurrence of the response. So far, the most plausible explanation for the late alpha decrease would be as a correlate to an externally triggered, non-voluntary movement, as which the delayed button press may be considered.

Regarding the differences between the *standard-* and the *dissociated* condition, the grand average figures would suggest a stronger alpha decrease in the former compared to the latter. However, none of the two stimulus conditions yielded a statistically significant effect. Again, it could be speculated that the effect of the motor response occurring in both conditions is dominating the alpha response in such a way, that the additional modulation by the perceptual process during the *standard* condition does not make a sufficient difference for the overall alpha activity level.

In any case, regarding the aim of the present study, a lack in a statistically significant difference between the conditions for the second time window is not as relevant as it is for the *early* time window, as only the latter permits conclusions on reversal-related activity.

7.3. Conclusion

The present thesis set out to investigate perceptual related EEG activity independently from motor related activity during a paradigm of multistable visual perception, by separating the subject's motor response from their perceptual reversals through a special experimental setup. It was proposed that modulations in the delta and alpha frequency band, reported previously using a conventional experimental setup, would still occur during the time course of a pattern reversal, even in absence of a motor response.

In line with the previous works, the delta band showed a distinct and statistically significant response during the course of perceptual reversals alone (no accompanying motor response) as compared to periods of stable visual perception.

As for the alpha band response, a statistical significant difference between stable perception and reversals could be shown for the *ambiguous* stimulus, but not for the disambiguated control condition. Taken together, the data strongly suggests that the so far reported delta and alpha band responses are indeed an electrophysiological correlates of perceptual reversals, and independent of overlapping motor processes.

7.4. Limitations

Quite obviously, one of the main features of the present study, the delayed button press, can also be considered as it's major shortcoming. In the first place, this is due to the strategy by which subjects estimated the desired delay period. Although they were explicitly asked not to actively count through the three cycles of the SAB if possible, six out of the 14 subjects included in the analysis reported to have done so. This quite certainly introduces correlates of the counting to the EEG record between reversal and button press. The remaining eight subjects reported to have used their rhythmic feeling, entrained by the metronomic flashing of the SAB, to estimate the correct delay time. However, even if engaging less cognitive resources than conscious, active counting, this process will leave some sort of trace in the EEG signal.

Besides the actual strategy by which participants realized the delayed button press, the mere anticipation of a motor response will contribute to the EEG as well. As first reported by Walter and colleges (1964), a conditional stimulus predicting a subsequent imperative stimulus is accompanied by a characteristic slow potential, the Contingent Negative Variation (CNV). The CNV starts out about 500 ms - 2000 ms after the conditional stimulus, continuously rises up to the point of the imperative stimulus and drops abruptly with the onset of the motor response. In the present case, the pattern reversal could be considered as the conditional stimulus, while the fourth cycle of the SAB serves as the imperative signal. However, a difference between the two paradigms certainly is the length of the delay period. In usual CNV studies, conditional- and imperative stimuli are separated by 6000 ms or more, which is considerably longer than the 1500 ms used in the present work. Thus, the possibility for a sufficient negativity to arise in this short amount of time is debatable. Besides the CNV, the buildup of the early

Bereitshaftspotential (Kornhuber & Deecke, 1965, see section 3.4) also falls into the period between reversal and button press of the dissociated condition. However, both CNV and Bereitschaftspotential are usually recorded using DC (direct coupled) amplifiers, while the analog high-pass filter of the amplifier used in the present study certainly removed most of the slow potential shifts.

Taken together, while the effects of counting and response anticipation may be negligible to the most extent, they still have to be taken into consideration when interpreting the results of the *dissociated* condition.

Although not in the focus of the present study, an issue worth considering is the comparability of the *ambiguous*- and *non-ambiguous* stimulus conditions. First, as presented in the methods-section, the number of *non-ambiguous* pattern changes was not matched to the individual-multistable reversal rate of each subject, but set consistently for all participants according to previous studies. In practice, this led to an above-average respectively below-average pattern change for most of the subjects. Drawing from the P300-related interpretation of the PSP, this fact potentially influenced the individual response amplitude to the *non-ambiguous* pattern change. However, concerning statistical effects and the appearance of the grand average figures, these differences overall much likely canceled each other out. A number of studies also found quite different electrophysiological and BOLD (Blood Oxygen Level Dependent) responses for externally versus internally triggered movements (Papa et al., 1991; Cunnington et al., 2002). Considering the internal origin of the perceptual reversal in the *ambiguous*-, compared to the imperative, external pattern change in the *non-ambiguous* condition, a different course of the pre-motor EEG may be arguable. If so, these differences may only occur in the *standard* condition, as the button press in the *dissociated* condition is, not a direct response to the pattern change but to the completion of the delay period, which is externally demanded by the task.

Finally, the differences in the alpha activity time-course during the *early* time window between the *standard* and *dissociated* conditions of the *non-ambiguous* may be captured more properly by the use of a narrower time-window and/ or a t-test conducted only occipital ROI's.

7.5. Perspectives

An elaborate study of endogenous processes, such as pattern reversions in multistable perception, without any sort of motor response by the subject may only be possible, if one manages to detect those processes with high accuracy in single trials by their electrophysiological correlates only. A possible candidate for those correlates would be a distinct spatio-temporal pattern of brain oscillations in different frequency bands, occurring only during the time course of a perceptual reversal and thus differentiating the latter from all other cognitive processes.

A different, currently more feasible approach could make use of blind source separation algorhythms such as Independent Component Analyses (ICA) (Delorme & Makeig, 2004). ICA linearly decomposes multivariate signals into a series of additive components. Applied to a multi-source EEG signal such as the one recorded during the *standard* condition of the present study, this method might successfully separate motor-related from perceptual components by their different time course and localization. However, due to technical limitations (mainly the number of electrode channels available) this approach could not be used in the present work.

Considering the overall way in which the brain processes and disambiguates visual input, still much remains unclear. While there is increasing knowledge on the responses in single frequency bands, interaction and cross-communication between those frequencies are yet to be investigated. Several recent studies reported cross-frequency correlations in a number of different perceptual and cognitive processes, such as the orienting response (Isler et al., 2008), mental arithmetic (Mizuhara et al., 2005) or memory matching (Sauseng et al., 2008), as well as in the spontaneous EEG (Nikulin & Brismar, 2004). From those empirical findings, as well as from theoretical accounts such as the one by Basar and colleges (2001), some kind of interaction between the oscillatory responses reported so far for multistable perception seems highly probable.

Knowledge on those issues, especially the direction of the interaction, along with a more accurate localization of the involved oscillations, will hopefully also shed light on the actual Top Down and Bottom Up processes going on during the emergence and decay of orderly visual patterns, and –in the end- meaningful representations of our world.

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8.2. Figures

Figure 1.:
(a) Fründ, I. (2004) Untersuchung visueller Wahrnehmung mithilfe eines multistabilen Musters: Phasenkorrelationen im EEG-Gamma-Band. Diplomarbeit, Universität Bremen.
(b) Braun, J. (2000) Computational Neuroscience: Intimate Attention. *Nature*, 408, 154-155.
(c) Online source:
http://www.seabury.edu/faculty/akma/2002_06_30_blogarch.html
(last access on 14.08.2009)
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Figure 3:
Online source:
http://www.borderland-tours.com/content/view/31/54/
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Figure 4:
Gleick, J. (1987), Chaos: Making a New Science, *Penguin*, New York, NY, .

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Appendix

9.1. Deutsche Zusammenfassung

In den vergangenen Jahren wurden eine Reihe spezifischer oszillatorischer EEG-Komponenten beschrieben, welche im Zuge einer Wahrnehmungsreversion während des Betrachtens eines multistabilen visuellen Reizes auftreten.
Die für die vorliegende Arbeit relevanten Komponenten sind: (a) eine langsame positive Welle im Delta Band (0-4 Hz), welche ihr Maximum etwa 250 ms nach einer Wahrnehmungsreversion (angezeigt durch einen Knopfdruck der Probanden) erreicht, und als Abschluss des Reversionsprozesses bzw. als die Etablierung einer neuen stabilen Wahrnehmung interpretiert wurde; (b) eine Abnahme der Aktivität im Alpha Band (8-12 Hz), welche etwa 1000 ms vor einer Wahrnehmungsreversion beginnt und als Destabilisierung des aktuellen Perzepts interpretiert wurde.
Da das Auftreten eines Wahrnehmungswechsels in den bisherigen Studien jedoch über einen Knopfdruck der Probanden rückgemeldet wurde, ist unklar in welchem Ausmaß elektrophysiologische Korrelate der motorischen Aktivität die beschriebenen perzeptuellen Komponenten beeinflussen oder überlagern.

In der vorliegenden Arbeit wurden die reversionsgebundenen EEG-Komponenten im Delta- und Alpha Band unabhängig von motorischer Aktivität untersucht, indem Wahrnehmungsreversion und rückmeldender Knopfdruck durch ein spezielles experimentelles Design getrennt wurden.
Die Ergebnisse zeigen klar, dass die zuvor beschriebenen oszillatorischen Komponenten im Delta- und Alpha Band während einer Wahrnehmungsreversion auch in Abwesenheit einer motorischen Antwort auftreten. Sie können daher als Teil jenes neuronalen Mechanismus gesehen werden, durch dessen Hilfe das Gehirn mehrdeutige visuelle Reize disambiguiert und verarbeitet.

9.2. Curriculum Vitae

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