Daniel Senkowski: Neuronal Correlates of Selective Attention. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences, 2004 (MPI Series in Human Cognitive and Brain Sciences; 42)

# Neuronal correlates of selective attention: An investigation of electrophysiological brain responses in the EEG and MEG

# Neuronal correlates of selective attention: An investigation of electrophysiological brain responses in the EEG and MEG

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie
der Universität Leipzig genehmigte

D I S S E R T A T I O N

zur Erlangung des akademischen Grades
doctor rerum naturalium
Dr. rer. nat.,

vorgelegt von
Diplom-Psychologe Daniel Senkowski
geboren am 22. August 1974 in Hannover

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Tag der Verteidigung: 14. Januar 2004

# Acknowledgements

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# Chapter 1

# Introduction

Most everyday live situations contain a number different objects which can not all be processed by the sensory systems at the same time. For this reason, it is necessary to select relevant and to suppress irrelevant information. How does selective attention (SA) contribute to these processes and what are the neuronal correlates of SA? These are the two main questions of the present work.

Starting from relatively simple models of SA, for example the *spotlight metaphor* (Fig. 1.1), modern theories of SA give a much more sophisticated picture of the topic (Desimone, 1999; Hillyard et al., 1999). In Cognitive Neurosciences, the development and application of different methods like the electroencephalography (EEG), the magnetoencephalography (MEG) and functional Magnetic Resonance Imaging (fMRI) allowed a precise investigation of SA processes. Studies in humans are thereby supported by data from single cell recordings in animals. However, most modern theories of SA focus on specific task demands, for example the processing of spatial or object information. The goal of the present work was to examine more general electrophysiological and electromagnetic correlates of SA in event-related potentials (ERPs) and fast oscillatory responses in the gamma-band (30-80 Hz, mainly 40 Hz)[1]. To do this, a series of four EEG and MEG experiments was performed in the context of SA. The four experiments cover different paradigms of attention in two sensory modalities (visual and auditory). Comparable findings in these studies would therefore allow a more general interpretation of the results.

Chapter 2 of the present work will give a theoretical background of the experiments. In this context, relevant theories and important findings will be described. Probably the most prominent correlate of SA in the EEG and MEG is the amplification of ERP amplitudes. It has been suggested that the amplification of signals improves the signal-to-noise ratio of attended stimuli and hence increases their discriminability from

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[1]A methodological introduction in ERPs and oscillatory gamma-band activity is given in Chapter 3
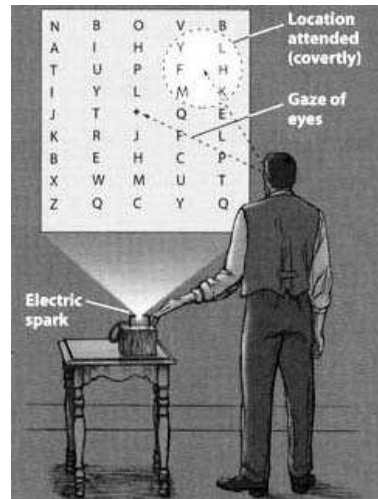
Figure 1.1: Illustration of the setup which was used by Herrmann von Helmholtz (1821-1894) to study visual attention. Helmholtz showed that subjects are able to "covertly" attend to any location on the screen during a brief illumination while they fixate the center of the screen. This finding demonstrated that subjects can shift their attention from one location to another without making overt eye movements (Source: Gazzaniga, 1998, p. 210)

unattended inputs (Hawkins et al., 1990). Different components in the ERP showed enhanced amplitudes for attended as compared to unattended stimuli. Interestingly, the same effect has also been found for oscillatory responses in the gamma-band, indicating that amplification of attended inputs might be a general correlate of SA. This is one assumption that will be investigated in the present work. A methodological background of the EEG and MEG and the respective analysing methods are given in Chapter 3. EEG and MEG allow a measurement of neuronal processes with a temporal resolution of a few milliseconds and are therefore appropriate methods to investigate the dynamics of attentional processes. Chapter 4 will give an outline of the present work, including specific hypotheses. Furthermore, general working hypotheses are formulated. The subsequent Chapters 5 to 8 constitute the empirical part where the four experiments will be presented. A detailed theoretical background is given at the beginning of each experiment and the results of each experiment are discussed separately in the respective chapters. Two of the Chapters (5 and 7) contain broad parts of published articles (Senkowski and Herrmann, 2002; Herrmann, Senkowski, Maess and Friederici, 2002). The other two Chapters (6 and 8) contain broad parts of submitted manuscripts (Senkowski, Röttger, Grimm and Herrmann, submitted; Senkowski,

Talsma, Herrmann and Woldorff, submitted). Finally, Chapter 9 summarizes the main findings of the present work and discusses the working hypotheses. In addition, a conclusion and perspectives for future research are given.

# Chapter 2

# Theoretical background

This chapter will give an introduction in modern theories of SA. Basically, two types of SA theories can be distinguished: General models of SA (Section 2.1.1) and specific models of SA (Section 2.1.2). Due to the complexity of the topic, it is only possible to give a general overview about SA theories here. The more interested reader may be referred to literature sources which introduce SA theories in more detail (Humphreys, Duncan, and Treisman, 1999; Pashler 1998a,b; Parasuraman and Davies, 1984). Another differentiation of SA models, namely the distinction of early and late SA models will be described in Section 2.1.3. In the second part of this chapter, electrophysiological and electromagnetic correlates of SA in event-related potentials (Section 2.2.1) and oscillatory gamma activity (Section 2.2.2) will be reported.

A short comment on frequently used terms in the present work should be given here. The terms bottom-up and top-down are used in the classical sense (Egeth and Yantis, 1997). Bottom-up thereby means that a process is primarily driven by the stimulus properties. In contrast, top-down describes processes that are affected by the internal state of a person. For example, a typical top down process is when the same stimulus material is used and the same behavioral motor responses are required in two blocks with different task instructions. Another frequently used term in the present work regards oscillatory activity in the gamma range. The terms *activity in the gamma range*, *gamma activity*, *gamma-band responses*, and *oscillatory gamma activity* are widely used as synonyms.

## 2.1   Modern theories of selective attention

### 2.1.1   General models

The central point of the first modern theories of SA was an investigation of capacity limitations of the sensory system. These theories came up in the early 1950s and are in broad parts motivated by the discovery of limitations in the handling of simultaneous messages by air-traffic controllers and by findings in dichotic listening tasks. Experimental situations at that time were designed to induce perceptual overload with the goal to explore how the assumed limited resources of the attentional system are directed to relevant information. The earliest and best known theory of these years was the *filter theory* by Broadbent (1958). As a basic idea, Broadbent proposed that the sensory system processes all incoming stimuli to a point at which certain physical attributes (e.g., loudness, pitch and location of an auditory stimuli) are analyzed (Figure 2.1). However, a subsequent system that identifies stimuli (e.g. recognizes a word and comprehends its meaning), was suggested to handle only one or a few items at a time. For this reason, Broadbent suggested that a filter mechanism selects only relevant items (or channels) for high-level processing in a so-called *limited capacity decision channel*. In contrast, irrelevant items are filtered out. The capacity limits of the system were interpreted as a limitation of the processing rate of information units rather than as a limitation of the processing rate of sensory inputs. This concept is closely related to mathematical theories of communication which had a strong influence on psychological theories at this time (Shannon and Weaver, 1949).

The basic idea of Broadbent's theory is that irrelevant sensory inputs are completely rejected by the filter mechanism. First empirical evidence for this idea came from dichotic listening experiments in which subjects had to attend to speech information from a designated ear while ignoring simultaneously presented information from the other ear (Cherry, 1953). Cherry reported that subjects had only few problems in remembering inputs from the attended ear, indicating the ability of humans to selectively attend to a designated input channel. In contrast, only few information from the unattended ear were remembered, indicating a filter mechanism of unattended inputs. A famous example in this context is the *cocktail party phenomenon* (Cherry, 1953). The *cocktail party phenomenon* describes the ability to listen selectively to a specific voice in the midst of other conversations (for example a person at a party who has a conversation is able to ignore other conversations around). However, the first version of the filter theory was quickly amended when it was found, for example, that people sometimes automatically respond to their name on a filtered channel (Moray, 1959). This finding suggested that information from unattended channels can be processed
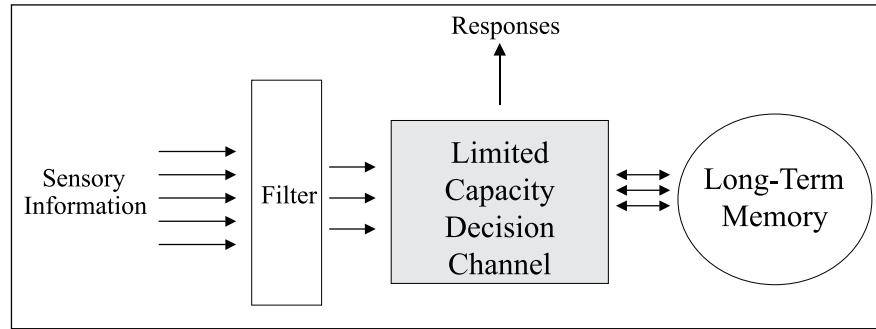
**Schematic illustration of Broadbent's filter theory (1958)**

Figure 2.1: The main component of Broadbents filter theory is the limited capacity decision channel. This channel is only able to process a limited amount of sensory information. For this reason, irrelevant sensory information were rejected by a filter mechanism. Relevant information which pass the filter were processed attentively referring to information from long-term memory. Finally, the processed information can lead to a behavioral outcome (response).

under specific conditions. Due to this findings, Broadbent presented a new version of his *filter theory* in 1971. In this new version he assumed that information from the filtered channels is sometimes sufficient to activate highly primed mental processes, thereby capturing attention. However, the new *filter theory* lacked more and more in explaining the empirical findings in the 1970s. For example, it had been demonstrated that divided attention is possible, particularly when the concurrent tasks differ sufficiently from each other (Allport et al., 1972; Neisser, 1976; Treisman and Davies, 1973). These findings did not fit with the idea of a simple bottleneck filter mechanism which allows the processing of only one single channel at a time. For this reason, new theories on attention were formulated.

One prominent work in this context was the book about *unspecific capacity* by Kahneman (1976). Kahneman did not suggest that attention is limited to the processing of one specific channel. Instead, the attentional system was proposed to be based on *unspecific capacities* which can spread over different channels at any given time. However, Kahneman suggested that the attentional system has also its limitations, particularly the part of the *unspecific capacity* which can be directed to relevant inputs. Directing of attention thereby was suggested to be closely related to the effort of the attentional system. This effort can be improved (for example as a learning strategy). Another central postulate of Kahnemans theory was the assumption that the interference between inputs from different tasks is primarily related to their demands (which need unspecific capacity). However, it has been shown that the processing of different tasks

can result in specific interferences. Allport et al. (1972) reported that it is easier to perform an audio-verbal information task and a parallel picture order detection task, than an audio-verbal information task and a parallel second verbal tasks. More recent studies also indicate that interference is usually observed in dual task experiments (for a review see Pashler, 1994a). Allport et al. (1972) suggested that the attentional system consists of multiple processors which have their own capacity limits and are able to work in parallel. However, this idea has also been critizised. Allport (1980) himself mentioned that it is only possible to estimate performance functions of multiple processors when it is ad-hoc known that the different tasks require the same demands. However, this assumption is hard to control. Therefore, Neumann (1987) concluded that the interference patterns, as for example in dual tasks, can not be explained by a sufficiently small number of different main processors. Thus, Allport's idea of multiple processors with specific limitations of their resources has probably a more descriptive than an empirically measurable character. However, the limited resources approach still influences current models of SA, although these models focus more on the functional aspects (including the advantages) of a system with limited attentional resources.

Interestingly, different studies also investigated the relationship between attentional resources and ERPs in the EEG (Ullsperger et al., 2001; Wickens et al., 1984) Thereby, various ERP components, including the N1 and P3, have been related to attentional resources. The effects of attentional resources on EEG activity were also investigated in the present Experiment 1. This experiment consists of three tasks which require a different amount of attentional resources. The goal thereby was to analyse the effects of attentional resources on oscillatory responses in the gamma-band and ERPs. Of particular interest was the examination of gamma-band responses. Such responses have not been investigated with relation to attentional resources before.

### 2.1.2   Specific models

Limited capacity models, as described in the previous chapter, suggest that SA is first of all necessary to assign processes to a a limited amount of attentional resources. Thus, SA acts as an administrator. In contrast, specific models of attention focus more on the functionality of SA mechanisms. Very important in this context is a direct relationship between selective attentional processing and motor behaviour, respectively action. LaBerge (1995) suggested three main functions of SA: simple selection, preparation and maintenance of action. Thus, SA is suggested to be an active mechanism which allows us to choose an appropriate behaviour by weighting the relevance of inputs in several different situations. In the 1980s, an increasing number of studies investigated SA effects in different sensory modalities and various theories on auditory and visual

| Theory | Basic idea | Key literature |
|---|---|---|
| **Experiment 1** — Attentional ressources approach | Attentional resources are limited. For this reason, selection mechanisms are necessary. | Broadbent, 1958 and 1971; Kahneman 1976 |
| **Experiment 2** — Feature Integration Theory | Attention to a stimulus is necessary in order to synthesize its features into a coherent pattern. | Treisman and Gelade, 1988; Treisman (1998) |
| **Experiment 5** — *What* and *where* processing in the visual and auditory modality | Anatomical differentiation between *what* and *where* pathways in the brain | Claude et al. 2001; Mishkin et al, 1983; Romanski et al, 1999; Ungerleider and Mishkin 1982 |
| **Experiment 6** — Crossmodal integration in the human brain | Investigating factors of multisensory integration, like selective attention | Calvert 2001; Eimer and Schröger 1998; Giard and Peronnet 1999 |

Figure 2.2: Relevant theories for the four experiments of the present work. Notice that the theoretical background of Experiment 1 is described in section 2.1.1.

attention were developed (including those which are important for the present work). Fig 2.2 summarizes the relevant attention models for the experiments in the present work.

A prominent theory of visual attention which is important for Experiment 2 is the *Feature Integration Theory* of Treisman and colleagues (Kahneman and Treisman, 1984; Treisman and Gelade, 1980; Treisman, 1998). Treisman suggested that spatial attention is necessary for feature binding processes. In a later Section (6.1) this will be called the *attention-first model*. The *binding problem* deals with the question of how we combine different features of an object into one single coherent object. The *Feature Integration Theory* assumes that the visual system codes one object at a time at an early level of information processing where the receptive fields are small. The

object is thereby selected on the basis of its location. In visual search for example, it is proposed that homogeneous groups of items can be processed in parallel (Treisman, 1982). Treisman (1998) suggests that these parallel stages of vision are related to later attentional stages. Visual inputs are thereby coded in a so-called *master map* which includes information about the location of regions, whereas information about the features (e.g. color, depth and motion) are represented in a separate set of *feature maps*. It is hypothesized that the locating and binding of features requires retrieval of their connections to the master map. An attention window thereby moves serially within the master map and selects the features which are currently linked to the attended location. Thus, the *Feature Integration Theory* assumes that attention helps to bind together the individual features of an object. In addition, there is a second, *alternative*, model which suggests that binding processes themself can evoke an automatic shift of visual attention. This model will be called the *binding-first model*. Evidence for this model came from visual search tasks where an illusory target stimulus had to be detected among distractor stimuli (for example a Kanizsa figure which requires visual binding, Fig. 2.3b). It has been shown  that the detection time of a Kanizsa



a)                                                          b)
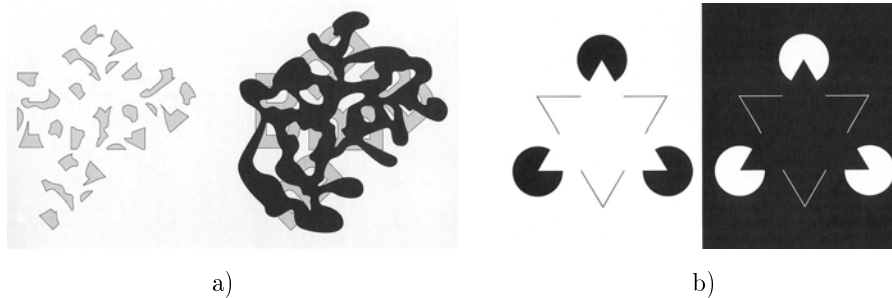
Figure 2.3: Examples for figures which require binding processes. a) Hidden objects (Bs),  b) Illusory Kanizsa Triangles (Adapted from Nieder, 2002, p. 212)

figure increases only slightly with increasing number of items in a visual search array (less than 10 ms per item; Davis and Driver, 1994). This has been interpreted as evidence for an automatic pop out of Kanizsa figures among distractor stimuli, which is likely to be the result of an early binding process. In the present work, the temporal order of feature binding and attention has been investigated a visual cueing paradigm where illusory Kanizsa figures among distractor stimuli were used as stimulus material (Experiment 2). In this experiment, EEG waves were measured and analyzed with respect to oscillatory gamma-band activity and ERPs. Particularly GBRs have been

closely related to attention and binding (Gray, 1999; Engel et al., 2001). For this reason, the analysis of gamma activity was of special interest.
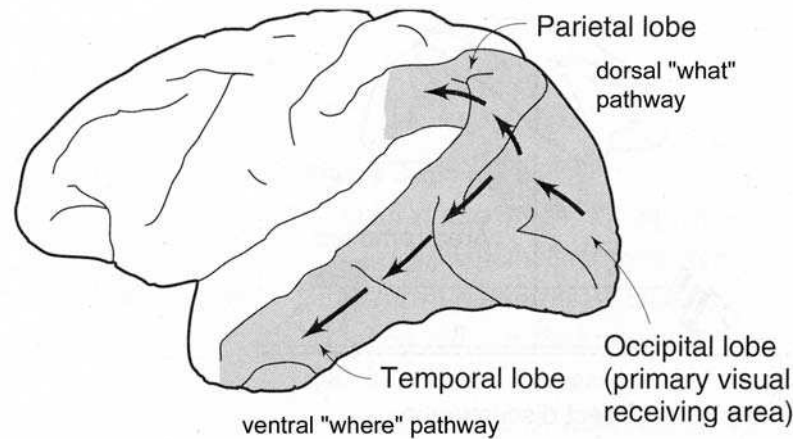


Figure 2.4: Schematic illustration of the visual *what* and *where* model by Ungerleider and Mishkin, 1982. (Source: Goldstein, 1996, p. 105)

One approach which is theoretically relevant for Experiment 3 is the visual *what* and *where* processing model by Ungerleider, Mishkin and colleagues (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994). This model assumes that visual processing can be functionally separated into a ventral *what* and a dorsal *where* pathway (Fig. 2.4). First evidence for an anatomical differentiation between *what* and *where* processing in the visual modality came from animal studies (Ungerleider and Mishkin, 1982; Mishkin et al., 1983). Ungerleider, Mishkin and colleagues set local lesions in the posterior parietal lobe and the inferior temporal lobe of monkeys and investigated the effects of the lesions in two different tasks. The first task was an object discrimination task where an object was presented in a first step. After a delay period, the same object was presented together with an unknown object. Monkeys were rewarded when they chose the unknown object (non-matching-to-sample-task). The second task was an object location task where monkeys had to choose the one out of two food boxes which was located closer to a cylinder. Ungerleider and Mishkin (1982) showed that monkeys with a lesion at the inferior temporal lobe had no problems in performing the object discrimination task. However, the same monkeys had trouble in the object location task. In contrast, monkeys with lesion in the posterior parietal lobe had no problems in performing the object location task, but failed in the object discrimination task. These results indicate an anatomical differentiation between a ventral *what* and a dorsal *where*

pathway in the visual system. The assumption of an anatomical differentiation between *what* and *where* processing has been supported in several subsequent monkey and human studies (for an overview see Ungerleider, 1994). Interestingly, recent animal and human fMRI studies have indicated that an anatomical distinction between *what* and *where* processing also exists in the auditory modality (Tian et al., 2001; Maeder et al., 2001; Romanski and Goldman-Rakic, 2001). In Experiment 3 of the present work possible differences between feature object and feature location processing in the auditory cortex were investigated (Chapter 7). By using magnetoencephalography (MEG) and 3-D head models which were reconstructed from individual MRI data, the location and strength of dipole sources in the auditory cortex were investigated in an object location task and an object feature discrimination task.

Experiments 1 to 3 of the present work investigated SA effects either in the visual or in the auditory modality. Experiment 4, examined SA effects in crossmodal audiovisual processing. Recent EEG studies reported different relationships between SA and audiovisual integration (Berti and Schröger, 2001; Eimer and Schröger, 1998; Eimer and van Velzen, 2002; Giard and Peronnet, 1999). Calvert (2001) reviewed several fMRI, EEG and MEG studies and suggested that a widespread network of brain areas including the superior temporal sulcus, the insular cortex, the claustrum and regions of the frontal brain are involved in crossmodal processing (Fig. 2.5). However, it is not clear when and where very early attention effects on crossmodal processing occur in the brain. First evidence came from ERP studies which showed that attention can affect very early audiovisual processing (Giard and Peronnet, 1999; Molholm et al., 2002). However, these findings have been recently criticized by Teder-Sälejärvi et al. (2002), who showed that the reported very early ERP effects might be caused by a methodological artifact. The goal of Experiment 4 was to investigate very early spatial attention effects on oscillatory GBRs and ERPs in audiovisual processing. So far, early SA effects on audiovisual GBRs have not been investigated before. Of special interest was the question when and where any such effects may occur.

### 2.1.3   Early and late selective attention

The question whether SA affects early or late stages of information processing is directly related to the present work. Since the EEG and MEG allow a measurement of activity with a time resolution of a few milliseconds, it was of particular interest to investigate when and where the earliest attention effects may occur. In the literature, some theories suggest that attention acts at very early stages of information processing, while others assume that it acts at later stages (for an overview see Pashler, 1998,
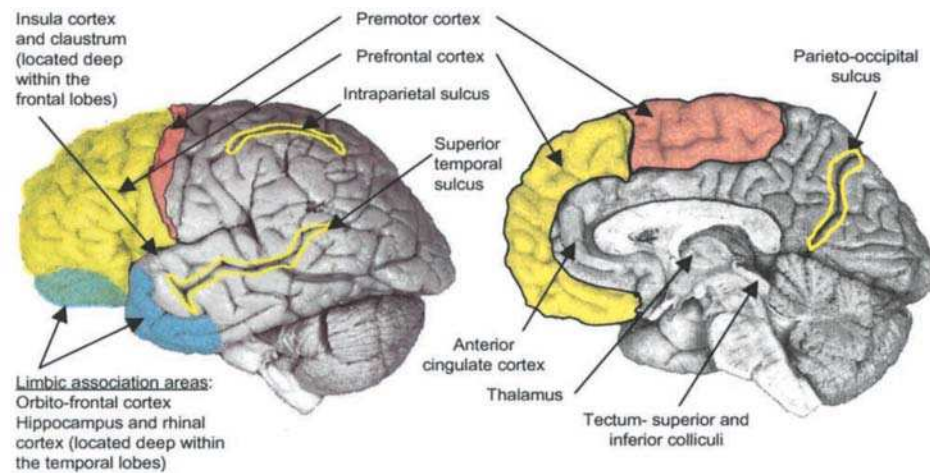
Figure 2.5: Several brain structures have been consistently found to be involved in crossmodal processes, indicating the existence of a widespread multisensory network. Lateral (left) and medial (right) view. (Source: Calvert, 2001, p. 1112)

Chapter 5). Fig. 2.6 shows schematically two contrasting models of SA. The *attenuation theory* by Treisman (1960, 1964) suggests that irrelevant sensory inputs are filtered out at a perceptual level, before the analysis of verbal content. This idea is comparable with Broadbents filter theory (Section 2.1.1). In contrast, the late selection theory by Deutsch and Deutsch (1963) suggests that the perceptual analysis of sensory inputs operates without capacity limitations and without voluntary control. This information is then selected by a response filter before selection and reorganisation processes prepare a response. The model assumes that even when a subject tries to ignore a stimulus, for example in a filtering task, all stimuli are automatically analyzed on verbal content. The *Stroop effect*, where subjects had to name the letter color of a color word is such an example. Subjects usually have difficulties in naming the letter color if this color does not match with the color word. This may indicate that the stimuli were first analyzed with respect to verbal content (the color word) and the relevant information (the color of the letters) is selected subsequently. However, it is also possible to explain the *Stroop effect* with learning strategies and habits. Furthermore, different experiments demonstrated that Deutsch and Deutsch's theory of a late selection is not valid in various situations. Particularly the assumption that the perceptual analysis is involuntary and capacity free does not fit with empirical findings. Subjects are not able to process an unlimited number of inputs at a time. This has been shown for example in divided attention tasks. However, there is a large body of evidence showing that SA
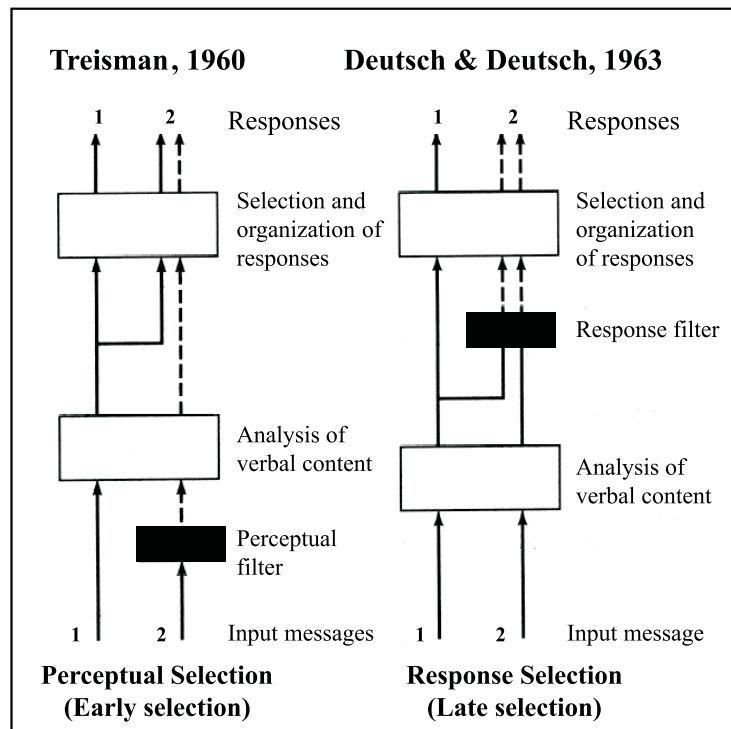
Figure 2.6: Schematic illustration of the early selective attention model by Treisman, 1960, and the late selective attention model by Deutsch and Deutsch, 1963. (After Treisman, 1967)

affects later stages of information processing (Treisman, 1998; Driver et al., 2001). Late SA mechanisms are often labelled as top-down processes (in contrast to early stimulus driven SA mechanisms which are labelled as bottom-up processes). An interesting question thereby is how bottom-up and top-down modulated processes interact with each other. On the neurophysiological level, this question can be best answered by using methods with high temporal resolutions like the EEG or MEG in humans or single cell recoding in monkeys. The use of these methods allows an insight investigation of the physiological nature of attentional bottom-up and top-down processes (Desimone, 1999; Fries et al., 2001; Hillyard et al., 1999).

Modern theories on bottom-up and top-down processes in the visual cortex suggest complex feedforward-feedback mechanisms between higher and lower cortical areas. Fig. 2.7 shows the integrated model of visual processing by Bullier (2001a,b). This model assumes that some neurons in higher order areas in the temporal and parietal

lobe can be activated very rapidly by lower order areas of the visual cortex. For ex-
ample, feedforward connections from area V1 to MT have been reported to conduct
information in nearly the same time as connections between V1 into V2 (Movshon and
Newsome, 1996). In addition, there are also fast backward connections from area MT
to V1 and V2, which are fast enough to allow a feedback modulation in a time range
of a few milliseconds (Girard et al., 2001). Bullier (2001b) suggests that visual areas
V1 and V2 may act as 'active black-board' for higher order areas. The assumption of
an important fast feedback mechanism in visual processing differs from the classical
view which suggests that the visual system is structured as a pure feedforward model.
The classical feedforward model proposes that visual areas V1 and V2 first perform
local computations of a visual scene whereas higher order areas compute a more global
3D representation (van Essen and Maunsell, 1983). However, a pure feedforward model
can hardly explain how the visual system identifies objects or human figures in a noisy
and cluttered scene, a task which is easy for the visual system (Mumford, 1994). In
contrast, a feedback mechanism from higher order areas sharpening the information
which is processed in V1 and V2 could explain how the visual system identifies objects
in a noisy scene. The integrated model of visual processing could also explain how SA
affects processing in primary visual cortex. EEG studies consistently reported that SA
does not modulate very early visual processing in the ERP, namely the C1 compo-
nent which was suggested to be generated in striate visual cortex (Butler et al., 1987).
However, recent fMRI and monkey studies reported SA effects in the primary visual
cortex (Di Russo et al., 2003; Luck et al., 1997; Tong, 2003). The integrative model
of visual processing would suggest that SA influences the later processing in primary
visual cortex by cortical feedback mechanisms (Bullier, 2001b).

## 2.2 Electrophysiological and electromagnetic correlates of selective attention

### 2.2.1 Event-related potentials

Different components in the ERP have been associated with SA in specific ways (Hill-
yard et al., 1973; Mangun and Buck, 1998; Schröger et al., 2000). This indicates that
the investigation of ERPs may allow a precise measurement of successive attentional
mechanisms. Fig. 2.8 shows an early attention effect on visual ERPs. In the respec-
tive task, subjects were instructed to detect occasional targets at an attended side
(left or right) and ignore stimuli from the unattended side. ERP responses are plotted
for physically identical stimuli which were attended or unattended. The figure shows
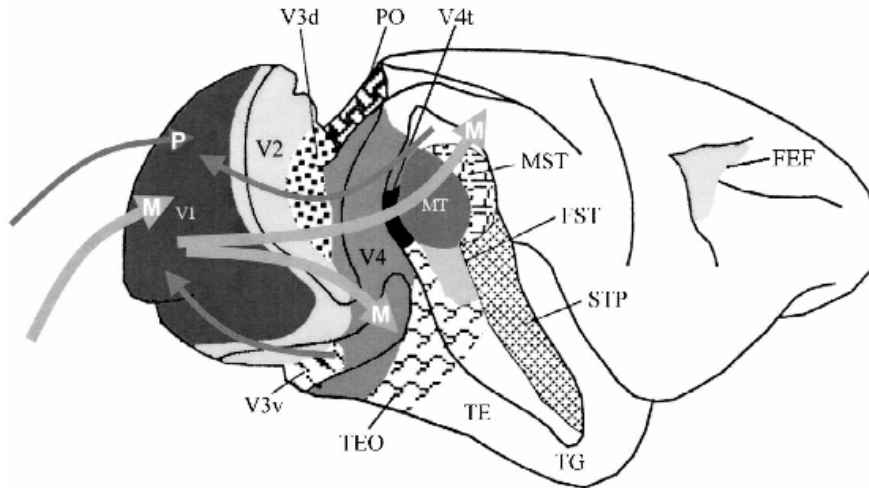
Figure 2.7: Schematic illustration of the integrated model of visual processing by Bullier. The large $M$ arrow on the left represent activity which is transfered through magnocellular neurons of the thalamus to the visual cortex. This activity is rapidly transfered to the temporal and parietal cortex. Fast feedback connections from the temporal and parietal cortex (narrower arrows pointing to V1) allow the system to regulate further processing in the visual areas, for example, later incoming inputs from parvocellular (P) neurons of the thalamus (narrow $P$ arrow on the left). (Source Bullier, 2001, p. 100)

enhanced positive P1 and more negative N1 amplitudes for attended as compared to unattended stimuli, indicating that both components are affected by SA. Early attention effects on ERPs have been consistently found in different paradigms like color detection (Anllo-Vento et al., 1998), spatial priming (Luck et al., 1994; Mangun and Hillyard, 1991), visual discrimination (Vogel and Luck, 2000; Ritter et al., 1988), and visual spatial attention (Mangun et al., 1998). For example, spatial attention effects on P1 amplitudes have been related to activations in extrastriate visual areas of the occipital lobe (Heinze et al., 1994; Martinez et al., 1999). Woldorff et al. (1997) suggested that sustained visual spatial attention results in a preset top-down biasing of early sensory input channels. This biasing leads to an amplifying of attended information (as expressed in enhanced P1 amplitudes). Attention effects on early P1 amplitudes have been primarily found in visual spatial paradigms. In the present work, the question whether early P1 amplitudes may also indicate an automatic shift of spatial attention in a visual cueing paradigm was investigated in Experiment 2.

Visual spatial attention effects have also been observed for the N1 component (Heinze et al., 1990; Yamaguchi et al., 1995). A study by Luck et al. (1990) yielded
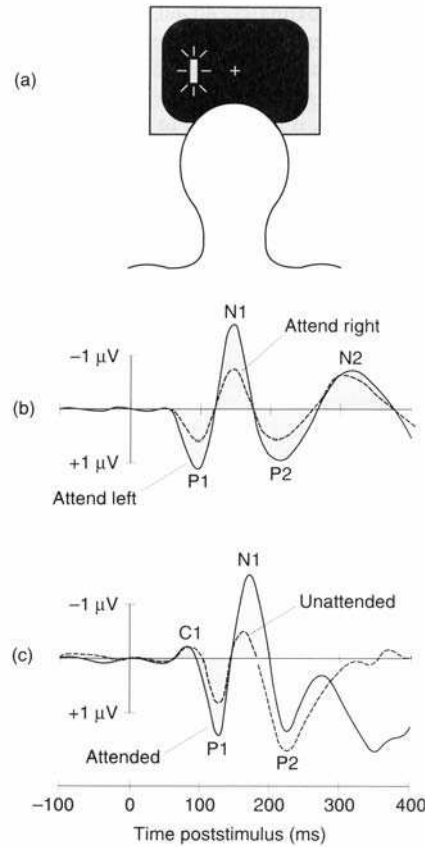
Figure 2.8: Typical ERP waveform for standard stimuli in a visual spatial attention experiment. (a) Subjects had to attend to a designated side and detect occasional targets in a stream of bars on that side (e.g. slightly smaller bars). (b) Idealized responses to a standard bar. Higher P1, N1 and P2 amplitudes were elicited by attended (solid line) as compared to unattended stimuli (stimuli which occur at the unattended side, dashed line). (c) Results from a study of Gomez Gonzales et al., 1994. Selective attention modulates P1, N1 and P2 amplitudes, but not the early C1 component (Source: Luck, 1998, p. 273).

enhanced posterior P1 and N1 components in response to attended as compared to unattended unilateral stimuli. However, the attention effect on N1 amplitudes was reduced when a preceding stimulus contained elements in the attended field. Interestingly, this was not the case for the amplitudes of the P1 component. Therefore, Luck et al. (1990) suggested that the P1 and N1 components may reflect different mechanisms of spatial attention. Luck, Hillyard and colleagues found more evidence for a functional

dissociation of the P1 and N1 components in subsequent studies (Hillyard et al., 1998; Luck and Hillyard, 1995). In a visual cueing paradigm, Luck et al. (1994) reported that valid and neutral cue trials evoke higher P1 amplitudes as compared to invalid cue trials. In contrast, N1 amplitudes were enhanced for valid as compared to invalid or neutral cue trials. Thus, Luck and Hillyard suggested that the reduced P1 amplitudes may reflect a suppression of unattended inputs, whereas the enhanced N1 amplitudes may reflect an amplification of attended inputs (Hillyard et al., 1998). SA effects on N1 amplitudes have also been found in other attention paradigms (Anllo-Vento et al., 1998; Hopf et al., 2002). A study by Vogel and Luck (2000) showed enhanced N1 amplitudes in visual choice reaction tasks as compared to a simple reaction task for the same stimuli. Thus, the N1 amplitude may also indicate a discrimination processes. In the present work, SA effects on N1 amplitudes were investigated in Experiments 1 to 3. Furthermore, SA effects on a later negative N2b component were analyzed in Experiments 1 and 2. The N2b has a latency of about 240-280ms and an amplitude maximum over the vertex. In the context of attentional paradigms, N2b amplitudes have been related to different processes like the discrimination of shape, orientation and color (Smid et al., 1999; van der Veen et al., 2000). Thus, N2b amplitudes possibly reflect a feature non-specific selection process. In addition, it has been suggested that N2b amplitudes may also indicate an attentional orienting (Wijers et al., 1989a).

As well as for the visual modality, SA effects on ERPs have been found in the auditory modality. Possible differences between early object and location processing for the auditory evoked N1m component were investigated in Experiment 3 of the present work. The main sources of the auditory N1 component have been located in the supratemporal plane, including the auditory cortex (Gallinat and Hegerl, 1994; Pantev et al., 1995b; Reite et al., 1994; Senkowski et al., 2003a). Näätänen and Picton (1987) gave an overview about the auditory N1 component in a famous review article. More recent experiments revealed further information about SA effects on the auditory N1 component (Arthur et al., 1991; Berti et al., 2000; Talsma and Kok, 2001). Since recent animal studies indicated that object and location information are likely to be processed in different areas of the auditory cortex (Romanski et al., 1999; Tian et al., 2001), it was expected to find such anatomical differences also for the auditory N1m component in the present work.

Another component which has been consistently related to attentional processes is the P3 (Herrmann and Knight, 2001). Amplitudes of the P3 have been associated with attentional processing in target detection (Comerchero and Polich, 1999; Katayama and Polich, 1999). Target effects on P3 amplitudes (enhanced amplitudes) have been
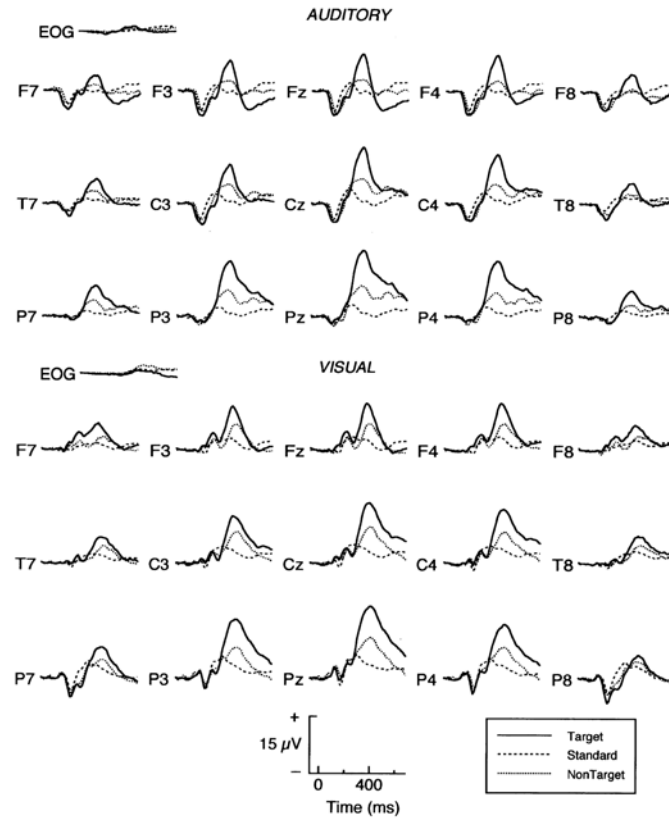
Figure 2.9: Grand average ERP data from an auditory (upper) and a visual (lower) 3
stimulus paradigm for different stimulus types (target, standard, non-target). Target
stimuli evoke a classical P3 amplitude in both modalities after about 300-500 ms. Note
that positive amplitudes are plotted upwards (Source: Katayama and Polich, 1999, p.
465).

found for ERPs in different sensory modalities like visual (Herrmann et al., 1999), au-
ditory (Polich, 1987), somatosensory (Bruyant et al., 1993), and even olfactory evoked
potentials (Pause et al., 1996). Fig. 2.9 shows P3 amplitudes from an auditory and
a visual 3 stimulus paradigm (Katayama and Polich, 1999). Event-related potentials
are plotted in response to target stimuli (target probability 10%), standard stimuli
(probability 80%) and non-target control stimuli (probability 10%). Subjects were in-
structed to press a button when a target stimuli occurs. Katayama and Polich (1999)
reported higher P3 amplitudes in response to targets as compared to standard and non-
target control stimuli in both modalities, indicating a positive relationship between P3

amplitudes and target processing (Fig. 2.9). In general, the P3 component has been in-
terpreted as a correlate of context updating or context closure within working memory
(Donchin, 1981; Donchin and Coles, 1988). While earlier ERP components (e.g. P1 and
N1 amplitudes) are mainly generated in the respective sensory corticies, the sources of
the P3 component seem to be widely distributed over different brain regions (He et al.,
2001). Interestingly, the scalp topography of the P3 is comparable for different modal-
ities, suggesting a more general cognitive mechanism underlying the P3 component.
The target P3 usually showed a maximum over posterior scalp regions which indicates
a crucial involvement of parietal cortex areas in target detection (for a review about
the P3 see Herrmann and Knight, 2001). Target P3 amplitudes were investigated in
Experiment 1 of the present work.

## 2.2.2   Gamma-band responses

As well as ERPs, oscillatory responses in the gamma-band have been associated with SA
processes (Herrmann and Knight, 2001). Furthermore, GBRs show a close relationship
with feature binding processes (Gray and Singer, 1989). This indicates a direct link
between binding, attention and gamma activity. For this reason, the analysis of GBRs
was of special interest in the present work. In Experiments 2 and 4, attention effects
on oscillatory GBRs were investigated with relation to feature binding and binding in
crossmodal integration, respectively. Furthermore, the effects of attentional resources
on gamma activity were investigated in a visual discrimination task (Experiment 1).
Important findings in the context of oscillatory GBRs, feature binding and SA are
discussed now.

Early studies on GBRs first showed a relationship between GBRs and feature bind-
ing (for a review see Gray, 1999 and Singer, 1999). Linking together the different fea-
tures of a single object is one of the most important functions of binding. The features
can thereby be processed in different brain regions (or modules). For example, when
a subject perceives a moving green ball, the color of the ball is mainly processed in
area V4, whereas the motion of the ball is mainly processed in area MT (V5). Each
submodule contains the complete information about the respective feature. The ques-
tion is how do these different features become a coherent representation of a single
object? This question has been called the *binding problem* (see also Section 2.1.2). In
the 1980s, von der Malsburg and colleagues presented a model which tries to explain
how binding mechanisms can be coded on the neuronal level (von der Malsburg, 1986).
This model assumes a time-based coding mechanism. The main idea is that neurons
which belong to the same neuronal assembly are bound together by synchronized ac-
tion potential firing (Fig. 2.10). The relative timing of the synchronized assembly also

allows that different functional networks can be active in parallel. Slight differences
in timing can distinguish the function of even neighbouring neurons. Such a fast and
flexible mechanism would allow a huge number of feature combinations. Simultaneous
neuronal activity on the single cell level may also correspond to synchronous activity
of associated networks at the level of field potentials and EEG. First evidence for a
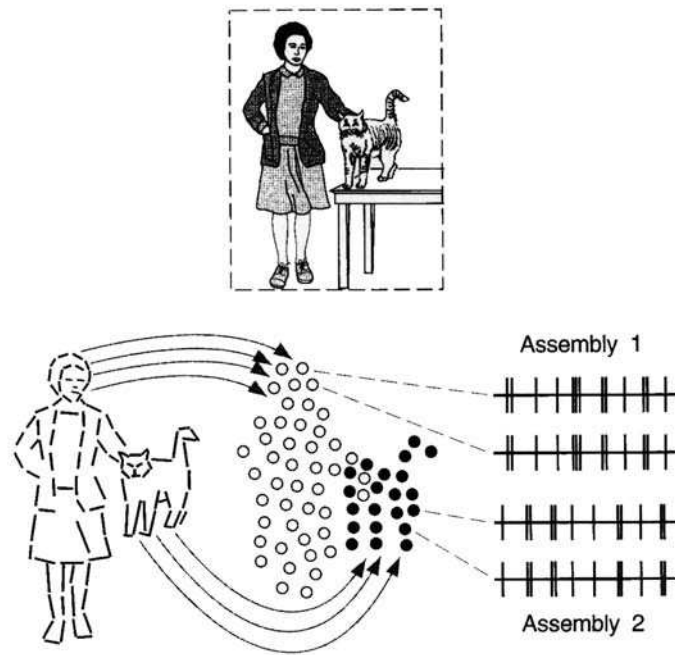


Figure 2.10: The temporal binding model assumes that neuronal assemblies of syn-
chronously firing neurons code different features of a single object (lower right). The
woman in the upper picture, for example is represented in one assembly, while the cat
is represented by a second assembly (lower panel). Thereby, neurons from the same
assembly are suggested to fire in synchrony. (Source: Engel et al., 1999, p. 131)

relationship between oscillatory GBRs and binding processes came from intracranial
recordings in the visual cortex of anesthized cats. Gray, Singer and colleagues reported
that coherent movements of two bars evoke a synchronized activity of neurons in sep-
arate columns (Gray and Singer, 1989; Gray et al., 1989). In contrast, the same bars
which do not move coherently did not evoke such synchronization. Müller et al. (1996)
investigated the same paradigm in a human EEG experiment. The authors reported an
increase of induced GBRs for coherent moving bars. Because the EEG picks up activity
from a large number of neurons, this result indicates that the coherently moving bars

cause a synchronization of gamma responses of a whole assembly of neurons. Interestingly, less synchronization was found for incoherently moving bars. Synchronization of neuronal responses in the visual cortex have also been found within and between striate and extrastriate cortex (Engel et al., 1991; Friedman-Hill et al., 2000) and between the two hemispheres of the primary visual cortex observed synchronization of visual (König et al., 1995). Castelo-Branco et al. (1998) responses between the cortex, the lateral
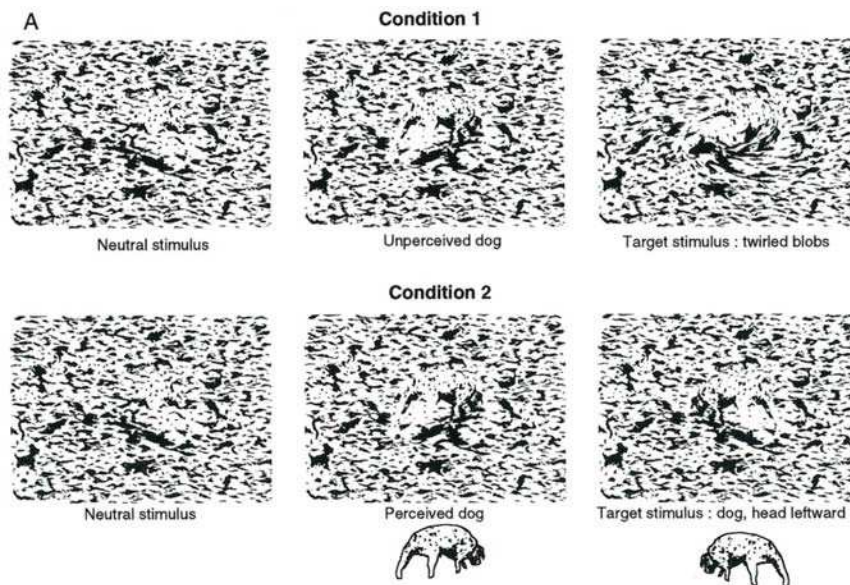


Figure 2.11: The figure shows two experimental conditions. In the first condition (top panel), subjects had to count the number of twirled blob stimuli (top right) among a continuous stream of neutral stimuli (top left) and stimuli containing unperceived dogs (top middle). In a second condition (bottom row), subjects were instructed to count the number of stimuli showing a dog which with a head leftward (bottom right). In this block the dogs with a head rightward (bottom middle) were perceived. For the perceived dog with the head rightward in the second condition (bottom middle), induced EEG gamma activity was found. However, for the same stimulus (top middle) no gamma activity was observed in the first condition. This finding indicates a relationship between object representation and gamma activity (Source: Tallon-Baudry et al., 1999, p.157)

geniculate nucleus (LGN) and the retina in cats. The authors found evidence for two independent mechanisms which seem to interact with each other. The first mechanism is a transient feedforward synchronization to high-frequency retinal oscillations (range 60-120 Hz). The second mechanism induces more sustained synchronization and operates at a lower frequency range (30-60 Hz). This mechanism was suggested to group

neuronal responses that are represented at the cortical level according to their fea-
tures. Findings like these indicate a close relationship between oscillatory GBRs and
object representation (Fig. 2.11). Such a relationship has been found also for humans
(Bertrand and Tallon-Baudry, 2000; Tallon-Baudry et al., 1997).

Oscillatory GBRs have also been related to target detection in object processing
(Herrmann et al., 1999; Herrmann and Mecklinger, 2001) and to target detection in
spatial processing (Fries et al., 2001; Tiitinen et al., 1993). Herrmann and Mecklinger
(2001) suggested that gamma activity is associated with a comparison process of work-
ing memory contents to the perceived stimuli. Thus, a perceived stimulus which matches
the memory templates (for example a relevant target stimulus) leads to a reinforcement
of gamma activity. This model assumes an amplification of task relevant signals. Sim-
ilarly, Fries et al. (2001) reported an enhanced synchronized gamma activity in visual
area V4 for behaviorally relevant stimuli. The Fries et al. study furthermore demon-
strated that oscillatory GBRs can occur at higher cortical regions. The lack of findings
which reported gamma activity in higher order regions on the single cell level has been
previously critizised by Shadlen and Movshon (1999). SA effects on gamma activity
have been primarily reported for top-down processes (Engel et al., 2001). However,
Elliott and Müller (1998) reported that stimuli which were presented with a rate of
about 40 Hz facilitate visual binding processes. This result may indicate a preattentive
coding of visual objects which can capture attention.

# Chapter 3

# Methodological background

The electroencephalogram (EEG) and the magnetoencephalogram (MEG) allow a measurement of brain activity in a time range of a few milliseconds and are therefore appropriate methods to investigate the temporal dynamics of attentional processes. The present chapter will give an introduction to the methods of the EEG (Section 3.1) and MEG (Section 3.2). A frequently used way to analyse EEG and MEG data is averaging the activities of the same stimuli. The result of this averaging process is called the event-related potential. Details about the averaging technique are described in Section 3.3. Finally, the wavelet transformation, a relatively new approach in the analysis of EEG and MEG data, will be described (Section 3.4).

## 3.1 Electroencephalography (EEG)

### 3.1.1 A brief history of the EEG

Electrical brain wave activity was first described by the English physician Richard Caton in 1875 (Brazier, 1957). Caton presented visual stimuli while recording from electrodes which were placed directly on the cortex surface of rabbits and monkeys. He described that visual stimulation evokes a change of electrical activity in the occipital cortex. Furthermore, Caton noticed that weak oscillations occurred in his recording while he did not present any stimuli. However, at that time, Caton's observations did not receive much attention. Twenty-seven years later, Hans Berger began his work on brain waves with dogs in Jena. In 1920, Berger began to record electrical brain waves from the human EEG (Fig. 3.1). His goal was to detect the same waves in humans that could be obtained in animals. By using a Galvanometer, Berger successfully recorded the EEG from a young male subject in 1924. Finally, in 1929, Berger published his findings on human EEG activity in his famous paper 'Über das Elektroenkephalogramm

*des Menschen I'* (*'On the Electroencephalogram of Man'*). In this paper he identified two basic patterns of brain waves. The first pattern consists of relative large and regular waves which occur with a frequency of about 10 to 11 Hz. Berger termed these waves alpha waves. The second pattern of activity was faster, with a frequency of about 20 to 30 Hz, and smaller than the alpha waves. Following the Greek alphabet, Berger termed these frequencies beta waves. Later, investigators identified further frequencies-ranges
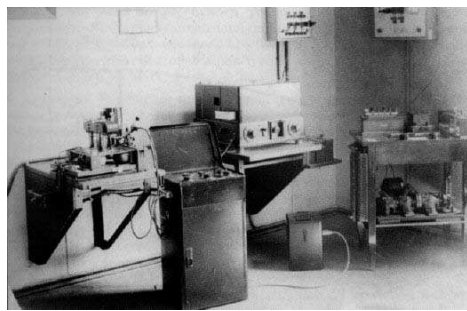


Hans Berger                    Berger's system for EEG recordings, 1926

Figure 3.1: The German psychiatrist Hans Berger was the first person who recorded EEG waves from the human scalp surface. (source: http://chem.ch.huji.ac.il/~eugeniik/history/berger.html)

which have been functionally related to different cognitive processes. The following list gives a brief overview of the most prominent frequency ranges of oscillatory activity and their presumed functions:

- $\delta$  < 4 Hz: These waves are characterized by high amplitudes and low frequencies. The person who gave delta waves their name was the neurophysiologist Grey Walter (1936). Delta waves have been related to cognitive functions like signal detection and decision making (Başar et al., 2001a). Furthermore, it has been shown that delta waves play a crucial role in specific sleep stages (particularly during non-Rapid Eye Movement sleep).

- $\theta$  4-7 Hz: It was Grey Walter (1953) again who gave theta waves their name. Experimental data suggest that theta activities are, for example, related to associative and search processes in working memory (Bösel, 1993; Demiralp and Başar, 1992). Such processes require cortico-hippocampal feedback loops. It has been demonstrated that such loops are activated in the theta frequency range during memory processes (Tesche and Karhu, 2000), indicating that theta activity is closely related to working memory processes.

- $\alpha$ 8-12 Hz: After his first EEG observations in humans, Berger suggested that frequencies in the alpha-band constitute the basic rhythm in the EEG. For example, alpha waves can be observed when subjects do not perform a task and have their eyes closed. Interestingly, as soon as subjects open their eyes, alpha activity disappears and is replaced by activities in different frequencies (as for example the faster beta activity). The replacement of the alpha rhythm is also called *alpha block* and is probably caused by a desynchronization of synchronized alpha-band activity. Thus, alpha activity might represent the resting state of the brain. However, it has been suggested that alpha activity can be functionally distinguished in an upper and a lower alpha (Bösel et al., 1990). The upper alpha activity (at about 10.5-12 Hz) primarily occurs at relaxed mental states when no task has to be performed. A desynchronization of this alpha activity may indicate a focusing of attention on specific aspects of a task (Klimesch et al., 1998). Lower alpha waves with a frequency of about 8-10.5, however, have been related to processes like concept learning, working memory and long-term memory. Of particular importance in memory processes seems to be the interplay between the lower alpha desynchronization and the synchronization of theta activity (for a review see Klimesch, 1999).

- $\beta$ 12-30 Hz: Low-amplitude activities in the frequency range of the beta-band were, for example, found in sensorymotor areas after somatosensory stimulation and after voluntary movement (Neuper and Pfurtscheller, 2001). Interestingly, it has been demonstrated that beta activity has also been related to attentional processing (Gomez et al., 1998; Wrobel et al., 1994). Bekisz and Wrobel (1999) observed a coupling of beta and gamma activity in the cortico-thalamic system of cats during the processing of attended visual stimuli. This may indicate that these frequencies are closely related to attentional processes.

- $\gamma$ 30-80 Hz: Gamma activity was analyzed in three experiments of the present work. As described before (Section 2.2.2), gamma-band activity has been associated with binding processes and attention. According to Başar-Eroglu et al. (1996), the research on gamma activity can be divided in the following four phases: The first phase was initiated by Adrian (1942) who observed oscillatory gamma activity (30-60 Hz) in hedgehogs after olfactory stimulation. In the next phase (between 1960-1980) more evidence for a close relation between sensory processing and oscillatory responses in the gamma-band was found. Furthermore, first studies showed a relationship between gamma activity and sensory processing in human (Başar et al., 1976). The third phase started with a publication by

Galambos et al. (1981). This publication was the beginning of a series of different works which investigated gamma activity in humans. The fourth and so far last phase of gamma-activity research started with the investigation of oscillatory gamma activity on the single cell level (Gray and Singer, 1989; Gray et al., 1989).

### 3.1.2   Measurement of the EEG

Electrical activity, as measured by the EEG is caused by a summation of various electrical processes in the brain (for an overview see Başar, 1998, Chapter 2). In particular, the EEG seems to pick up activity which is caused by dendritic inhibitory (IPSP) and post-synaptic excitatory (EPSP) potentials. EEG waves are not generated by the activity of single neurons or synapses. Instead, it has been suggested that the EEG measures the activity of a large number of synchronously active synapses (about 1 million). For the recording of electrical activity with the EEG, variable potential differences between two electrodes are recorded. In monopolar recordings, as used in the studies of the present work, the active electrode is placed on the scalp, whereas a second reference electrode is attached to an electrically inactive tissue. This means that only very few electrical brain activities should be measured by this electrode. Usually there are several active electrodes which record the electrical brain activity over different scalp regions. All active electrodes are normally referenced to the same reference electrode(s). For the measurement of EEG, electrodes are often placed according to the international standardized 10-20 system (Fig. 3.2). The original 10-20 system contains 21 electrodes which are placed at specific relative distances (10% or 20% steps) to standard points on the scalp. The standard points are usually the nasion, the inion and the preauricular points. To get more information about the spatial topography of EEG activities, additional electrodes are often used in cognitive experiments as suggested by the American EEG Society (1991). In the present work, a total number of up to 64 EEG channels was used.

## 3.2   Magnetoencephalography (MEG)

Each flow of electrical activity, including electrical brain activity, evokes a weak electromagnetic field. The strength of this field is measured in Tesla (T). Compared to the magnetic field fluctuation of the environment ($\sim 10^{-4}$ Tesla), evoked field activity of the brain shows a much smaller strengths ($\sim 10^{-15}$ Tesla). For this reason, elaborate instruments and procedures are necessary to screen out the interference of the fluctuations in the surrounding environment (Fig. 3.3). One method which allows the measurement
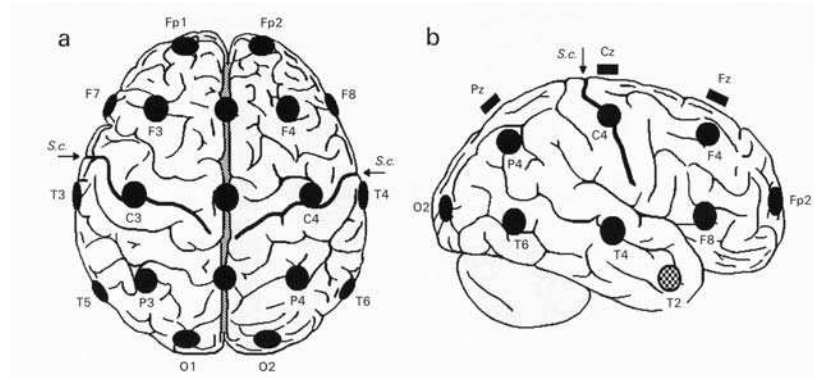
Figure 3.2: Topography of electrodes with relation to underlying brain structures according to the international EEG 10-20 system (Jasper, 1958). a) Top view. b) lateral view. (source: Zschocke, 1995, p. 60)

of the weak evoked field activity from the brain is the superconducting quantum interference device (SQUID). The magnetoencephalography (MEG), which was developed in the late 1970s, mostly uses SQUID (Näätänen et al., 1994). The MEG has some advantages as compared to the EEG, particularly in dipolar source analysis (for more information about dipole source analysis cf. Scherg, 1986 and 1990). This is caused by the following characteristics of the MEG measurement: (a) The magnetic fields are less influenced by tissue lying between the source and the magnetic sensors. For example, the skull and the skin which strongly attenuate and distract the electrical signal of the EEG do not influence the magnetic signal in such a strong manner. (b) No reference electrode is necessary for the analysis of the electrical field. (c) Usually the MEG picks up only those activities which have a tangentially orientation in relation to the scalp. Brain sources with a radial orientation are not measured by the MEG (In case of activity with complete radial orientation). This has the disadvantage that some brain sources are not measurable by the MEG. However, the advantage is that sources with a tangential orientation in relation to the scalp can be measured without overlapping activity of radial sources. For this reason, the MEG is particularly suitable for measuring tangential oriented sources. Such sources were often found in sensory cortical areas.

Of special interest for anatomical questions is the fusion of MEG and magnetic resonance tomography (MRT) data. For example, the combination of individual 3D head models, created from individual MRT images, and magnetic field potentials, measured by the MEG, allow a calculation of specific dipole sources with a spatial resolution in a range of a few millimeter and a temporal resolution in a range of milliseconds.

In the present work the fusion of MRT and MEG data was used to investigate an early anatomical separation of object and location processing in the auditory cortex (Chapter 7).



MEG recording

Figure 3.3: MEG apparatur. The MEG measures electromagnetic activity which results from the flow of electric activity. This method allows a precise measurement of brain activity in a time range of a few milliseconds.

## 3.3   Event-related potentials

The occurrence of an event[1] evokes a time locking of a specific part of electric brain activity in the EEG. This time locked activity can be calculated by averaging the EEG responses to the repeated presentation of the same event (for example 50-100 repetitions of the same event are averaged for a time window between 100 msec before to 1000 msec after event-onset). By averaging the EEG responses to the same event type, the activity which is not time locked to the event (the background EEG) is cancelled out. The resulting activity is called an event-related potential (ERP, Fig. 3.4). The event-related potential consists of different successive components which have been related to different stages in information processing (Rugg and Coles, 1995). Vaughan (1969)

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[1] An event, for example, can be a specific stimulus or also the omission of an expected stimulus.

classified ERPs as sensory ERPs, motor potentials, steady potential shifts, and long-latency potentials. Sensory ERPs are early components which are primarily related to the physical properties of a stimulus (for example visual, auditory, somatosensory and olfactory stimuli). The motor potentials are suggested to be related to voluntary movement. In contrast, the steady potential shifts contain components, for example the contingent negative variation (CNV), which can be observed during the preparation of a task (Leynes et al., 1998). Finally, long-latency responses are those components which occur at later latencies. These components have been primarily related to cognitive processing of a stimulus. An example for a long-latency response is the P300 which can be observed in target detection tasks.
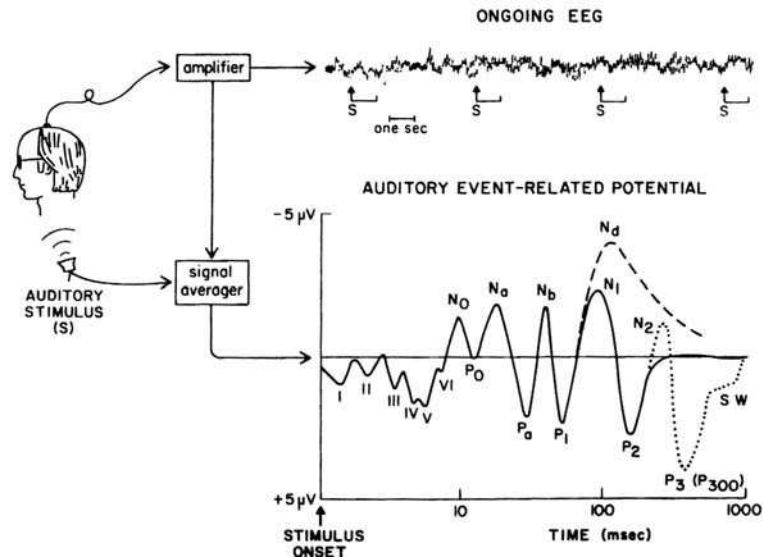


Figure 3.4: Schematic illustration of EEG recording of auditory evoked potentials. Event-related activity, which occur phase-locked to stimulus onset is often to small to be detected in the ongoing EEG (top). By averaging several trials of the same type, the non-phase locked EEG activity cancelled out and different components of the event-related potentials can be found (low). (Source: Hillyard and Kutas, 1983, p. 35)

In general, scalp-recorded ERPs represent electric fields in the brain which are related to a large number of synchronously active neurons. These fields have a certain geometric configuration in such a way that they sum up to yield a dipolar field. The dipolar fields in the brain are often called dipolar sources (Scherg and von Cramon, 1986). For those components of the ERP which are likely to be generated by only a few sources, dipole source analysis (Scherg and Picton, 1991) can reveal a good estimation of the strength and the location of these sources. However, it is necessary to specify ad-hoc

some parameters prior to the dipole source analysis (as for example the number of dipole sources). This is called the forward solution of the inverse problem. The inverse problem describes the fact that no unique dipole solution can be found for scalp-recorded data (for example, the scalp-recorded activity can always be perfectly explained when the number of sources corresponds with the number of scalp-recorded electrodes). For a more detailed description on the inverse problem and possible strategies to handle this problem see for example Scherg and Berg (1991).

## 3.4   Wavelet transformation

In recent years wavelet transformation became a popular and powerful new approach in the analysis of EEG and MEG data. Compared to classical Fast Fourier Transformation (FFT; for an introduction see Bösel, 1996), the wavelet transformation gives information about the temporal dynamics of activity in specific frequency ranges. This allows an investigation of different frequencies with relation to different stages of information processing. For the wavelet transformation of high frequency activity short time windows have to be analyzed. Wavelet transformations for higher frequencies yield a good temporal resolution, whereas the frequency discrimination is not good. However, the high temporal resolution is an advantage for the analysis of selective attentional processes. For the interpretation of the gamma activity it is important to distinguish whether the activity occurs phase-locked to a stimulus (evoked activity) or with variable phase relative to a stimulus (induced activity). For the analysis of gamma activity, a wavelet transform based on Morlet wavelets was employed. According to Galambos (1992), at least three types of gamma activity can be distinguished: *spontaneous*, *induced* and *evoked*. *Spontaneous* gamma activity is completely uncorrelated with a stimulus. This activity is probably due to neuronal processes that do not relate to the task at hand. Furthermore, *spontaneous* gamma activity usually cancels out completely when an average ERP is computed across enough trial repetitions. For this reason, this type of activity is not the focus of the gamma analysis in the present work. In contrast to the *spontaneous* gamma activity, the *induced* and *evoked* gamma activity are related to the onset of a stimulus. Thereby, *induced* activity is not phase-locked to a stimulus, whereas *evoked* activity is phase-locked to a stimulus. This is illustrated in Fig. 3.5. The sum of *induced* and *evoked* activity is called the *total* activity. The analysis of the *total* activity can give important information about the characteristics of the activity (amplitude increase vs. phase-locking, see Chapter 8). In the present work, *induced*, *evoked*, and *total* gamma activity were computed with Morlet wavelet transformation of the raw EEG signals. Morlet wavelets were calculated
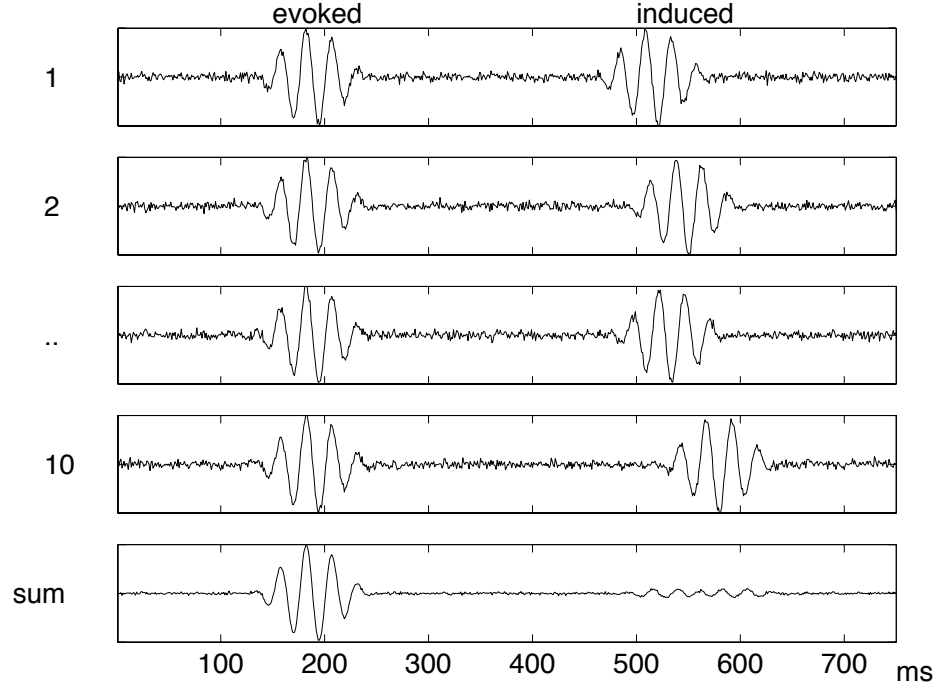
Figure 3.5: Oscillations which occur at the same latency after stimulus onset with the same phase relative to stimulus onset in multiple trials (rows 1-4) are considered evoked by the stimulus (left). This evoked activity sums up in the average (bottom row). Oscillations with latency or phase jitter relative to stimulus onset (right) are considered to be induced by the stimulus. These oscillations nearly cancel out in sum. (Source: Herrmann, 2001a, p. 471)

using the following formula:

$$\Psi(t) = e^{j\omega_0 t} \cdot e^{-t^2/2}$$

The term $e^{j\omega_0 t}$ represents a sinusoidal function which is multiplied with the envelope function $e^{-t^2/2}$. Fig. 3.6 shows that the resulting product is a wavelet.

A specific target frequency has to be defined for the wavelet analysis. To do this, the wavelet can be compressed by a scaling factor $a$. Of further interest is the calculation of the wavelet amplitude over time. This can be done by shifting the wavelet using the parameter $b$:

$$s_a(b) = \frac{1}{\sqrt{a}} \int \overline{\Psi}\left(\frac{t-b}{a}\right) \cdot x(t) \ dt$$

To scale the wavelet prior to the convolution, a scaling factor $\frac{1}{\sqrt{a}}$ is used. The term $\overline{\Psi}$

$$\Re(e^{j\omega_0 t}) \qquad\qquad e^{-t^2/2} \qquad\qquad \Re(\Psi(t))$$

a)                                        b)                                        c)
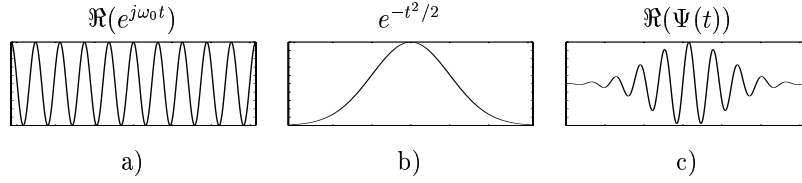
Figure 3.6: The product of the absolute part of the sinusoidal function (a) and an envelope function (b) is the wavelet (c). (Adapted from Herrmann, in press)

is the conjugate of the complex wavelet and $x(t)$ represents the original EEG signal. The result of the compressed wavelet shifting is a new signal $s_a(b)$, where the absolute values constitute the amplitude of the wavelet. The *evoked* gamma activity can now be calculated by computing the absolute values of the wavelet transformation over single trials (WTAv). In other words, the wavelet transformation is computed for the average signal, respectively the event-related potential. Therefore, the following formula is used:

$$\text{WTAv} = \left| \frac{1}{\sqrt{a}} \quad \int \overline{\Psi}\left(\frac{t-b}{a}\right) \cdot \frac{1}{n}\sum_{i=1}^{n} x_i(t) \; dt \right|$$

The term $\frac{1}{n}\sum_{i=1}^{n} x_i(t)$ represents the average of single trials which is multiplied with the wavelet. The single trial average of gamma activity contains only activity which occurs phase-locked to stimulus onset. This activity is called *evoked*. In order to compute the *total* activity which includes both phase-locked and non phase-locked gamma activity, the absolute values of the wavelet transforms of single trials are averaged (AvWT).

$$\text{AvWT} = \frac{1}{n}\sum_{i=1}^{n} \left| \frac{1}{\sqrt{a}} \quad \int \overline{\Psi}\left(\frac{t-b}{a}\right) \cdot x_i(t) \; dt \right|$$

The absolute value wavelet transforms over single trials are averaged together which is expressed by the term $\frac{1}{n}\sum_{i=1}^{n}$. The term $x_i(t)$ represents the original EEG signal of one single trial. Subtracting the *evoked* activity (phase-locked activity) from the *total* activity (phase-locked + not phase-locked) results in the *induced* activity (non-phase locked activity).

   To calculate the exact frequency of the gamma activity, time-frequency planes are calculated (see for example Fig. 5.2, p. 46). In the present work the time-frequency planes for gamma-band activity are plotted for a frequency range between 30-80 Hz. Morlet wavelet transformations are calculated for these frequencies and are plotted into one single plane for a specific time interval. Time-frequency planes allow a good estimation of possible target frequencies which are involved in the data.

## 3.5 Statistical analysis

In case of nonspherity all calculated analyses of variances (ANOVAs) in the present work were adjusted with the Greenhouse-Geisser epsilon correction for nonsphericity (Jennings and Wood, 1976). Furthermore, all ANOVAs were calculated with a two-tailed $\alpha = 5$ %.

# Chapter 4

# Outline of Experiments 1 to 4 and working hypotheses

The theoretical and methodological background of the present work was described in the previous Chapters 2 and 3. The present chapter will give a brief outline of the conducted four experiments and their respective hypotheses. Furthermore, unspecific working hypotheses will be formulated.

Four experiments constitute the empirical part of the present work (Fig 4.1). Experiment 1 investigated the relationship between the demands of attentional resources and electrophysiological responses in the EEG. The demands of attentional resources were systematically manipulated by varying the difficulty of a visual discrimination task. As an indicator of a longer stimulus processing, delayed electrophysiological responses in the ERPs and GBRs were expected for higher demands of attentional resources. In addition, it was expected to find attention modulated amplitudes for the N1, N2b and P3 component. The temporal order of attention and visual feature binding was examined in Experiments 2. It is a longstanding debate whether attention is necessary for feature binding or whether binding processes themselfs can initiate an automatic shift of attention. There are several behavioral studies which showed that feature binding can occur at early stages of information processing and that these processes may automatically capture attention (Davis and Driver, 1994, 1998). For this reason, it was expected to find evidence for the *binding-first model* also in the ERPs and gamma activity. Experiment 3 examined the influence of attentional top-down processes on early auditory processing. By combining MEG and anatomical MRI data, dipole sources of the auditory N1m component were fitted in dipole source analyses for a feature object and a feature location task. Based on previous studies in monkeys, it was assumed to find an early functional separation of feature object and feature location processing

|  | Empirical question | Hypothesis | Focus of analysis |
|---|---|---|---|
| **Experiment 1** | Investigating the relationship between electrical brain responses and attentional ressources | Higher demands of attentional ressources lead to delayed responses in the EEG. | EEG: Gamma-band responses; visual N1, N2b, and P3 amplitudes<br><br>Behavioral: RTs and error rates |
| **Experiment 2** | Feature binding and visual spatial attention in figural processing | Early feature binding in figural processing can capture spatial attention. | EEG: Gamma-band responses; visual P1, N1, N2b amplitudes<br><br>Behavioral: RTs and error rates |
| **Experiment 3** | Early anatomical separation of object and location processing in areas of the auditory cortex | Selective attention causes a functional separation of object and location processing in the auditory cortex. | MEG and MRI: Location and strength of N1m dipole sources in the auditory cortex<br><br>Behavioral: RTs and error rates |
| **Experiment 4** | Early selective attention effects on crossmodal audiovisual processing | Very early Attention effects are stronger on multisensory than on unisensory stimuli. | EEG: Gamma-band responses in auditory, visual and audiovisual processing; auditory and audiovisual P1 amplitudes<br><br>Behavioral: RTs and error rates |

Figure 4.1: Outline of the empirical questions, hypotheses, and focus of the four experiments.

in areas of the auditory cortex (Rauschecker and Tian, 1999). Finally, very early SA effects on crossmodal audiovisual processing were examined in Experiment 4. The main focus of this experiment were attention effects on oscillatory GBRs. GBRs have been closely related to feature binding and selective attention (Engel et al., 2001; Gray, 1999). Binding processes are also necessary to integrate crossmodal inputs. For this reason, it was expected to find higher attention effects on GBRs for multisensory as compared to unisensory stimuli. A more detailed description of the four experiments and the discussion of the results is given in the respective Chapters 5 to 8. Next to the

specific hypotheses for the experiments (Fig 4.1), more general hypotheses can be formulated for the present work. These hypotheses are based on previous EEG and MEG findings in attentional paradigms (Section 2.2). The following working hypotheses were investigated in the present work:

*Hypothesis I:*    Amplification of attended signals and hence an increase of their signal-to-noise ratio is expected to be a direct correlate of selective attention in ERPs (Experiment 1, 2 and 4). Furthermore, it is assumed that top-down processes can cause an early functional separation of activity sources in the auditory cortex (Experiment 3).

*Hypothesis II:*    As well as for the ERPs, it is expected to find enhanced oscillatory gamma activity as a correlate of selective attention (Experiment 1, 2 and 4).

*Hypothesis III:*    Regarding the temporal order of attention and visual feature binding, it is expected to find evidence for the *binding-first model* in behavioral data, ERPs and gamma activity (Experiment 2).

The working hypotheses will be explicitly discussed in the general discussion of the present work (Chapter 9).

# Chapter 5

# Experiment 1: Attentional resources and electrophysiological brain responses

The relationship between attentional resources and electrophysiological responses was investigated by varying the effort which is necessary to perform a task[1]. The effort was investigated by manipulating the level of task difficulty. Electrical brain responses were measured in two visual discrimination tasks (easy/hard condition) and in a passive control task. The same stimulus material was used in all three tasks. For this experiment, it is assumed that the demands of attentional resources are positively related to the difficulty of a task. Thus, a comparison of the three tasks should yield information about neuronal processes with relation to attentional resources.

## 5.1 Introduction

Oscillatory activity in the gamma-band has been related to different cognitive processes (Başar, 1999). However, the relation between gamma activity in the EEG and task difficulty has not yet been examined. Some evidence for a relation between GBRs in the EEG and task difficulty came from studies which compared GBRs for target and non-target stimuli in visual discrimination tasks. Evoked GBRs in visual discrimination tasks were found to be higher in targets than in non-targets (Herrmann et al., 1999; Herrmann and Mecklinger, 2000). Longer reaction times (RTs) and higher error rates for targets as compared to non-targets furthermore indicate that targets are more

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[1]The results of the present experiment were published in Senkowski and Herrmann (2002). The chapter contains main parts of this article. For stylistic reasons the format was adapted.

difficult to discriminate than non-targets. However, targets in previous experiments
were compared with non-targets. Therefore the increased GBRs could also have been
related to the infrequent response to the target stimulus. Further evidence for a relation
between GBRs and task difficulty resulted from memory tasks which showed that GBRs
in the EEG gamma-band are positively related to memory load (De Pascalis and Ray,
1998). So far no study has explicitly examined the relation between task difficulty in
visual discrimination processes and oscillatory GBRs.

The relation between event-related potentials and task difficulty has been inves-
tigated in various studies. Task difficulty has been mainly associated with the ERP
components N1, N2 and P3. With regard to the latency of the N1 in visual discrimi-
nation tasks this component will be refereed as N170. Ritter et al. (1982, 1988) found
an increased negative deflection in the time interval of the N170 and N2 component
in a choice-RT task as compared to simple-RT tasks. The N2 has also been associated
with discrimination processes (Breton et al., 1988; Ritter et al., 1983). Smid et al.
(1999) compared the latencies of the posterior N2 component (N2b) in an easy and a
hard color discrimination task. Latency of the N2b was delayed when color was hard
to discriminate compared with when it was easy to discriminate. The N2b, which has
its maximum over the vertex (Näätänen et al., 1978), seems to be be a marker of the
intensity of discrimination processes. Another ERP component which has been associ-
ated with discrimination tasks is the P3 (Mecklinger et al., 1998). Most studies which
investigated the visual or auditory evoked P3 found a delay of latency and a decrease of
amplitude for more difficult discrimination processes especially when comparing target-
stimuli with non-target stimuli (Polich, 1987; Palmer et al., 1994; Hoffman et al., 1985).
The P3 latency and amplitude effects were found at frontal and posterior electrode sites
(Comerchero and Polich, 1999).

In the present study ERPs and GBRs were investigated in three tasks with dif-
ferent levels of difficulty. In all tasks the identical color stimuli were used as stimulus
material. GBRs and ERPs of the same non-target stimulus were compared between all
tasks. The influences of different factors which are related to GBRs in the EEG, such
as motor responses (Crone et al., 1998) and differences in the processing of different
colors (Krüger et al., 2002) were controlled by comparing the same stimulus over all
task. Possible differences in GBRs and ERPs are therefore mainly attributable to the
difficulty of the visual discrimination task.

## 5.2  Methods

**Participants**

Fifteen subjects ($23.4 \pm 2.0$ years, 8 female) participated in the experiment. Six of the subjects had to be rejected from the analysis because their EEG data failed a criterion of at least 50 valid trials for each condition (see below). The remaining 9 subjects ($23.4 \pm 1.7$ years, 6 female) were included in the data analysis. All subjects were right-handed and had normal or corrected-to-normal vision. They showed no signs of neurological or psychiatric disorder and all gave written informed consent to participate in the study.

**Procedure**

The experiment consists of three different tasks (Fig 5.1). All tasks employed a red circle and two green circles as stimulus material. Even though the luminances of all colors were equal, the two green stimuli will be referred as 'light green' and 'dark green' to differentiate them verbally. The circles were presented 100 times each, in random order. Furthermore, the stimuli were presented with a duration of 800 ms and a varying inter-stimulus interval between 300-500 ms (mean 400 ms). In the first task (passive task) subjects were instructed to keep their eyes still and watch the stimuli without any task. An easy and a hard discrimination task followed the passive task. The order of the two discrimination tasks was randomized across subjects. In the easy task subjects were instructed to respond with a button press of their right thumb to the red circle and with a button press of their left thumb to both green circles. In the hard task subjects were instructed to respond with a button press of their right thumb to the light green circle and with a button press of their left thumb to the other two circles. After each response, a feedback 'right', 'wrong' or 'out of time' was visually presented. In contrast to the easy task, subjects had to discriminate the two similar green circles in the hard task. Reaction times and EEG data were recorded during the tasks. Focus of the EEG and wavelet analysis was the comparison of the dark green circle across all three tasks since it served as non-target in all tasks. Response requirements and frequency of this stimulus were equal in both discrimination tasks.

**Stimuli**

Three circles with different colors were used as stimulus material. Circles were presented separately. Size of the circles was $6.5°$ visual angle. All circles had a luminance of about $4.5\ cd/m^2$ and were presented on a white background with a luminance of about 53
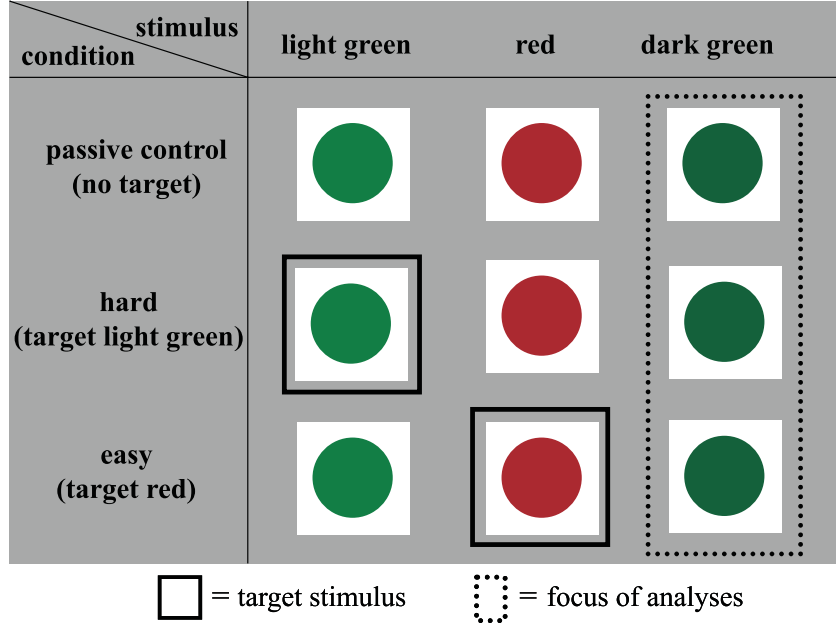
Figure 5.1: Design of Experiment 1. The experiment consists of three tasks (a passive control task, and a hard and an easy discrimination task). Three different circles (light green, red, dark green) were presented in a random order in each task. Subjects were instructed to press a right button in response to the target, and a left button in response to the non-target stimuli in the two discrimination tasks. No response was required in the passive control task. Focus of the EEG analysis was the 'dark green' circle which served as non-target in all three tasks.

$cd/m^2$. According to the Commission International d'Eclairage (CIE) the colors had the following $X, Y$ coordinates: Red (X = 0.584; Y = 0.345), light green (X = 0.291; Y = 0.536) and dark green (X = 0.257; Y = 0.468). CIE coordinates and luminances were measured with a Minolta Chroma Meter CS-100. Stimuli were presented for 800 ms with randomized inter-stimulus-intervals ranging from 1150 to 1350 ms. In the two discrimination tasks a feedback '*right*' or '*wrong*' was presented for 400 ms at the center of the screen succeeding each trial.

## Data acquisition

The EEG was recorded with NeuroScan amplifiers using 26 Ag/AgCl–electrodes electrodes mounted in an elastic cap. Electrodes were placed according to the international 10-10 system. The ground and reference electrode were placed near the left mastoid

(M1). Electrode impedance was kept below 5kΩ. Horizontal and vertical electrooculogram (EOG) recordings were registered with four additional electrodes. Data were
sampled at 500 Hz and analog-filtered with a 0.05 Hz high-pass and a 100 Hz low-pass
filter. Data were further off-line filtered with a digital 0.5 Hz high-pass filter before
analysing. An additional digital 20 Hz low-pass filter was applied before displaying
the ERP data. Baselines were computed for each trial in a time interval 100 ms prior
to stimulation and subtracted from raw data before averaging. Averaging epochs for
ERP and GBRs lasted from 100 ms before to 800 ms after stimulus onset. For artifact
suppression, trials were automatically excluded from averaging, if the standard deviation within a moving 200 ms time interval exceeded 30 $\mu$V in any one of the channels.
After the automatic artifact rejection all trials were visually inspected and rejected if
eye-movement artifacts or electrode drifts were visible. A criteria of at least 50 valid
trials per condition for data analysis was set.

**Data analysis**

Selected electrode sites were pooled to four topographical regions of interest (ROIs)
to avoid a loss of statistical power that is inherent when repeated measures ANOVAs
are used to quantify multi-channel EEG data. The left anterior region (LAR) was
comprised of electrodes FP1, FC3, F3 and F7 while the left posterior region (LPR)
included electrodes P3, O1, CP5 and P7. Regions over the right hemisphere included
the homologous electrodes. For statistical analyses, ERP amplitudes were pooled across
the electrodes in each of the ROIs. Fig. 5.4 shows ERPs of the standard dark green
circle in the three tasks. In all tasks, a N170 was evoked around 170 ms after stimulus
onset. In the two discrimination tasks an additional posteriorly pronounced negative
ERP deflection at about 260 ms was evoked, the so called N2b component. Targets in
both discrimination tasks also evoked a target P3. Latencies of P3 were about 350 ms
in the easy and 550 ms in the hard task (Fig. 5.5). For data analysis ERP components
were defined as mean amplitudes in the following time intervals: 150-190 ms (N170),
240-280 ms (N2b), 300-500 ms (early P3) and 500-700 ms (late P3). For the dark green
stimulus, which served as standard in all three tasks, ANOVAs were computed for
these time intervals comprising factors task and ROI. A further ANOVA investigated
differences between the two target stimuli for the two discrimination tasks.

For the analysis of gamma activity, wavelet transform based on Morlet wavelets
were conducted. To differentiate between evoked and induced activity, each subject's
ERP was transformed to yield evoked GBRs and averages of transforms of single epochs
were computed to yield induced activity (see Section 3.4 for details). The frequency
of GBRs used for the wavelet analysis was individually adapted via time-frequency

planes of the O1 and O2 electrodes in response to the red target circle in the easy task
(Fig 5.2). The individual frequency of GBRs was defined as the highest activation in
a frequency range of about 20 to 80 Hz in a time range of about 60-200 ms. Using
this definition the individually adapted GBRs ranged from 25 to 45 Hz. In analogy
to previous studies of Herrmann and Mecklinger (2001) the GBRs evoked by the dark
green standard stimulus were analyzed in an early (60-120 ms) and in a late time-
interval (150-250 ms) by means of an ANOVA using the same factors as for the ERP
data. A further ANOVA investigated the differences between the two target stimuli. In
order to examine the relations between the latencies of the GBRs and the P3 component
of the ERPs a Pearson correlation coefficient was calculated.
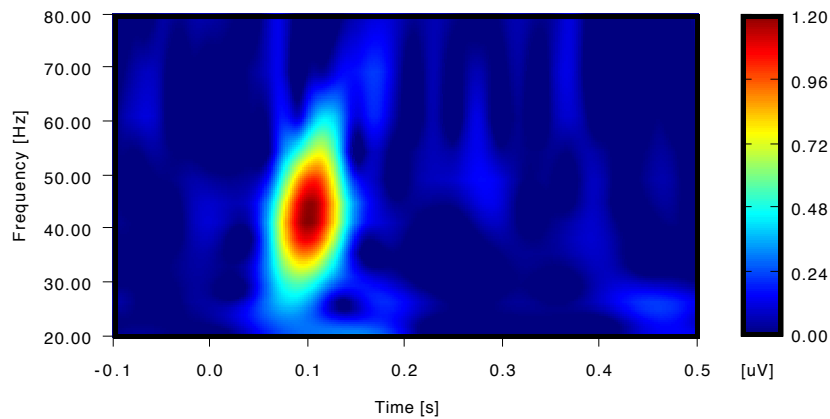


Figure 5.2: Time-frequency plane of the electrode 'O2' (in one subject) after the pre-
sentation of a visual target stimulus. After 100 ms an early peak of gamma activity
was evoked at a frequency of about 43 Hz. (Adapted from: Senkowski and Herrmann,
2002, p. 1745)

## 5.3   Results

**Behavioral Data**

Mean RTs and error rates of the easy and the hard discrimination task are shown in
Fig. 5.3. A comparison of RTs between the standard dark green stimulus in the hard
(570 ms) and the easy (408 ms) task yielded longer RTs in the hard task ($F(1,8) =
78.9, p < 0.0001$). The same effect was found for the targets in the two tasks. RTs
of the target circle (light green) in the hard task (614 ms) were significantly longer as

compared to the target circle (red) in the easy task (428 ms; $F(1, 8) = 117, p < 0.0001$). The delay of RTs in the hard task indicates longer stimulus processing.

At the next step the error rate of the two discrimination tasks was analyzed. Thereby a higher error rate was found in the hard (8.8 %) as compared to the easy task (2.0 %). Comparing the error rate of the standard circle (dark green) in the two tasks yielded a significantly higher error rate in the hard (9.8 %) as compared to the easy task (1.1 %; $(F(1, 8) = 17.50, p < 0.005)$. A higher error rate was also found for the target in the hard (15.0 %) as compared to the target in the easy task (3.3 %; $F(1, 8) = 22.72, p < 0.005$). Longer reaction times and higher error rates indicated that the hard task was in fact harder to perform than the easy task.



Figure 5.3: Mean RTs and error rates in the easy and hard discrimination task. Upper figure shows reaction times with standard error of mean. Lower figure shows error rate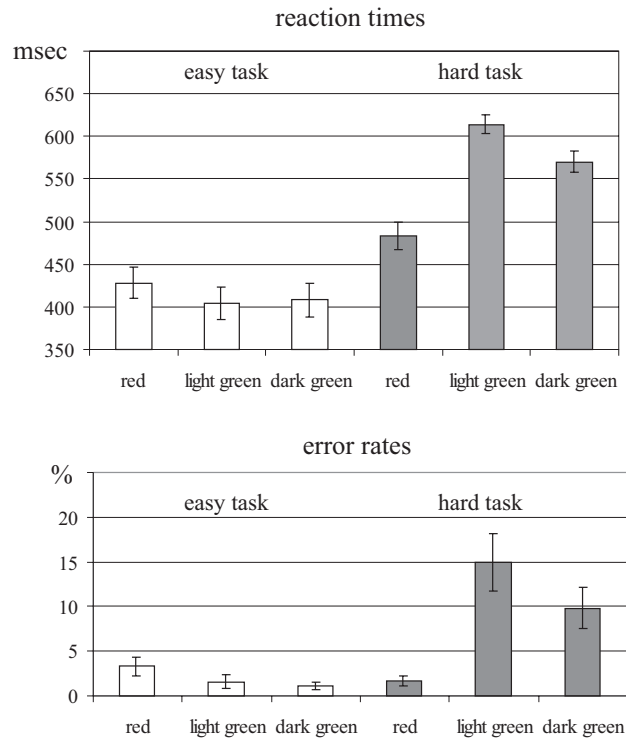s with standard error of mean. Notice higher error rates and longer RTs for the target stimulus (red circle in the easy, light green circle in the hard task) and dark green standard stimulus in the hard task. (Source: Senkowski and Herrmann, 2002, p. 1746)

**ERP Responses**

An ANOVA of N170 amplitudes in response to the standard dark green circle yielded a significant main effect of task ($F(2, 16) = 10.25, p < 0.005$), indicating larger amplitudes for the easy (-1.51 $\mu$V) and the hard (-1.78 $\mu$V) discrimination tasks as compared to the passive task (0.02 $\mu$V; Fig. 5.4). A significant task x ROI interaction revealed that this effect is pronounced at posterior ROIs ($F(6, 48) = 3.82, p < 0.05$). Post-hoc comparisons showed no significant differences between the dark green circle in the easy and in the hard task ($F(1, 8) = 0.35, p < 0.6$). However, compared with the control condition higher N170 amplitudes were found for the easy ($F(1, 8) = 10.89, p < 0.05$) and the hard task ($F(1, 8) = 24.84, p < 0.005$), indicating that the N170 has a generally higher amplitude when performing a discrimination task, but is not associated with the level of difficulty. Amplitudes in the time interval of the N2b also differed between the three tasks ($F(2, 16) = 5.06, p < 0.05$). Furthermore, a significant task x ROI interaction was found for N2b amplitudes ($F(6, 48) = 5.04, p < 0.05$), indicating that N2b effects were pronounced at posterior ROIs. A post hoc comparison for anterior and posterior regions of the easy and the hard task revealed a significantly enhanced N2b amplitude in the hard task for posterior regions ($F(1, 8) = 15.65, p < 0.005$), but not for anterior regions ($F(1, 8) = 0.03, p < 0.9$). Amplitude differences of the standard dark green circle were also found in the time interval of the early P3 ($F(2, 16) = 9.49, p < 0.005$). As for the N2b, a significant task x ROI interaction was found ($F(3, 24) = 6.45, p < 0.05$). This interaction emerges due to the fact that only posterior P3 amplitudes were enhanced in the easy (2.69 $\mu$V) as compared to the hard task (1.25 $\mu V; F(1, 8) = 10.71, p < 0.05$), whereas no differences between the anterior P3 amplitudes were found ($F(1, 8) = 0.82, p < 0.4$). For the time interval of the late P3 component no significant differences were observed for the standard dark green circle between the three tasks ($F(2, 16) = 2.81, p < 0.1$).

A comparison of the target P3 for the early P3 time interval between the easy and the hard task (Fig. 5.5) revealed higher amplitudes for the easy (0.93 $\mu$V) as compared to the hard task ($-0.19$ $\mu V; F(1, 8) = 21.39, p < 0.005$). Furthermore, a significant task x ROI interaction ($F(3, 24) = 11.52, p < 0.005$) indicates that this effects was strongest at posterior sides. Post-hoc comparisons between anterior and posterior regions showed higher posterior P3 amplitudes in the easy (3.40 $\mu$V) as compared to the hard task (0.75 $\mu V; F(1, 8) = 10.75, p < 0.05$). No significant differences were found for anterior regions. An ANOVA for the target P3 in a later time interval showed higher amplitudes for the difficult (0.92 $\mu$V) as compared to the easy task ($-0.21$ $\mu V; F(3, 24) = 20.61, p < 0.005$). A significant task x ROI

Figure 5.4: Averaged across 9 subjects in response to the dark green standard stimulus in the control task (solid), easy task (dashed) and hard task (dotted). (Source: Senkowski and Herrmann, 2002, p. 1747)

interaction ($F(3, 24) = 6.45, p < 0.005$) further indicates that this effect was pronounced at posterior sites. Post-hoc analyses revealed enhanced late target P3 amplitudes for the hard task in anterior ($F(1, 8) = 9.31, p < 0.05$) and posterior regions ($F(1, 8) = 17.58, p < 0.005$). As for the P3, a significant task x ROI interaction was found for the N2b amplitudes of the targets ($F(3, 24) = 6.60, p < 0.05$). However, no significant differences were found between the hard and the easy task for anterior and posterior regions, indicating that N2b in targets was not enhanced in the hard task. No significant differences between the target amplitudes were found for the N170.
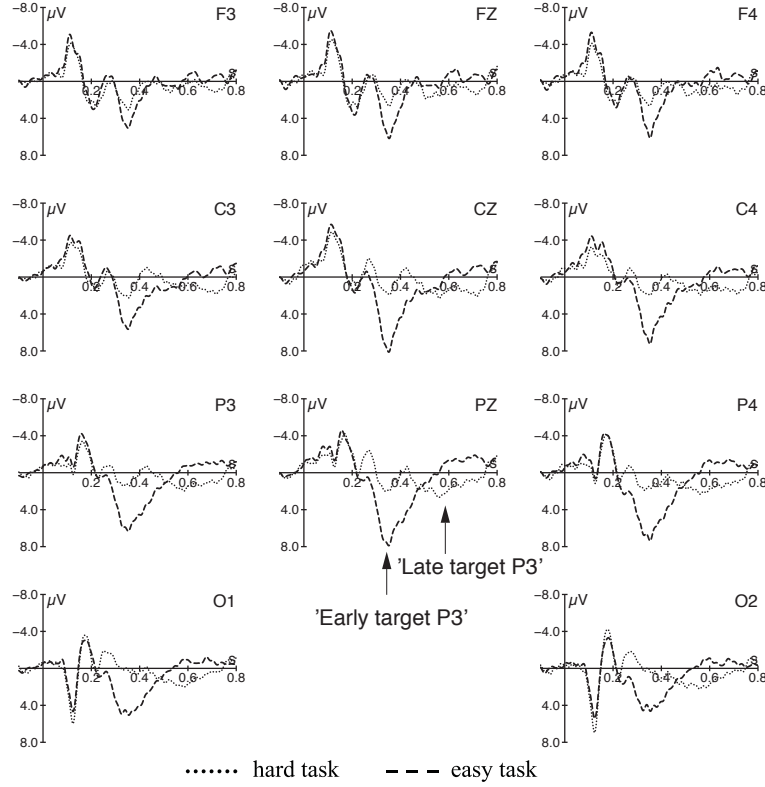
Figure 5.5: ERPs averaged across 9 subjects in response to the light green target stimulus in the hard task (dotted) and target red stimulus in the easy task (dashed). (Source: Senkowski and Herrmann, 2002, p. 1748)

## Gamma-band responses

Bursts of GBRs after stimulus onset were only found for the evoked gamma activity. The total gamma activity did not increase after stimulus onset. Interestingly, the increase of evoked GBRs accompanies a decrease of induced GBRs. Evoked GBRs at some selected electrodes are shown in Fig. 5.6 for the standard dark green circles. In all three tasks a peak of gamma activity was found in a post-stimulus time interval between 60 and 100 ms. An ANOVA for this time interval revealed a significant main effect of task ($F(2, 16) = 4.77, p < 0.05$). Post-hoc comparisons revealed that the GBRs for the dark green circle in the easy task (0.34 $\mu$V) were larger than the GBRs in the hard task (0.28 $\mu$V; $F(1, 8) = 7.13, p < 0.05$) and larger than the GBRs in the passive task (0.24 $\mu$V; $F(1, 8) = 11.17, p < 0.05$). A significant task x ROI interaction indicated that these differences were most pronounced over posterior electrodes

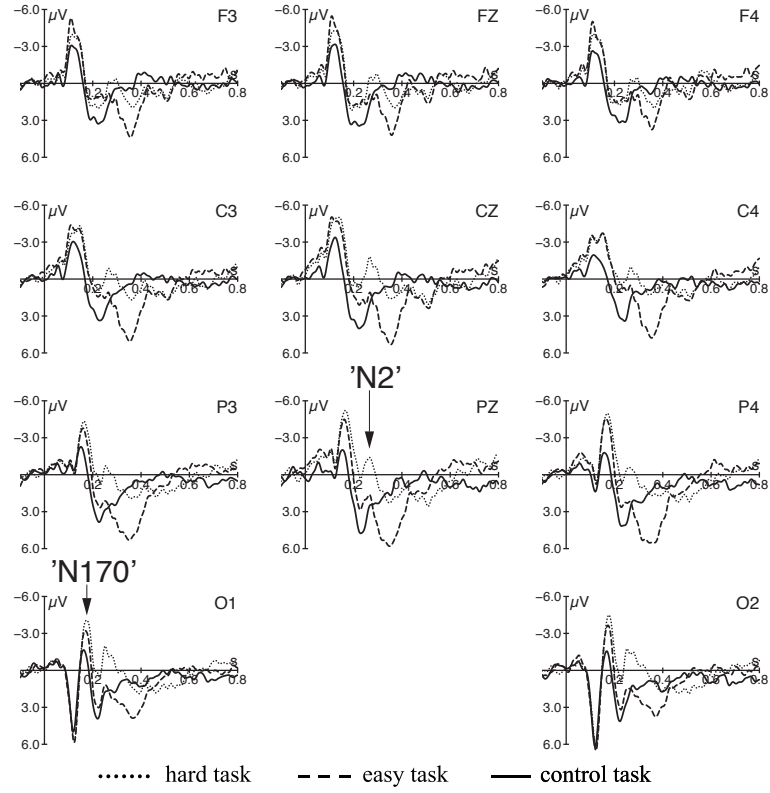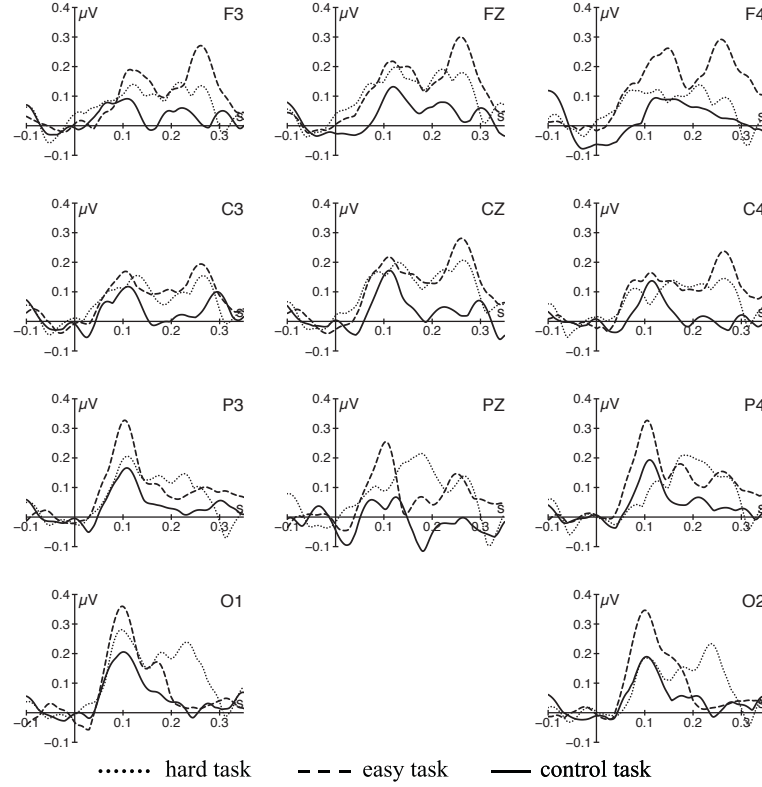Figure 5.6: Evoked EEG gamma-band responses averaged across 9 subjects in response to the standard dark green stimulus in the control task (solid), easy task (dashed) and hard task (dotted). Notice the second peak of gamma activity in the hard task at about 200-250 ms at posterior electrodes. (Source: Senkowski and Herrmann, 2002, p. 1749)

$(F(3, 24) = 4.33, p < 0.05)$. No GBR differences were found between the hard and the passive task in this time interval.

A second peak of gamma activity was found in the time interval between 150 and 250 ms. An ANOVA for this time interval revealed a significant main effect of task $(F(2, 16) = 9.12, p < 0.005)$. Largest amplitudes for this time interval were found for the hard task (0.29 $\mu$V). Post-hoc comparisons revealed that the amplitudes for the hard task were larger as compared to the amplitudes for the easy task $(0.23 \ \mu V; F(1, 8) = 5.58, p < 0.05)$. Furthermore, post-hoc tests also revealed larger amplitudes for the easy as compared to the passive task $(0.17 \ \mu V; F(1, 8) = 6.38, p < 0.05)$. The ANOVA for the target stimuli revealed no significant differences in evoked GBRs.

**Latency of evoked gamma-band responses and P3 amplitudes**

For the examination of the relation between evoked GBRs and P3 amplitude the latency differences of the posterior Pz electrode between the hard and the easy task for the gamma activity (highest activity in a time range between 60-300 ms) were correlated with the latency differences of the P3 component (highest activity in a time range between 300 and 700 ms). In this analysis, a high ($r = 0.53, p < 0.15$) but not significant correlation was found. However, the lack of correlation may be explained by the small number of subjects (n=9) which were included in the calculation of the correlation.

## 5.4   Discussion

**Behavioral Data**

Higher error rates and longer RTs in the hard as compared to the easy task indicated that the hard task was in fact more difficult to perform than the easy task (Fig. 5.3). Longest RTs and highest error rates in both discrimination tasks were found for the target stimuli. This effect has also been reported in previous experiments (Teichner and Krebs, 1974; Herrmann and Mecklinger, 2000). A higher error rate and longer RTs for the standard dark green stimulus in the hard task further demonstrated the effect of task difficulty. Longer RTs for the dark green stimulus and the target stimulus additionally indicated a longer duration of stimulus processing in the hard task.

**ERP Responses**

The results replicated previous examinations, which found a positive relation between specific ERP components and task difficulty. Most sensitive to task difficulty was the posterior N2b. The N2b component, which has its maximum amplitude at electrode Cz at about 260 ms, was associated with attention to color and target detection effects (Ruijter et al., 2000; Potts and Tucker, 2001). Eimer (1996) examined two visual discrimination tasks with colored stimuli, where he presented targets among various distractors. He found an enhanced negativity in the time range of the N2 for the target, which he interpreted as a neuronal correlate of an attentional filtering process. Following this interpretation, it can be proposed that the enhanced N2b in the hard task is a marker of the demands of a visual discrimination task. In the present study the demands differ between the two tasks. In the hard task subjects had to perform a color discrimination within one color category (light vs. dark green) and further had to produce the same response to two non-target stimuli (light green and red circle) belonging to two different categories. Especially the discrimination within the same

color category (light vs. dark green) make the hard task more difficult than the easy task, in which a response can be made based simply on differentiating two major color categories (green and red).

Another component which was associated with task difficulty was the N170. A study which observed timing of color-based attentional processes indicates that this component was probably generated in inferior occipito-temporal cortex (Anllo-Vento et al., 1998). Vogel and Luck (2000) reported an enhanced negative deflection of the N170 component in choice-RT tasks with colorful letter arrays. In their study the influence of task difficulty has been investigated by varying the distractor colors in an easy and in a hard choice RT-task. The target in both tasks was a non-specific red letter. Colors of the distractor letters could either be blue, gray, green or violet (easy task), or shades of purple and pink (hard task). Compared to simple RT-task, the N170 was increased in both choice-RT tasks. No differences in the time range of the N170 component were found between the easy and hard task. The present study replicated this finding, which indicates that N170 is generally enhanced in visual discrimination processes.

Amplitude differences in the study of Vogel and Luck (2000) were also observed for the time interval of the P3 component. It was suggested that more difficult discriminations tend to produce smaller and later P3s (Polich and Bondurant, 1997; Grillon et al., 1990). In the present study, P3 was also delayed in the hard task as compared to the easy task (Fig. 5.5). This effect was primarily found at posterior electrodes, which is in line with previous ERP findings (Mangun et al., 1998; Karayanidis and Michie, 1997). The observed delay of P3 amplitude could indicate a longer duration of stimulus evaluation (Donchin and Coles, 1988). This assumption was supported by higher RTs in the hard task.

**Gamma-band responses**

The main purpose of this experiment was to investigate the relation between the difficulty of visual discrimination tasks and GBRs in the EEG. Higher evoked GBRs were found in two color discrimination tasks as compared to a passive control task. Evoked GBRs in an easy discrimination task were found in a time range of about 100 ms. In a hard discrimination task, however, evoked GBRs were found in a later time range of about 200 ms. The delay of GBRs suggests a longer duration of stimulus processing in the hard discrimination task. This interpretation fits well with the assumption of a relation between GBRs and the processing demands, respectively demands of attentional resources, of a task (Simos et al., 2002; Yordanova et al., 1997b). Simos et al. (2002) examined the influence of task complexity on GBRs by manipulating the complexity

of a target stimulus which had to be detected. In an easy task, subjects had to decide whether they saw a specific animal (a dog or a cat) after the presentation of different animal pictures. In more complex tasks, subjects had to detect a stimulus with specific features (e.g. a four-legged animals among the animal pictures). The authors reported a linear increase in absolute power in the GBRs over right temporoparietal, left occipital, and left frontal regions with increasing task complexity. These regions showed also a relation with task difficulty in the present study, where strongest GBR effects were found at posterior sites (Fig. 5.6). Posterior GBRs have been associated with attentional processes in selective visual attention (Fries et al., 2001), in a paired stimuli paradigm (Shibata et al., 1999a) and in target detection (Herrmann et al., 1999). Clinical studies (Miceli et al., 2001; Schoppig et al., 1999), Positron Positron Emission Tomography (PET) examinations (Gulyas and Roland, 1991), fMRI studies (Engel et al., 1997) and animal studies (Hanazawa et al., 2000; Johnson et al., 2001) further showed that different posterior regions like visual cortex, inferior temporal lobe and left superior parietal cortex are crucially involved in visual discrimination processes. It is therefore likely that the delayed posterior GBRs are related to such discrimination processes.

The finding that only the evoked but not the induced GBRs were related to the onset of an experimental condition goes well in line with previous EEG and MEG examinations in visual discrimination tasks (Herrmann et al., 1999; Herrmann and Mecklinger, 2000). In these studies, Herrmann and collagues also failed to find induced GBRs related to the experimental conditions. However, enhanced induced GBRs have been found in cognitive processes like visual short term memory (Tallon-Baudry et al., 1998) and learning processes (Gruber et al., 2001). Yordanova et al. (1997a) and Fell et al. (1997) reported a higher degree of phase-locking to targets than to standard stimuli, indicating that task difficulty may alter gamma phase-locking. This may be the reason why there were only evoked but no induced GBRs in the present data: since both color discrimination tasks are at least as hard as simple target discrimination task, both lead to phase-locked GBRs.

**General Discussion**

When interpreting the results with relation to task difficulty, and hence attentional resources, one has to keep in mind that the easy and the hard task require different kinds of processing. In the easy task, subjects had to perform a simple color category comparison between the target red and the two non-target green circles. Similar reaction times and error rates (Fig. 5.3) indicate that the two standard stimuli (light and dark green circle) were both processed in a similar way in the easy task. This result contrasts

with that found for the hard task, where higher RTs and a higher error rate were found for the dark green circle as compared to the red circle. To execute the hard task, a comparison of two color categories is required. For the detection of the light green circle subjects had to perform a discrimination within the same color category (light green vs. dark green). This discrimination makes the task more difficult to perform. In addition to discrimination within one color category the same response to different color categories (red and green) has to be executed for the two non-target stimuli. This raises following question: which differences on the behavioral side are most relevant in explaining the presented data?

One factor which might be related to the GBR effects in the present experiment is the different RT of the easy (408 ms) and the hard task (570 ms). Could the delayed motor responses in the hard task be an explanation for the delayed GBRs? Crone et al. (1998) examined event-related synchronization for the gamma-band of the sensorimotor cortex with subdural electrocorticographic electrodes. They found that gamma synchronization began slightly before or during the motor responses. The GBR effects (60-250 ms) in the present study were found long before the motor response of the subjects. It is therefore unlikely that different latencies of the motor responses could explain these effects.

Another aspect which might explain the delayed GBRs in the hard task is a possible inhibition of a target response in the hard task. The two green circles had a very similar color and were therefore difficult to discriminate. For this reason, it is likely that the processing of the non-target green stimulus in the hard task requires an inhibition of a target response. Longer RTs and a higher error rate in the hard task for the non-target dark green stimulus as compared to the non-target red stimulus may be indicative of this inhibition of the target response.

The inhibition of a target response has been examined extensively in the go/nogo paradigm where a target response has to be suppressed (Pfefferbaum et al., 1985). In go/nogo studies, an enhanced frontocentral N2 can be observed for the nogo trials (Bokura et al., 2001; Jackson et al., 1999). In the present study the N2 for the non-target dark green stimulus was also enhanced in the hard task as compared to the easy task in frontal regions. This could indicate the inhibition of a target response for the non-target green stimulus. However, the strongest N2 differences were found at posterior sites and not at frontal sites (Fig. 5.4), indicating that the enhanced posterior N2 in the hard task is directly related to the difficulty of visual discrimination tasks. Inhibition of behavior has also been related with relation to GBRs in the EEG (Shibata et al., 1999b). In that study, enhanced GBRs were found in central regions (C3, C4 and Cz) in a time range at around 230 ms. Interestingly, this is the same time range where the

enhanced GBRs for the hard task were found (Fig. 5.6), indicating that the enhanced GBRs in the hard task might be explained by an inhibition of a target response. However, since target inhibition processes have been primarily related with anterior regions, it is unlikely that these processes explain the posterior GBR effects in the present experiment. The delayed posterior evoked GBRs might rather indicate a longer duration of the discrimination process due to the additional complexity of the hard task (stimulus discrimination within one color category and response discrimination across color categories).

Interestingly, GBRs already reveal the difference in task difficulty before 100 ms whereas ERPs only reflect this difference after about 260 ms, indicating that oscillatory EEG activity may be a better indicator of task difficulty than ERPs are. There are remarkable similarities between evoked GBRs and ERP data with respect to task difficulty. Evoked GBRs of the standard dark green stimulus showed a delay of about 100 ms in the hard task (Fig. 5.6). This delay of GBRs was similar with the delayed latency of the P3 component in ERPs (Fig. 5.5). Thus, the delayed P3 and evoked gamma activity might both reflect a longer duration of stimulus processing. This would indicate a close functional relation between evoked GBRs and the P3 component. A high but not significant correlation between the latency differences (hard task vs. easy task) of the P3 amplitude and evoked GBRs is consistent with this conclusion. The assumption of a close relation between oscillatory processes and ERP components was also strongly supported by recently published data (Başar et al., 2001b; Makeig et al., 2002).

## 5.5   Summary

Experiment 1 examined oscillatory brain activity of the EEG gamma-band and event-related-potentials (ERPs) with relation to the difficulty of a visual discrimination task. Three tasks with identical stimulus material were performed by 9 healthy subjects. The tasks comprised a passive control task, an easy, and a hard visual discrimination task, requiring discrimination of the color of circles. EEG was recorded from 26 electrodes. A wavelet transform based on Morlet wavelets was employed for the analysis of gamma activity. Evoked GBRs were enhanced by both discrimination tasks as compared to the passive control task. Within the two discrimination tasks, the latency of the evoked gamma-band peak was delayed for the harder task. Higher amplitudes of the ERP components N1 and P3 were found in both discrimination tasks as compared to the passive task. The N2b, which showed a maximum activation at about 260 ms, was increased in the hard discrimination task as compared to the easy discrimination task. Furthermore, delayed GBRs in the hard task indicated a longer duration of stimulus

processing, whereas the amplitude of the N2b directly indicates the level of task diffi-
culty. These results indicate that early evoked GBRs and N2b are directly related to
the difficulty of visual discrimination processes and thus to the attentional resources
necessary to perform a task.

# Chapter 6

# Experiment 2: Spatial attention and visual feature binding

Binding different features of an object together is an important process in visual perception. Experiment 2 of the present work investigated how those processes are temporally related to attention[1]. To do this, illusory Kanizsa figures among distractors were used as cue-masks for a subsequent choice-reaction task. The perception of Kanizsa figures require visual binding processes. Based on the results of previous behavior studies (Davis and Driver, 1994; Herrmann, 2000), it was expected to find electrophysiological evidence for the assumption that Kanizsa figures automatically capture visual spatial attention in visual displays in the present experiment. This would indicate that early visual binding processes can initiate subsequent shifts of spatial attention.

## 6.1 Introduction

Visual feature binding and attention are crucial processes affecting the perception of our environment. Linking together and integrating the separate features of a single object in the correct combination is one of the most important functions of binding (Treisman, 1998). Furthermore, it has been demonstrated that binding processes are closely related to attention (Driver et al., 2001; Robertson, 2003). However, it is still not clear how exactly these two mechanisms operate and there are two current models regarding the temporal relation of feature binding and attention:

One model, which will be called the *binding-first model*, proposes that visual binding

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[1]The results of this experiment were described in a manuscript which is submitted to an international peer review journal (Senkowski, Röttger, Grimm and Herrmann, submitted). The chapter contains broad parts of this manuscript. However, the results of a gamma-band analysis which are not included in the manuscript are added to this chapter. For stylistic reasons the format was adapted.

operates at very early, parallel stages in human information processing. Evidence from
visual search experiments, using Kanizsa subjective figures suggests that binding can
lead to automatic shifts of selective visual spatial attention (Albert, 1993; Davis and
Driver, 1998). The edges of the inducer disks of Kanizsa figures can be bound together
to form one coherent object (Fig. 6.1). It has been reported that the detection of
a Kanizsa figure among a varying number of distractor items leads to flat reaction
time (RT) slopes smaller than 10 ms/item (Davis and Driver, 1994, 1997). This result
indicates the pop out effect of Kanizsa figures, which is presumably the result of a
parallel visual search. These findings in behavioral data are well in line with the results
of monkey studies, showing that illusory contours are coded already at very early
stages in visual processing (area V1 and V2) (Grosof et al., 1993; von der Heydt et al.,
1984). These experiments lead to the conclusion that object feature binding of illusory
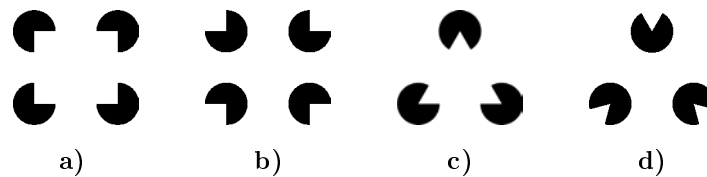contours can occur preattentively.



Figure 6.1: Examples of frequently used Kanizsa figures and their corresponding dis-
tractor stimuli: a) Kanizsa square, b) distractor square, c) Kanizsa triangle, and d)
distractor triangle.

The second model, which will be called the *attention-first model*, proposes that vi-
sual feature binding requires top-down modulated selective attention. Davis and Driver
(1994), and other authors have been criticized for supplying sufficient information in
their search displays to support a parallel search independent of illusory contour pre-
sentation (Gurnsey et al., 1992, 1996). The critical points were that Davis and Driver
(1994) used a prefield to indicate subsequent presentation locations and that the items
of the figures were presented in a fixed distance from the fixation point. Further critical
points were the use of relatively small set sizes, the large number of practice trials, and
the higher luminance of gradients inside the target Kanizsa subjective figures as com-
pared to the luminance of gradients inside the distractors items. Gurnsey et al. (1996)
ran a series of three experiments, in which they tried to control some of these factors.
In these experiments, the authors did not find evidence for a pop out of illusory figures,
indicating that attention is may be necessary for illusory contour processing.

In the present experiment, the relationship between visual binding and selective
spatial attention was investigated by measuring electric brain waves and behavior data

in a visual cueing paradigm. For this experiment, some of the displays from a visual
search study by Herrmann (2000) were used as stimulus material in the present exper-
iment. Herrmann (2000) showed that Kanizsa figures pop out among distractor stimuli
even when factors like luminance, symmetry or configurational aspects are controlled.
In Experiment 2 the displays from Herrmann's first visual search study were used as
cue-masks for a subsequent target choice-reaction task. The cue-masks thereby either
included or did not include a Kanizsa figure. The Kanizsa figure could occur at one
of two fixed positions (right or left) in the display. Three conditions were compared:
(1) A valid cueing condition where the target occurs inside the Kanizsa figure. (2) An
invalid cueing condition where the target occurs contralateral to the Kanizsa figure. (3)
A no-cue condition where the cue-mask did not include a Kanizsa figure. Importantly,
the Kanizsa figures themselves gave no information about the position of the subse-
quently presented target and were therefore not relevant for the target processing. Thus,
if the Kanizsa figure in the cue-mask does not attract attention automatically, then
there should not be differences between valid, invalid and no cue trials in the EEG
and behavioral data. However, since Davis and Driver (1994) and Herrmann (2000)
demonstrated that Kanizsa figures pop out of the visual displays, it was expected that
Kanizsa figures lead to an automatic shift of visual spatial attention, even if they are
not task relevant. This attention shift should lead to an enhanced performance in the
validly cued trials as compared to the invalidly cued trials and to differences in the
event-related potentials (ERPs). Based on previous ERP findings, amplitude effects in
response to the cue-masks were expected for the P1, N1 and N2 components (Eimer,
1994; Nobre et al., 2000; Yamaguchi et al., 1994b). Of particular interest for the analysis
of the target stimuli was the early N1 response. In a spatial cueing paradigm, Mangun
and Hillyard (1991) found enhanced contralateral N1 amplitudes for validly as com-
pared to invalidly cued stimuli. This indicates that visual spatial attention is closely
associated with enhanced contralateral N1 amplitudes in cueing paradigms. Thus, if
the non-informative Kanizsa figures in the present study automatically capture visual
spatial attention, the same effect on the N1 component as described by Mangun and
Hillyard would be expected. Another focus of the EEG analyses was on the investiga-
tion of oscillatory responses in the gamma-band. GBRs have been positively related
to attention and to feature binding processes (Section 2.2.2). Thus, it was expected to
find enhanced GBRs in the valid cueing as compared to the invalid cueing condition.
This would indicate that attention shifts toward Kanizsa subjective figures.

## 6.2 Methods

**Participants**

Thirteen student subjects ($23.5 \pm 2.7$ years, 8 female) participated in Experiment 2. Three of the subjects were rejected from the further analyses because their EEG data contain to much eye movement artifacts (A criterion of at least 40 artifact free trials for each condition was set). The remaining 10 subjects ($23.6 \pm 3.6$ years, 6 female) were included in the data analyses. All subjects had normal or corrected-to-normal vision and showed no sign of any neurological or psychiatric disorder. While two of the subjects were ambidextrous, all others were right handed. Subjects were paid for participating in the experiment and gave written informed consent.

**Procedure**

Fig. 6.2 shows the procedure of the experiment. Each trial started with the presentation of a cue-mask after a variable inter-trial-interval between 500 ms and 1500 ms (mean 1000 ms). This cue-mask consists of an arrangement of 5x5 inducer disks, which either included a Kanizsa figure (Fig. 6.2, upper and middle panel), or did not include a Kanizsa figure (Fig. 6.2, lower panel). 370 ms after cue-mask onset a target triangle, which either pointed to the right or to the left, was presented at a fixed right or left location inside the cue-mask. The probability of target location right (50 %) and target location left (50 %) was independent of the cue-mask. The target was only presented for a time period of 50 ms. Subjects were instructed to indicate the pointing direction of the target triangle by pressing the right button with their right thumb when the triangle pointed to the right, or the left button with their left thumb when the triangle pointed to the left. The response time was limited to 2000 ms after target onset and after each response, a feedback 'right', 'wrong', or 'out of time' was visually presented. Subjects were instructed to look at the center of the screen, which was indicated by a red fixation cross during the experiment. The cue-masks were shown during the whole length of a trial (2000 ms). Using this experimental design, three cueing conditions can be distinguished. Validly cued targets where those which were presented inside a Kanizsa figure (Fig. 6.2, upper panel). Invalidly cued targets where presented contralateral to the Kanizsa figure (Fig. 6.2, middle panel). Finally, no-cue trials were targets in a cue-mask which did not include a Kanizsa figure (Fig. 6.2, lower panel). For each of the three cueing conditions 100 target stimuli were presented at both possible target locations, adding up to a total number of 600 experimental trials. The experiment was run in 4 blocks with a lengths of 150 trials each. Prior to data acquisition, subjects performed 10 practice trials.
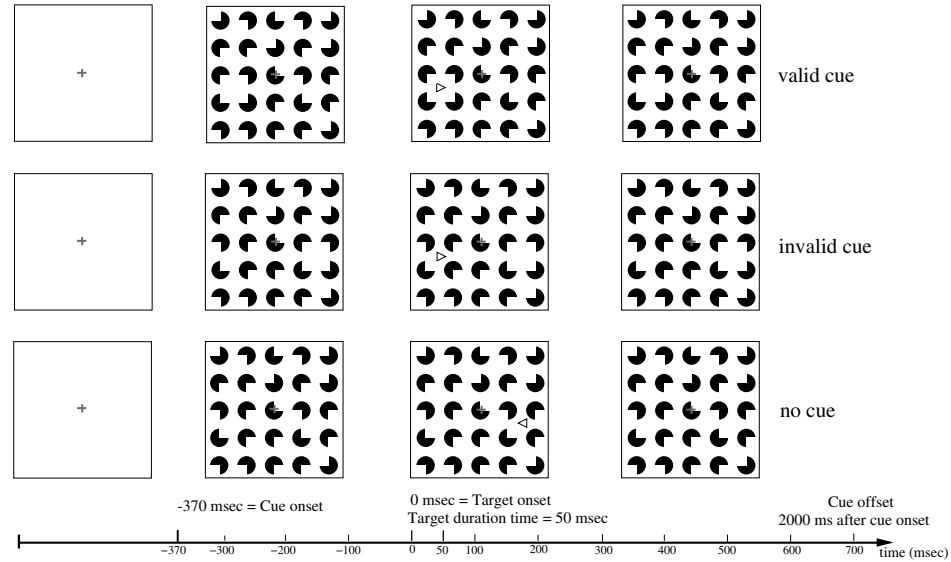
Figure 6.2: Procedure of Experiment 2. After a variable interval between 500 - 1500 ms, a cue-mask arrangement occur 370 ms prior to the target triangle. The cue-mask either included a Kanizsa square at the same location as the target triangle (valid cue, upper panel), at the contralateral position as the target (invalid cue, middle panel) or no Kanizsa square (no cue, lower panel). Subjects had to indicate the direction of the target triangle which pointed to the right or left.

### Stimuli

A 17" Sony Black Trinitron Monitor was used for visual stimulation. Stimulus presentation was controlled by the Experimental Runtime System (BeriSoft Cooperation, Germany). The cue-mask consists of 4x4=16 inducer discs which are symmetrically distributed (Fig. 6.2). The center of potential cue and target position was located at a 2.6° visual angle to the left and right of the screen center. The stimulus size was 0.25° visual angle for the target triangle, 1° for the inducer disks, and 2.2° for the Kanizsa squares. The background color of all arrangements was white.

### Data acquisition

The EEG was recorded with NeuroScan amplifiers using 28 Ag/AgCl–electrodes mounted in an elastic cap. Electrodes were placed according to the international 10-20 system.

The ground and reference electrodes were placed near the left mastoid (M1). Electrode impedance was kept below 5kΩ. Horizontal and vertical electrooculogram (EOG) recordings were registered with four additional electrodes. Data were sampled at 500 Hz and analog-filtered with a 0.05 Hz high-pass and a 100 Hz low-pass filter. Data were further off-line filtered with a digital 1 Hz high-pass and a 50 Hz notch filter before analyzing. An additional digital 20-Hz low-pass filter was applied before displaying the ERP data (Fig. 6.4 and 6.5). Averaging epochs for ERP activity lasted from 200 ms before cue presentation to 500 ms after target onset. For artifact suppression, trials were automatically excluded from averaging if the standard deviation within a moving 200 ms time interval exceeded 30 $\mu$V in any one of the channels. After the automatic artifact rejection, all trials were visually inspected and rejected if eye-movement artifacts or electrode drifts were visible.

**Data analyses**

The ANOVAs for the behavioral data were calculated using the factors Cue Validity (valid cue, invalid cue, no-cue) and Target Location (right, left). Trials with incorrect responses, as well as trials with a RT exceeding 2.5 standard deviations of the mean, were excluded from analyses. The time windows for the analysis of the ERP data were chosen according to the grand average ERP curves (Fig. 6.4 and 6.5). For the ERPs after cue-mask onset mean amplitudes were calculated in time windows between 90-110 ms, 160-180 ms and 240-320 ms for the P1, N1 and N2b components, respectively. For the ERPs after target onset mean amplitudes in a time window between 170 and 190 ms were calculated for the N1 component. Baselines were computed in the time interval 200 ms prior to cue-mask onset for each trial and subtracted from the raw data before averaging. For the ERP analyses, selected electrode sites for the occipito-parietal distributed activations of the P1 and N1 cue-mask and N1 target components were pooled to 2 topographical regions of interest. The right occipito-parietal region was comprised of electrodes P8, P4 and O2, while the left occipito-parietal region was comprised of homologous electrodes (P7, P3 and O1, respectively). For the cue-mask N2b component, which showed a maximum over the vertex, mean amplitudes of the Cz electrode were calculated for the respective time window and subjected to an ANOVA using the within subject factor Kanizsa Figure Location (figure right, figure left, no figure). For the analysis of the cue-mask P1 and N1 amplitudes repeated measures ANOVAs were computed using the within subject factors Kanizsa Figure Location (figure right, figure left, no figure) and ROI (right occipito-parietal region, left occipito-parietal region). Finally, for the target N1 component a repeated measure ANOVA was calculated including the following within subject factors: Kanizsa Figure

Location (figure right, figure left, no figure), Target Location (right, left), and ROI (right occipito-parietal region, left occipito-parietal region).

For the analyses of Gamma activity mean amplitudes of Morlet wavelet transformations for a frequency of about 40-Hz were calculated (Section 3.4). Since no increase of Gamma activity was found after target onset, GBRs were particularly analyzed for the time window after cue-mask onset (Fig. 6.7). Analyses for the GBRs were done for the same occipito-parietal ROIs as used for the analyses of cue-mask P1 and N1 and target N1 amplitudes (see above). Mean GBR amplitudes in a time window between 50-110 ms after cue-mask onset were subjected to a repeated measure ANOVA using the factors Kanizsa Figure Location (figure right, figure left, no figure) and ROI (right occipito-parietal region, left occipito-parietal region). Furthermore, the same baseline window as used for the ERPs were used for the analyses of GBRs.

## 6.3 Results

**Behavior**

Fig. 6.3 shows mean RTs and standard error of means for the three conditions. An ANOVA for the reaction times yielded a significant effect of the factor Cue Validity ($F(1, 06, 9.59) = 7.88, p < 0.02$). Post-hoc comparisons between the single conditions revealed faster RTs for validly cued targets (448 ms) as compared to invalidly cued targets (478 $ms$; $F(1, 9) = 8.38, p < 0.02$). Furthermore, no cue trials (461 ms) showed faster RTs as compared to invalidly cued trials ($F(1, 9) = 13.95, p < 0.005$), and validly cued trials showed a tendency for faster RTs as compared to no cue trials ($F(1, 9) = 4.32, p < 0.07$). No other effects were found for the RTs. An ANOVA for the error rate yielded no significant differences between the valid cue (2.5 %), the invalid cue (3.8 %) and the no-cue (2.5 %) trials. The overall error rate was 2.9 percent. There were no other significant main effects or interactions for with relation to the error rate.

**Event-related potentials**

Fig. 6.4 and 6.5 show ERPs for trials of the valid, invalid and no-cue conditions. The ANOVAs for the cue-mask P1 and N1 amplitudes revealed no significant main effects or interactions. However, for the later cue-mask N2b component a significant main effect of the factor Kanizsa Figure Location was found ($F(1.68, 15.11) = 15.57, p < 0.0003$), indicating more negative N2b amplitudes evoked by the cue-masks including a Kanizsa figure as compared to N2b amplitudes evoked by cue-mask which did not include a
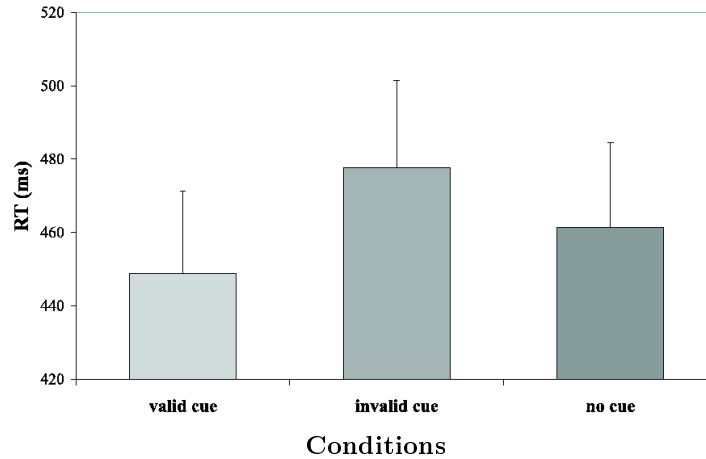
Figure 6.3: Mean RTs with standard error of mean for the three cueing conditions of Experiment 2. Notice the delayed RTs for the invalidly cued trials as compared with validly and no cued trials.

Kanizsa figure (Fig. 6.6a). Post-hoc ANOVAs revealed that N2b amplitudes for the cue-mask which included a Kanizsa figure at the right location (-4.38 $\mu$V) were significantly more negative than N2b amplitudes for the cue-mask which did not include a Kanizsa figure (-2.34 $\mu$V; $F(1,9) = 15.36, p < 0.004$). Also the cue-mask with the Kanizsa figure at the left location (-4.76 $\mu$V) evoked more negative N2b amplitudes than the cue-mask without a Kanizsa figure ($F(1,9) = 22.61, p < 0.0003$). No significant differences were found between the cue-mask which included a Kanizsa figure at the left and the cue-mask which did include a Kanizsa figure at the right location.

The ANOVA for the target N1 component yielded a significant main effect of the factor Kanizsa Figure Location ($F(1.32, 11.88) = 4.48, p < 0.05$). More negative N1 amplitudes were found for the cue-masks which included a Kanizsa figure at the left location (-3.82 $\mu$V) and right location (-3.55 $\mu$V) as compared to the cue-mask which did not include a Kanizsa figure (-2.99 $\mu$V). Furthermore, significant interactions between the factors Kanizsa Figure Location x Target Location ($F(1.13, 10.17) = 13.28, p < 0.004$) and Target Location x ROI ($F(1,9) = 117.07, p < 0.0001$) were found. More specifically, the Kanizsa Figure Location x Target Location interaction resulted from more negative N1 amplitudes for the validly cued trials as compared to the invalidly cued trials (Fig. 6.6b). The Target Location x ROI interaction resulted from more negative N1 amplitudes contralateral to the target location. Finally, a significant three-way interaction between the factors Kanizsa Figure Location x Target Location x ROI indicated that validly cued trials evoke more negative contralateral N1 amplitudes as compared
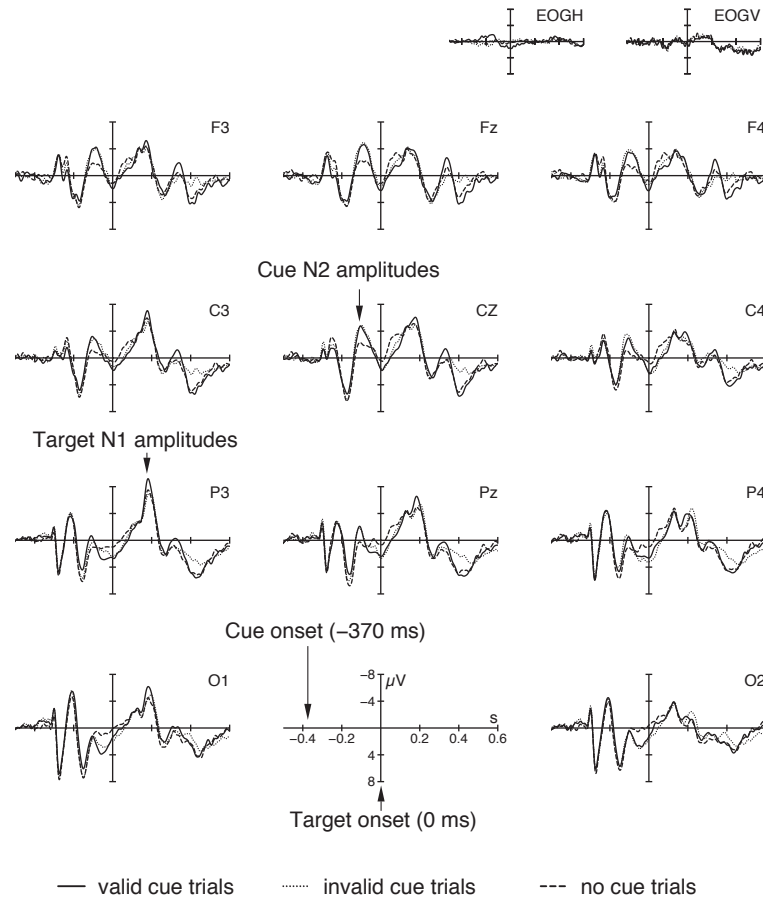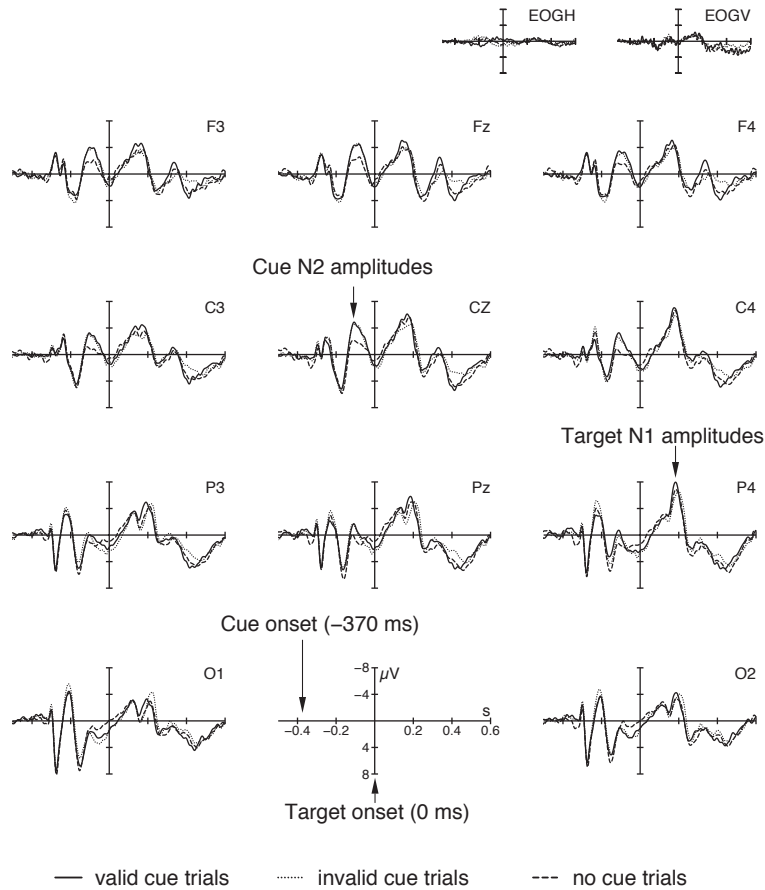
ERPs in response to target presentation right

Figure 6.4: ERPs averaged across ten subjects in response to target presentation right. The solid line represents validly cued trials, the dotted line invalidly cued trials and the dashed line no cue trials. Significant differences between the conditions for the cue-mask N2 and contralateral target N1 amplitudes indicate an attention effect of Kanizsa figures.

to invalidly cued trials $(F(1.91, 17.15) = 5.94, p < 0.02)$. The effects on N1 amplitudes suggest that visual spatial attention was shifted toward the Kanizsa figure.

**Gamma-band responses**

An increase of GBRs after cue-mask presentation was found for evoked gamma activity (Fig. 6.7). As in Experiment 1, there was no increase in total gamma activity.

ERPs in response to target presentation left

Figure 6.5: ERPs averaged across ten subjects in response to target presentation left. The solid line represents validly cued trials, the dotted line invalidly cued trials and the dashed line no cue trials. Significant differences between the conditions for the cue-mask N2 and contralateral target N1 amplitudes indicate an attention effect of Kanizsa figures.

Furthermore, the increase of evoked GBRs accompanies a decrease of induced GBRs. For this reason, only the evoked gamma activity was analyzed. The ANOVA for the evoked GBRs after cue-mask onset revealed no significant main effects of the factor Kanizsa Figure Location, indicating no differences in GBR amplitudes in response to cue-masks including a Kanizsa figure right, cue-mask including a Kanizsa figure left, and cue-masks not including a Kanizsa figure. Furthermore, no significant main effects
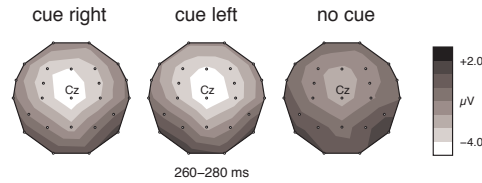
a) Topographies of the cue-mask N2b component
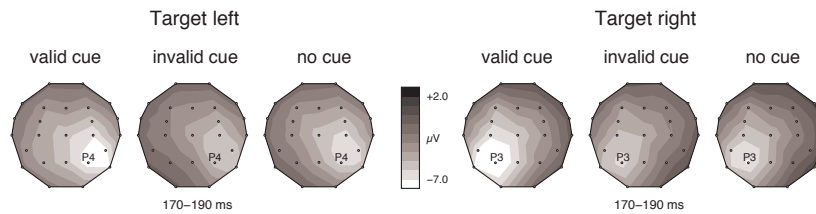


b) Topographies of the target N1 component

Figure 6.6: Panel a): Topographies of the event-related fields for the time interval of the cue-mask N2 component. Panel b): Topographies of the event-related fields for the time interval of the target N1 component.

of the factor ROI or interaction between the factors Kanizsa Figure Location x ROI were found.

## 6.4 Discussion

Shorter RTs and enhanced target N1 amplitudes for validly cued trials as compared to invalidly cued trials indicate a visual spatial attention shift towards the Kanizsa figure. An enhancement of N1 amplitudes for validly cued trials also has been reported in previous studies (Mangun and Hillyard, 1991; Yamaguchi et al., 1994a). In general these studies found the highest N1 cueing effects at posterior sites (Yamaguchi et al., 1995), which is in line with the results of the present study, where the target N1 effects were strongest over occipito-parietal regions. These regions have been closely related to visual spatial attention (Hillyard et al., 1999), indicating that the present N1 effects reflect an enhanced attentional processing of the target stimulus for validly as compared to invalidly cued trials. Next to the target N1 effects there were earlier differences for the N2b amplitudes after cue-mask presentation. The N2b component had a central topography and was more negative for cue-mask which included as compared to the
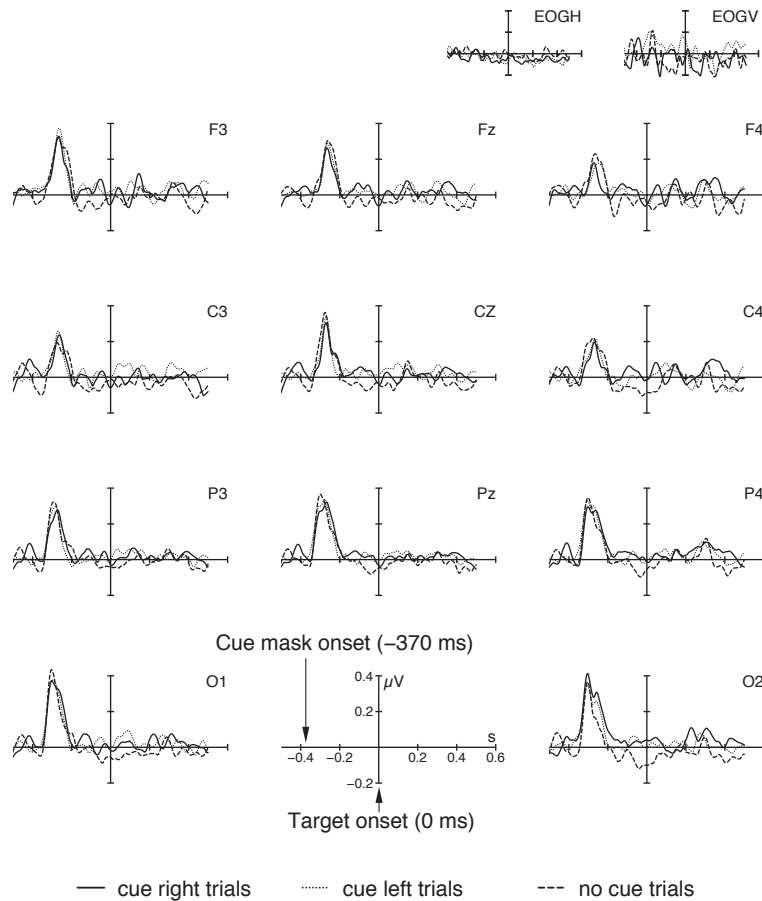
**Evoked gamma activity in response to the three different cue-masks**

Figure 6.7: Evoked GBRs averaged across ten subjects and collapsed over target trials which were presented in the right and left hemispaces. The solid line represents cue right trials, the dotted line cue left trials and the dashed line the no cue trials. Bursts of GBRs were found at about 50-110 ms after cue mask onset in all three cueing conditions. However, no significant differences between the three cue mask conditions were found.

cue-masks which did not include a Kanizsa figure. Lange et al. (1999) suggested that N2b amplitudes might reflect the activity of an integrative executive system which evaluates the results of a stimulus analysis with relation to the task instructions. The system is proposed to be comparable with the Posner's attention system (Posner and Raichle, 1994) which is involved in the directing of attention (including visual spatial

attention). The present N2b amplitudes might reflect the activity of such an attentional system, suggesting that illusory Kanizsa figures automatically initiate processes which are closely associated with the shifting of visual spatial attention. An alternative interpretation of the N2b effects would be that the enhanced N2b amplitudes indicate the existence of a Kanizsa figure after a successful top-down modulated visual search. In this case, spatial attention would initiate, or at least precede a feature binding processes, as it was suggested by the *attention-first model* (Treisman, 1999). However, Woodman and Luck (1999) showed that top-down modulated visual search is associated with a N2pc component which occur contralateral to the attended hemifield. Similarly, Woldorff et al. (2002) reported spatial attention effects on N2b amplitudes over contralateral occipito-parietal scalp areas. For this reason, it is likely that the present N2b amplitudes, which are centrally distributed, do probably not reflect top-down modulated processes. Instead, the N2b rather indicates an enhanced response of a spatial attention system that is sensitive to cue-masks which include a Kanizsa figure. Early automatic binding mechanisms of the single features of the Kanizsa figure may thereby play a crucial role.

In contrast to the N2b, no cue-mask differences for the early P1 and N1 amplitudes were observed. The visual P1 component has been closely related to selective spatial attention (Heinze and Mangun, 1995; Woldorff et al., 1997). Since the generators of the P1 amplitudes are probably located in the extrastriate cortex (Mangun et al., 1998), it is likely that early responses of these areas do not contribute to the cueing effects in the present experiment. There was also no cue-mask effect on the N1 amplitudes. Enhanced visual N1 amplitudes for illusory Kanizsa figures as compared to non-illusory figures have been reported previously (Herrmann and Bosch, 2001; Proverbio and Zani, 2002). However, the stimuli in these studies were presented centrally and were task relevant. Other studies which presented illusory figures or contours at a lateral position failed to find early effects in the latency range of the P1 and N1 components (Brandeis and Lehman, 1989; Murray et al., 2002). It is therefore possible that the lack of early cue-mask P1 and N1 amplitude effects are due to the lateral presentation of the Kanizsa figures.

As for the early cue-mask P1 and N1 amplitudes, there was no effect for GBRs. It might be that also the lateral presentation of the Kanizsa figures caused this lack. Edwards et al. (2001) reported that stimulus properties appear to influence visual GBRs. This finding is supported by a recent study which showed that identical visual stimuli evoke gamma activity when they are presented centrally (Senkowski et al., 2003b) as compared to when they are presented peripherally (see the present Experiment 4).

Thus, the present GBRs after cue-mask onset might be particularly affected by centrally presented distractor stimuli. The distractor stimuli did not differ between three cue-mask conditions (cue right, cue left and no cue), which might explain the lack of GBR effects in the present experiment. However, the lack of GBR effects may also indicate that gamma activity is not related to the processing of the Kanizsa figure in the present setting. The question about feature binding and oscillatory activity has been critically discussed by Shadlen and Movshon (1999). Further studies are necessary to investigate the relationship between oscillatory gamma activity, feature binding processes and spatial attention in more detail.

In general, the results of Experiment 2 demonstrated that Kanizsa figures can act as a visual spatial cue for a subsequently presented target. In order to perceive Kanizsa subjective figures, it is necessary to bind the separate features (i.e. the inducer disks) of the figure to a single object. It can be assumed that these binding processes are closely related to the effects on cue-mask N2b and target N1 amplitudes. Particularly the enhanced target N1 amplitudes for validly cued trials indicate a shift of spatial attention toward the Kanizsa figures. A theoretical model which could explain how early cortical processing may produce perceptual grouping was presented by Grossberg et al. (1997). Based on the results of single cell recordings in monkeys and electrophysiological and functional MRI studies in humans, the authors propose a complex cortical interplay between the lateral geniculate nucleus (LGN) and the visual areas V1 and V2. This is one possible model which could explain how bottom-up processes achieve perceptual grouping.

An alternative explanation for the results would be that the present attention effects were affected by a low-spatial-frequency blurring of the edges of the Kanizsa figure (Ginsberg, 1975). In fact, low-spatial-frequency blurring of the Kanizsa figure may contributed to the present results. However, in a series of four experiments, Davis and Driver (Davis and Driver, 1998) explicitly investigated whether the pop out effect of Kanizsa figures remains when factors like the low spatial-frequency blurring and the grouping of aligned edges were controlled (for example by using black crosses instead of inducer discs to form an illusory figure). Indeed, the pop out effect of Kanizsa figures was found even if these factors were controlled. Thus, Davis and Driver concluded that Kanizsa figures can be coded in parallel as occluding surfaces. Next to these results, Herrmann (2000) demonstrated that the Kanizsa figure pop out remains also when the luminance was controlled by inserted blank spots in the displays. Another factor which might contribute to the present result is the collinearity of aligned edges within the Kanizsa figures. ERP amplitudes in response to Kanizsa figures and non-illusory control stimuli with similar collinear aligned edges have been investigated in

a previous work by Herrmann and Bosch (2001). The authors showed that enhanced ERP amplitudes in response to Kanizsa figures can not be explained by collinearity. It might be that the present attention effects were mainly caused by an object feature binding of the inducer discs. To perceive a Kanizsa figure as a unique object, the edges of the inducer disks have to be bound together. Thus, the present data revealed behavioral and electrophysiological evidence for the assumption that visual feature binding processes, which are necessary for the perception of illusory Kanizsa figures, can lead to an automatic shift of spatial attention.

## 6.5  Summary

Object feature binding and attention are two of the most important processes that help to correctly perceive the outside world. Binding is necessary to link together the different features of single objects which are represented in a distributed fashion in the brain. The mechanism of attention serves to focus onto a small subset of the vast amount of incoming information. It is still not clear how exactly these two mechanisms operate and interact. Kanizsa subjective figures were used as stimulus material in order to investigate the temporal order of feature binding and attention in Experiment 2. Thereby, visual search displays, either including or not including a non-informative Kanizsa figure among distractor stimuli, constitute cueing-masks for a subsequent target choice-reaction task. In the EEG data, enhanced N2b amplitudes were found for cueing-masks which included a Kanizsa figure as compared to cueing-masks which did not include a Kanizsa figure. In addition, faster reaction times and larger contralateral target N1 amplitudes over occipito-parietal areas were found for validly cued trials (target presentation inside a Kanizsa figure) as compared to invalidly cued trials (target presentation outside a Kanizsa figure). To conclude, this is the first EEG study which showed that Kanizsa subjective figures automatically capture spatial attention in a visual cueing paradigm.

# Chapter 7

# Experiment 3: Spatial vs. object feature processing in auditory cortex

The goal of Experiment 3 was to examine early top-down modulated anatomical separations of feature object and feature location processing in the auditory cortex[1]. An early anatomical separation between feature object and feature location processing has been described before for the visual modality (Ungerleider and Mishkin, 1982). Recent findings indicate that such a differentiation also exists in the auditory modality (Rauschecker and Tian, 1999). In the present experiment, MEG and anatomical MRI data were combined to investigate the location and the strength of N1m dipole sources in an auditory spatial and an auditory feature processing task.

## 7.1   Introduction

Magnocellular projections from the retina via the lateral geniculate nucleus (LGN) into primary visual cortex form a dorsal visual stream into parietal cortex and parvocellular projections form a ventral visual stream into temporal cortex. The ventral stream processes mainly object properties and projects to ventrolateral prefrontal cortex (VLPFC) while the dorsal stream processes mainly spatial locations and projects to dorsolateral prefrontal cortex (DLPFC) (Ungerleider et al., 1998).

A similar division is also seen in the auditory cortex of monkeys. Within the lateral belt area of monkey auditory cortex, it has been shown that the anterior part projects to VLPFC while the posterior part projects to DLPFC (Romanski et al., 1999). Functionally this differentiation has been interpreted as a distinction between object and

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[1] The present work was published in Herrmann, Senkowski, Maess and Friederici, 2002. The chapter contains main parts of this article. For stylistic reasons the format was adapted.

spatial processing in monkey auditory cortex (Rauschecker et al., 1997). Subsequent findings supported the notion of a functional specialization of the anterior part for types of monkey calls (object specialization) and of the posterior part for the spatial direction of monkey calls (spatial specialization) (Tian et al., 2001). In humans, the middle frontal gyrus of DLPFC was activated bilaterally during auditory and visual spatial localization, indicating that auditory sound localization is processed in, or in the vicinity of, brain regions which are also involved in visual object localization (Bushara et al., 1999). Recently, distinct cortical pathways for either recognizing or localizing sounds have been reported for humans using fMRI (Maeder et al., 2001; Anourova et al., 2001). However, so far no study has dissociated such a specialization within human auditory cortex using identical stimulus material for spatial and non-spatial tasks. Here, data are presented which demonstrate that different parts of the human auditory cortex are activated as a function of different tasks either focusing attention on spatial or object features of the same stimuli as early as 120-160 ms after stimulus onset. The stimulus used in both tasks were identifiable sounds presented binaurally from at seven different locations.

## 7.2   Methods

### Participants

Five healthy male subjects participated in the study (ages ranging from 22 to 25 years, mean age 23 years). All subjects were right-handed and had normal or corrected-to-normal vision. They had no history of neurological or psychiatric disorder and all gave written informed consent to participate in the study.

### Procedure

Complex auditory stimuli were presented binaurally from 7 spatial locations (Fig. 7.1). Prior to the experiment, each sound was presented via loudspeakers from each spatial location and recorded with a stereo head with microphones inside the ears (HEAD acoustics, HMS III.0). During the experiment, the sounds recorded with the stereo head were presented via air pressure headphones inside the MEG chamber. Individual hearing thresholds were determined for both ears of each subject and stimuli were presented 50 dBb above. Each stimulus lasted 200 ms. In an object task, subjects had to identify object targets (horn from a car) among 6 standard stimuli (ringing phone, digital chirp, whistle, kid's trumpet, bike horn, cuckoo clock) irrespective of their spatial location. In a spatial task, all stimuli presented form 30 degrees to the right had to be

detected among the 6 other locations. The identical stimuli were used in both tasks. Subjects had to press a button with their right hand in response to targets and another button with their left hand in response to standards. All objects and locations were presented with equal probability. Each sound was presented 56 times, resulting in 336 trials for each standard condition which comprise either 6 objects or 6 locations.
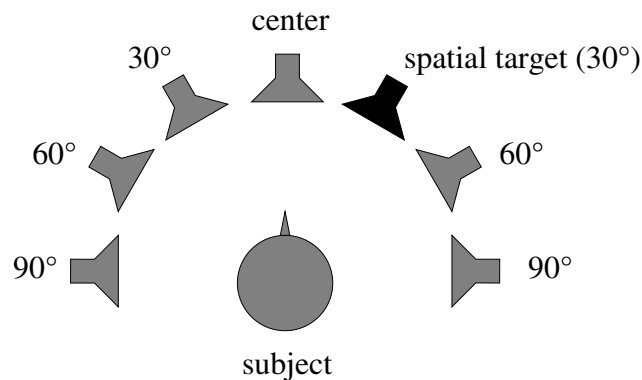


Figure 7.1: Configuration of sound sources relative to the subjects head.

**Data acquisition and data analysis**

Only responses to standards were evaluated, because of their higher signal-to-noise ratio and to avoid potential confounds with target detection. Mean values of reaction times and error rates were analyzed in an ANOVA with the factor task. Trials with reaction times exceeding 2.5 standard deviations from the mean were excluded. MEG was recorded with a BTI 148 channel whole-head system (MAGNES WHS 2500). Horizontal and vertical EOG was registered with four additional EEG electrodes. Data were sampled at 508.63 Hz (on-line 0.1 Hz analog high-pass and 100 Hz low-pass filtering) and digitally off-line filtered with a 20 Hz low-pass filter to reduce noise. Baselines were computed for each trial in the time interval 200 ms prior to stimulation and subtracted from the raw data before averaging. Averaging epochs lasted from 100 ms before to 900 ms after stimulus onset. All epochs were at first automatically and then manually inspected for artefacts and rejected if eye-movement artefacts or sensor drifts were detected. For automatic detection, the standard deviation in a moving time window was computed and epochs were rejected if a threshold was exceeded. EOG electrodes and MEG channels were checked with thresholds of 30 $\mu$V and 1100 fT with window sizes of 200 ms and 3 sec, respectively. Also, if the min-max value of any sensor exceeded a threshold of 3000 fT it was rejected. In case adjacent sensors (distance < 40 mm) showed

mean absolute correlations of the magnetic field strengths of less than 0.7 they were rejected as artefactual. Individual subjects' data were transformed to a standard gradiometer before dipole fitting to compensate potential movements between the object and the spatial condition which were recorded in different sessions (Maess et al., 2001). Dipoles were fitted for the individual averages of each subject using CURRY® (Neuro Scan Labs, Sterling (VA), USA). A realistically shaped boundary element model, was used as volume conductor for each subject. For this purpose, models of each subject's brain were reconstructed from individual anatomical brain recordings such that a net of small triangles represents the outer surface of the brain (Fig. 7.3). T1 weighted images from a 3 Tesla Bruker magnetic resonance imaging scanner were used for this purpose. One dipole was fitted into each hemisphere for the maximum of the global field power of each condition. The starting point of the dipoles was individually adjusted to lie on Heschl's gyrus. After fitting, dipole locations were transformed into Talairach space (Talairach and Tournoux, 1988) and superimposed onto the axial anatomical slice which best represented the location of the dipoles. Repeated-measures ANOVAs were carried out for the locations of the dipoles in Talairach space with factors $x$ (lateral/medial), $y$ (anterior/posterior), $z$ (inferior/superior), hemisphere (left/right), and task (object/spatial).
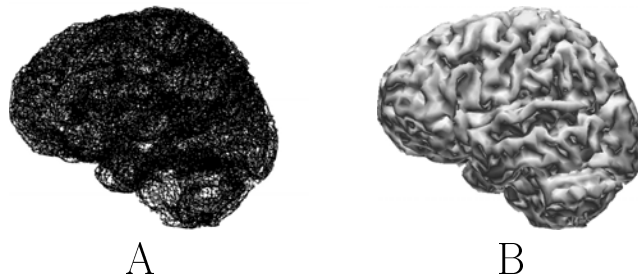


Figure 7.2: A: Realistic shaped boundary element model which was reconstructed from individual anatomical MRI data of subject 3. B: Surface of the boundary element model.

## 7.3   Results

**Behavioral data**

The reaction times revealed no significant differences between the two tasks ($object task$ : $501 \pm 70ms, spatial$ : $570 \pm 50ms$) as indicated by an ANOVA. The ANOVA of the

error rates yielded a significant effect of task ($F(1,4) = 34.60, p 0.005$), indicating fewer errors for the object task ($0.9 + -0.7\%$) than for the spatial task ($14.3 + -5.5\%$).

**Dipole source analysis**

Fig. 7.3 shows the event-related fields (ERFs) in response to standard stimuli in the object (blue) and spatial task (red). A clear M100 can be seen between 120 and 160 ms. The dipole fits resulted in a goodness of fit between 93 % and 94 % on average, reflecting a precise modelling of the data [13]. The ANOVA for the lateral/medial co-ordinate $x$ of the M100 dipoles yielded a significant interaction of hemisphere x task (F(1,4)=10.39, p<0.05). Post-hoc analyses revealed that, within the right hemisphere, M100 dipoles were localized more lateral for the 'spatial' condition than for the 'object' condition (F(1,4)=16.17, p<0.05, x(spatial) = 47 mm, x(object) = 41mm). Within the left hemisphere, differences of the lateral/medial coordinate (x) of the M100 dipoles were not significant  (x(spatial) = -39mm, x(object) = -37mm). Fig. 7.4a shows the
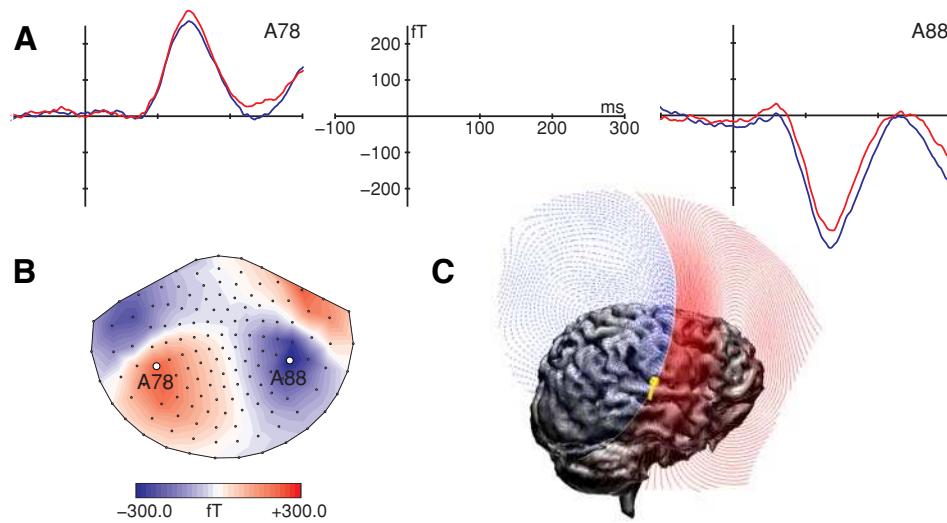


Figure 7.3: A: Averaged event-related fields for all five subjects over left (A78) and right (A88) auditory cortex for the object (blue) and the spatial (red) condition. B: The location of the sensors is shown in the map which displays the topographical distribution of the object condition in the time interval 120–160 ms (top view, nose at top). C: Magnetic fields and the fitted M100 dipole for the object task in the right hemisphere of an individual subject (side view, nose at right). (Source: Herrmann et al., 2002, p. 38)

specialization of the right hemisphere for spatial vs. object processing: M100 dipoles

of all 5 subjects are mapped onto the individual MR slices of all 5 subjects for the
mean z coordinate of the dipoles: all dipoles of the 'spatial' condition (yellow) are
more lateral than those of the 'object' condition (red) within the right hemisphere.
Fig. 7.4b shows the average dipole position mapped onto an averaged horizontal MR
slice, Fig.7.4c shows the averaged coronal slice. Both show a clear separation of the
'object' and 'spatial' dipoles within the right hemisphere. The ANOVA of the ante-
rior/posterior coordinate $y$ of the M100 dipoles yielded a significant main effect of task
($F(1,4)=10.86$, $p<0.05$). Dipoles were located slightly more anterior for the 'spatial'
condition ($y$(spatial) = -16mm) than for the 'object' condition ($y$(object) = -18mm).
No effects were found for the factor inferior/superior ($z=10$mm) or the dipole strengths.
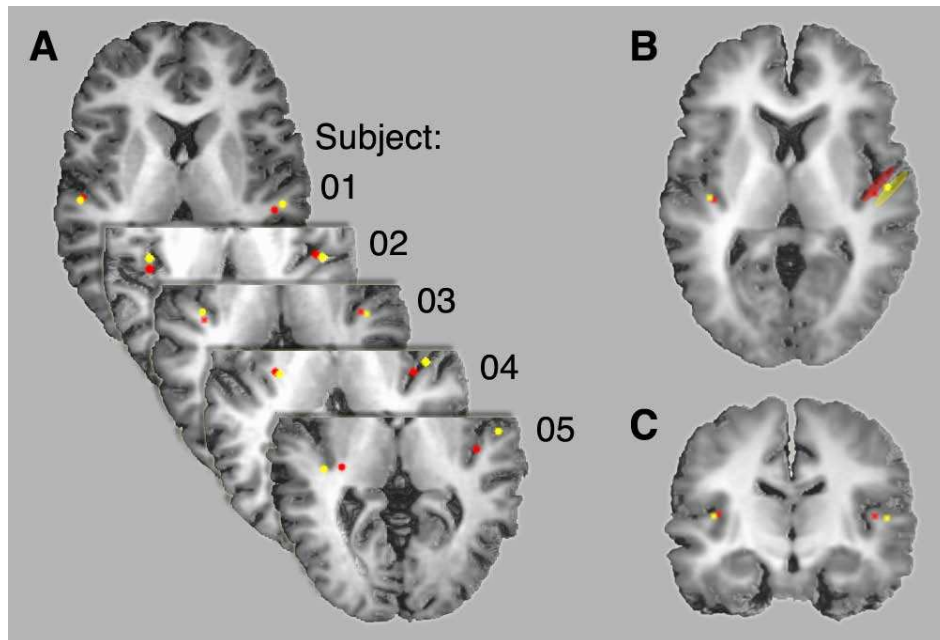


Figure 7.4: Figure 2. M100 dipole locations for auditory object identification ('object'
condition, red) and for localizing auditory objects in space ('spatial' condition, yellow).
A: Horizontal slices of the five individual brains. Horizontal (B) and coronal (C) slice
of a mean brain computed from these five subjects. In the right hemisphere a clear
separation of the two functional specialisations can be seen: objects are processed more
medially while space is processed more laterally. Red and yellow shadings represent
potentially different gyri involved in object and spatial processing, respectively (B).
(Source: Herrmann et al., 2002, p. 39)

Table 7.1 summarizes the mean dipole locations for both conditions and hemi-
spheres. The localization of the M100 dipoles in Heschl's gyrus replicates earlier results

which found M100 dipoles within the temporal plane, in Heschl's gyrus or slightly anterior or posterior (Scherg and von Cramon, 1986; Näätänen and Picton, 1987; Pantev et al., 1995a). The M100 probably represents the sum of activity in primary and non-primary auditory areas.

Table 7.1: Talairach coordinates of mean dipole locations. (Source: Herrmann et al., 2002, p. 39)

| Condition: | Hemisphere: | $x$: | $y$: | $z$: |
|---|---|---|---|---|
| Object | Left | -37 | -20 | 11 |
| Spatial | Left | -39 | -19 | 9 |
| Object | Right | 41 | -17 | 9 |
| Spatial | Right | 47 | -14 | 10 |

## 7.4   Discussion

Our results suggest that object features and spatial features are processed in different regions of human auditory cortex. The more lateral part processes predominantly spatial locations while the more medial part processes predominantly object information. This differentiation is more pronounced within the right hemisphere. Reaction times did not differ significantly between tasks while higher error rates in the object task indicated that localising one out of seven locations is somewhat more difficult than identifying one out of seven sounds. The same pattern of differential error rates has been found for comparing spatial auditory stimuli versus identifying environmental sounds (Maeder et al., 2001). Compared to other experiments investigating sound source localization, the obtained error rate of 14.3 % is lower, indicating a good performance of the subjects (Maeder et al., 2001; Bushara et al., 1999). However, it seems unlikely that the observed different spatial activation of auditory cortex results from task difficulty. Varying the amount of attention or difficulty does influence the magnitude of fMRI responses in auditory cortex but not the location of the activation (Jäncke et al., 1999). Even though fMRI activation need not behave in the same way as MEG dipoles this is an indication that attention did not confound the dipole localisation. The differential activation of auditory cortex for spatial and object tasks observed in the present study is taken to be related to different underlying neural mechanisms. It has been argued previously that auditory object identification relies upon frequency discrimination (Tian et al., 2001),

while detecting the spatial source of sounds depends upon interaural time differences (Fitzpatrick et al., 1997). These interaural time differences are already computed in the superior olivary complex, but also in the inferior colliculi, the medial geniculate nucleus of the thalamus and auditory cortex processes this information with increasing sensitivity as compared to subcortical areas (Fitzpatrick et al., 1997). Among others, frequency properties of sounds are known to influence the auditory M100 (Roberts and Poeppel, 1996). Low frequencies map to more lateral and high frequencies to more medial areas within Heschl's gyrus (Pantev et al., 1988). Since sound source localization depends upon computation of interaural time differences of the low-frequency components (up to 2 KHz) (Fitzpatrick et al., 1997) of the auditory signal, it makes sense that the 'spatial' dipole is located more laterally. Identification of sounds, however, requires the comparison of high frequencies, too, and thus leads to the more medial 'object' dipole. Of course, both regions might interact and fitting the data with just one dipole may be a simplification. The two different dipole locations might even represent two attentional foci within one tonotopic area rather than two completely separate streams. The finding that the right hemisphere shows a clearer separation of the two pathways in the present experiment is in line with the right-hemispheric dominance for processing the movement of auditory objects which is computed based on their location change (Griffiths et al., 1998). While monkeys show a similar differentiation of 'object' and 'spatial' processing also in the left hemisphere (Romanski et al., 1999), the human left hemisphere is specialized for language processing (Binder et al., 1997). In the present study, the object stimulus items represent nameable auditory events which have been shown to activate language-related brain areas in the left hemisphere (Opitz et al., 2000). Their perception may therefore activate temporal cortex in the left hemisphere independently of the task. This would leave the preference for differential processing of object and spatial properties of sounds to the right hemisphere. Thus the observed right hemispheric dominance in differentiating object and spatial processing in human auditory cortex may be related to the human ability to process language in the left hemisphere.

## 7.5  Summary

The human visual system is divided into two pathways specialized for the processing of either objects or spatial locations. Neuroanatomical studies in monkeys have suggested that a similar specialization may also divide auditory cortex into two such pathways. The identical stimulus material was used in two experimental sessions in which subjects had to either identify auditory objects or their location. Magnetoencephalograms were

recorded and M100 dipoles were fitted into individual brain models. In the right hemisphere, the processing of auditory spatial information lead to more lateral activations within the temporal plane while object identification lead to more medial activations. These findings suggest that the human auditory system processes object features and spatial features in distinct areas.

# Chapter 8

# Experiment 4: Spatial attention and multisensory integration

Experiment 4 examined SA effects on unisensory visual, unisensory auditory and multisensory audiovisual GBRs in one single paradigm.[1] Visual, auditory and audiovisual stimuli were compared when presented at an attended and an unattended side. The focus of the analysis was an investigation of early oscillatory responses in the gamma-band (see footnote). Gamma-band responses have been closely related to binding processes (Section 2.2.2). Binding mechanisms are also necessary to processes multisensory audiovisual stimuli. For this reason, it was expected to find the strongest attention effects for audiovisual stimuli.

## 8.1 Introduction

Perception of our environment is based on integrative processing of input from various sensory modalities. It is still unclear, however, whether this integration occurs for all stimuli, or only for relevant stimuli. Early selection theories predict that our brain has to amplify relevant information and suppress irrelevant information at very early stages of information processing. This amplification and suppression of sensory information allows us, for example, to direct attention to a specific stimulus in one sensory modality while ignoring stimuli from other sensory modalities (Eimer et al., 2002; Hackley et al.,

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[1]The data in this chapter are the result of a reanalysis of a study by Talsma and Woldorff (Talsma and Woldorff, submitted). The goal of this reanalysis was to examine early attention effects on oscillatory gamma activity. These effects were not investigated by Talsma and Woldorff. The result of this analyses are described in a manuscript which is submitted to an international peer review journal (Senkowski, Talsma, Herrmann and Woldorff, submitted). The present chapter contains broad parts of this manuscript. For stylistic reasons the format was adapted.

1990; Macaluso et al., 2002; Talsma and Kok, 2001, 2002). This suggests that multi-sensory processes and interactions can be affected by attention. Single cell recordings in cats and rhesus monkeys have shown that multisensory integration can also take place very early in the processing stream. For example, it has been reported that neurons in the superior colliculus integrate sensory inputs of different modalities (Wallace and Stein, 1997, 2001). Furthermore, electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings in humans, focusing on the integration of audiovisual information, have reported enhanced activations in various cortical areas, such as the superior temporal gyrus (Callan et al., 2001), temporo-frontal and occipito-parietal regions (Giard and Peronnet, 1999; Fort et al., 2002b; Molholm et al., 2002), and the temporo-occipito-parietal junction (Raij et al., 2000). These activations occur at various points in time, indicating that multisensory integration can occur at different stages in the processing stream, including very early stages. Talsma and Woldorff (submitted) described the temporal and topographical dynamics of attended and unattended multisensory integration processes as reflected in event-related potentials (ERPs). The main finding was that audiovisual integration, as reflected in the differences between multisensory audiovisual (AV) stimuli and combined unisensory auditory (A) and unisensory visual (V) stimuli, consisted of four phases of effects across time. The earliest effect was found at around 100 ms post-stimulus over frontal scalp areas. This effect was followed by three phases of centro-medially distributed effects, which started at 160 ms. All four phases of integration effects were found to be larger in amplitude for attended stimuli as compared to unattended stimuli.

Although Talsma and Woldorff (submitted) did not find early attention effects prior to 100 ms post-stimulus, it is possible that ERPs may not be sufficiently sensitive to how these early activations of multisensory integration may be reflected. Recent studies have indicated that ERPs might partly consist of a superposition of a phase resetting of multiple electroencephalographic processes that can be separated into oscillatory activations in specific frequency ranges (Makeig et al., 2002; Karakaş et al., 2000a). Interestingly, different frequencies of these oscillations have been associated with different cognitive processes (Başar et al., 2001a). The examination of oscillatory activations in specific frequency ranges constitutes a promising new additional approach in the analysis of electrical brain activity, which could include the possibility that these oscillatory activations might be more sensitive to some early modulations of cognitive processes than ERPs alone would be. The focus of the present Experiment 4 was on fast oscillatory responses in the gamma-band (30-80Hz, mainly 40Hz), which were analyzed by wavelet transformations of the EEG data. Evoked gamma-band-responses (GBRs)

usually peak first after about 40-80 ms in the auditory (Tiitinen et al., 1993) and af-
ter about 80-120 ms in the visual modality (Senkowski and Herrmann, 2002). In the
present Experiment 4 it was investigated whether selective attention affects these early
activations in multisensory processing.

With regard to multisensory integration, it is of interest to note that oscillatory
GBRs have been shown to play a role in binding the integration of different sensory
inputs features within the same modality (Singer, 2001; Engel et al., 1999). Studies
in cats and monkeys have demonstrated a synchronization of single neurons in the
gamma-band in auditory cortex during the integration of different auditory stimulus
features (de Charms et al., 1998), and in visual cortex during the integration of different
visual stimulus features (Gray et al., 1989). In addition, human studies have shown that
binding processes are likely to be related to oscillatory GBRs (Müller et al., 1996; Tallon
et al., 1995). Numerous daily life situations require multisensory binding of information
from different modalities, the mechanisms of which have been related to attentional
processes. For example, Davis, Driver and colleagues have demonstrated that bottom-
up processes and top-down modulations, due to attention, can facilitate and support
binding (Davis and Driver, 1994; Driver et al., 2001). For a review of binding processes
and spatial attention see Robertson (2003). Interestingly, GBRs have also been related
to spatial attentional processes in the visual (Gruber et al., 1999; Müller et al., 2000)
and auditory modalities (Tiitinen et al., 1993; Yordanova et al., 2000).

The studies described above suggest two key relationships. First, feature binding
processes, which are likely to play a crucial role in multisensory integration, seem to
be closely related to oscillatory activations, particularly in the gamma-band. Second,
GBRs also seem to show a close relationship with attentional processes. However,
this is the first Experiment that investigated the relationships between multisensory
integration, selective spatial attention, and GBRs.

The main purpose of the present work was to investigate such relationships. To do
this, the GBRs of the ERP data that are reported in Talsma and Woldorff (submitted)
are computed and analyzed. More specifically, the GBR activity on EEG data that
was collected when subjects were presented with a continuous stream of unisensory
auditory, unisensory visual, and multisensory audiovisual stimuli. These stimuli, which
were always unilateral, were presented in random order to the left and right hemispaces
while subjects focused their attention on a designated side to detect occasional target
stimuli on that side (which could occur in either one or in both of the modalities). In
this way it was possible to analyze the brain responses to the same set of unisensory
and multisensory stimuli when they were attended vs. when they were unattended,

with the only difference being the covert focusing of attention towards or away from those stimuli.

According to the results of previous studies on spatial attention and GBRs (Tiitinen et al., 1993; Yordanova et al., 2000; Gruber et al., 1999; Müller et al., 2000), it was expected to find enhanced GBR activity for the attended, as compared to unattended, stimuli in both the visual and auditory modalities. Moreover, since GBRs have been closely related to both attention and binding processes, it was expected to find even stronger selective attention effects for GBRs in response to multisensory (AV) stimuli than to unisensory auditory (A) and visual (V) stimuli. Such a finding would support the hypothesis that oscillatory-GBRs are particularly important for integrative binding processes of attended multisensory objects. The high temporal resolution of electrophysiological recordings was expected to provide data on the stage of processing at which any such effects might occur, and their topography was expected to provide some insight into the brain regions in which such audiovisual binding processes and their interactions take place.

## 8.2   Methods

### Participants

Sixteen subjects (21.1 ± 2.9 years, 9 female) participated in the experiment. From these sixteen subjects, two were rejected from the analysis because their EEG data contained too much high frequency noise due to muscle activity. The remaining fourteen subjects (21.9 ± 3 years, 8 female) were included in the full data analysis. All subjects were right-handed and had normal or corrected-to-normal vision. They had no history of neurological or psychiatric disorder and all gave written informed consent to participate in the study.

### Procedure

Streams of unisensory auditory, unisensory visual, and multisensory (audiovisual) stimuli were presented in random order to the left and right hemispaces, while subjects were attending on different runs to one or the other of these sides. The subject's task was to detect target stimuli on the attended side and report these by making a manual response with the right or left index finger (counterbalanced across runs), while ignoring all stimuli from the other side (Fig. 8.1). Target stimuli were highly similar to standards, but contained an intensity decrement half-way through the presentation of the stimulus, which caused the subjective impression that the stimulus appeared to flicker

(for visual targets) or to stutter (for auditory targets). Multisensory target stimuli contained both the visual and the auditory intensity decrements. All trials were presented with a randomly varying inter-stimulus-interval (ISI) between 350 and 650 ms (mean 500 ms). After a number of practice runs, subjects were presented ten experimental blocks of trials (five attend left and five attend right blocks, also counterbalanced across runs). For each condition (attend left/right), a total number of 700 visual, 700 auditory, and 700 multisensory stimuli were presented; 350 to the left hemispace, and 350 to the right). For each stimulus type, 70 out of these 350 stimuli were targets. To facilitate the elimination of distortion of ERP waves from overlapping responses of adjacent trials (Woldorff, 1993), a total of 350 "no-stim" (omitted) trials were included in each condition (Burock et al., 1998). For the analysis of the GBR, the bandpass filtering of the data around 40 Hz attenuates the longer-latency slow waves so substantially that the overlap of adjacent responses at these stimulus rates is essentially eliminated.
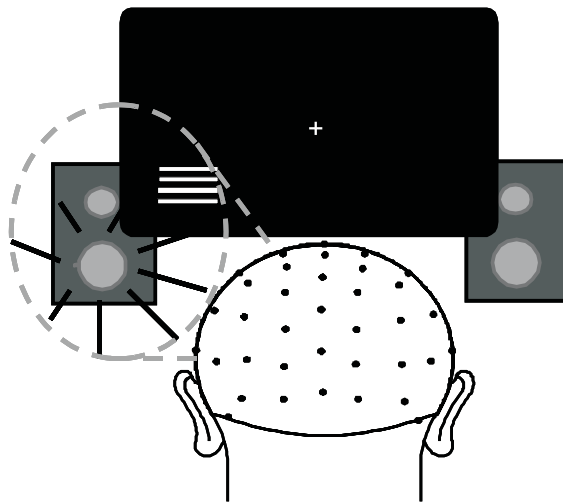


Figure 8.1: Experimental design of the attended left condition. The figure shows the presentation of an attended multisensory stimuli in the left hemifield. Unattended stimuli were presented in the right hemifield in this condition.

The degree of the mid-stimulus intensity reduction for the targets was determined for each subject individually during a training session prior to the experiment. The difficulty of the targets was adjusted for each subject, based on his or her accuracy, by increasing or decreasing the amount of intensity decrement, thereby making them either more similar or less similar, respectively, to the standards (i.e., nontargets). This

target-difficult titration was done separately for the auditory and visual stimuli to keep
the subject's accuracy near 90%

## Data Acquisition

Recordings took place in a sound attenuated, dimly lit, electrically shielded chamber.
Stimulus presentation was controlled by a personal computer running "presentation"
software (Neurobehavioral Systems, Inc., San Francisco, CA. USA). EEG was recorded
from 64 tin electrodes, mounted in an elastic cap (Electro-Cap International, Inc) and
referenced to the right mastoid during recording. Electrode impedances were kept below
2 k$\Omega$ for the mastoid and ground electrodes, 10 k$\Omega$ for the eye electrodes, and 5 k$\Omega$ for
the remaining electrodes. Horizontal eye movements were monitored by two electrodes
at the outer canthi of the eyes referenced to each other. Vertical eye movements and eye
blinks were detected by electrodes placed below the orbital ridge of both eyes, which
were referenced to two electrodes directly located above the eyes. During recording, eye
movements were also monitored though a closed-circuit video system. The EEG was
recorded using a NeuroScan (SynAmps) acquisition system with a band pass filter of
0.01 to 100 Hz and a gain setting of 1000. To suppress high-frequency background noise,
data were also off-line filtered with a 60 Hz notch filter. Raw signals were continuously
digitized and with a sampling rate of 500 Hz and digitally stored for off-line analysis.
Prior to averaging, all channels were re-referenced to the algebraic average of the two
mastoid electrodes. Averaging epochs for ERP and EEG gamma activity lasted from
200 ms before to 500 ms after stimulus onset. Baselines were computed for each trial in
the time interval between 150 ms and 50 ms prior to stimulation and subtracted from
the raw data before averaging. Trials containing artifacts were automatically excluded
from averaging when the standard deviation within a moving 200 ms time interval in
any channel exceeded 30 $\mu$V for the scalp electrodes and 40 $\mu$V for the eye electrodes.
After the automatic artifact rejection trials were visually inspected to ensure that eye-
movement artifacts or electrode drifts had been appropriately rejected.

## Stimuli

Unimodal visual stimuli consisted of white horizontal square wave gratings (5.8 by 5.8
cm, subtending a visual angle of about 6 degrees) presented against a black background.
These visual stimuli were presented laterally to the left or right of the display at an
angle of about 15 degrees from a centrally presented fixation point, in the lower visual
fields (about 6 degrees below the horizontal meridian), with a duration of 105 ms.
Unimodal auditory stimuli consisted of a 1600 Hz tone pip, with a total duration of
105 ms and linear rise and fall times of 10 ms). These stimuli were presented through

two speakers that were placed behind the monitor, such that the speakers were hidden from the subject's view and the observed location of the sound matched the location of the lateral visual stimuli. The auditory stimuli were presented with an intensity of about 65 dB sound pressure level. Multisensory stimuli consisted of the simultaneous presentation of both the auditory and visual stimuli.

## Data Analysis

### Behavioral Data

Reaction times (RTs) for correct detections of targets, hit rates (HR) and false alarm (FA) rates were computed separately for the different conditions. These measures were subjected to an ANOVA using the following subject factors: 'stimulus modality' (visual, auditory, audiovisual), and 'stimulus location' (left hemispace, right hemispace).

### Event-Related Potentials and Wavelet Transformations

The focus of the analysis of ERPs and triggered oscillatory activations was on the "standard" (i.e., non-target) stimuli. Since early multisensory integration effects have been described over occipito-parietal areas (Fort et al., 2002b; Giard and Peronnet, 1999), a topographical region of interest (ROI) was defined including these areas for the statistical analysis. This ROI includes the following electrodes: $Oz_i$, $Oz_s$, $Pz_i$, O1, O2, P01, and P02 ('i' indicates that the electrode was placed slightly inferior to the corresponding 10-20 system electrode, whereas 's' indicates it was placed slightly superior). Because maximum activations of early ERP and triggered GBRs were found over the medial frontal areas, and because previous studies have also implicated frontal regions as being involved in multisensory integration, a second ROI was defined using the following anterior electrodes: $Fz_p$, Cz, $Cz_a$, FC1, FC2, $C1_a$, and $C2_a$ (where 'a' indicates that it was placed slightly anterior to the corresponding 10-20 electrode and 'p' that it was placed slightly posterior). Based on the latencies of previously reported very early ERP and triggered oscillation effects (Tiitinen et al., 1993; Woldorff et al., 1993), ROI mean amplitudes in a time interval between 40-60 ms were computed for each stimulus type and submitted these to an ANOVA factors using the following within-subject factors: 'attention' (attended, unattended) and 'presentation side' (left or right hemispace). For the ERPs the time-locked average of the no-stim trials were subtracted out from that of the other trials prior to the analysis. This was done to eliminate the overlap from preceding trials (Talsma and Woldorff, submitted). Because early high-frequency effects are not sensitive to this kind of overlap (Woldorff, 1993), this subtraction was not done for the GBR analyses.

For the analysis of oscillatory GBRs, a wavelet transform based on Morlet wavelets was employed for the calulation of induced and evoked gamma activity (Section 3.4). In addition to the induced and evoked GBRs, the phases of oscillatory GBRs were analyzed. In this analysis, the resulting complex phase-angle were first plotted of each single trial as a point on a unit circle (Mardia and Jupp, 2000). This was done for each single time point and each frequency in the gamma-band separately. Secondly, it was tested whether the phases of single trials were uniformly distributed by subjecting these phases to the Rayleigh test of uniformity. If a stimulus onset does affect the phase of the GBRs, either by a phase resetting of ongoing oscillatory activity or by phase locked activity of additional generators, one would expect to find a non-uniform distribution of phase-angles. In other words, the phase-angles would not be randomly distributed and the test would be significant ($p > .05$). The results of the Rayleigh test were finally plotted into a time-frequency plane (Fig. 8.6).

## 8.3   Results

Fourteen out of the 16 subjects that participated in the experiment and whose ERP data were reported in Talsma and Woldorff (submitted) were included in the current report, with the other two excluded here due to unacceptable noise-levels in the gamma-band in their EEG data. Because the subject group was slightly different, behavioral and early-latency ERP data of the 14 subjects that are included in the present analysis were reanalysed.

### Behavioral Data

The ANOVA on the reaction time data revealed significant differences between unisensory auditory, unisensory visual and multisensory audiovisual stimuli, as indicated by a significant main effect of the factor 'stimulus modality' ($F(2, 12) = 13.09, p < 0.001$). Fastest responses were found for the audiovisual stimuli ($564 \pm 30$ ms), followed by auditory stimuli ($616 \pm 30$ ms) and visual stimuli ($690 \pm 37$ ms). Post-hoc comparisons revealed that audiovisual stimuli were processed significantly faster than auditory stimuli ($F(1, 13) = 7.29, p < 0.018$). In addition, shorter RTs were found for auditory stimuli as compared to visual stimuli ($F(1, 13) = 16.12, p < 0.001$). No other significant effects were found.

As for reaction times, the ANOVA for hit rates yielded significant differences between the three stimulus modalities ($F(2, 12) = 28.14, p < 0.001$). The highest hit rates were observed for audiovisual stimuli ($89.0 \pm 2.2$ %), followed by auditory stimuli ($86.6 \pm 2.7$ %) and visual stimuli ($72.9 \pm 4.0$ %). Post-hoc analyses showed that

hit rates for both multisensory audiovisual and unisensory auditory stimuli were significantly larger than hit rates for unisensory visual stimuli ($F(1, 13) = 51.09, p < 0.001$; $F(1, 13) = 21.48, p < 0.001$, *respectively*). Hit rates between audiovisual and auditory stimuli, however, did not differ significantly. Again, no other significant effects were found .

**Gamma Responses**

First, the evoked (phase locked) GBR activity was analyzed. To do so, time-frequency planes were calculated that gave an estimate of both frequency and latency of the evoked GBR activity for the various event types. Figure 8.2 shows time-frequency planes for audiovisual and auditory stimuli for attended, unattended, and attended minus unattended stimuli (collapsed over trials presented in the right and left hemispaces and averaged across 14 subjects). The figure indicates an early selective attention effect (at about 40-60 ms post-stimulus) for audiovisual stimuli in a frequency range of around 45-Hz. Figure 8.3 shows the wavelet transformed data for the evoked GBRs elicited by unisensory auditory, unisensory visual and multisensory audiovisual stimuli. To calculate whether the GBRs significantly changed in amplitude after stimulus onset, ANOVAs using the within subjects factors 'time window' (baseline window or post-stimulus window between 40-60ms) and 'presentation side' (left or right hemispace) were performed. This was done for the anterior and posterior ROIs and for the three stimulus types. The ANOVAs revealed an early increase of evoked GBR activity for the audiovisual (AV) and auditory (A) stimuli, as indicated by a significant main effect of the factor 'time interval' (AV anterior ROI: $F(1, 13) = 46.29, p < 0.0001$; AV posterior ROI: $F(1, 13) = 30.96, p < 0.0001$; A anterior ROI: $F(1, 13) = 42.11, p < 0.0001$; A posterior ROI: $F(1, 13) = 6.83, p < 0.05$). No effects were found for the factor 'presentation side'. In contrast to the audiovisual and auditory stimuli, no increase of evoked GBRs was observed for visual stimuli.

In further ANOVAs, the effects of the factor 'attention' on evoked GBRs were investigated. The mean GBR amplitudes (post-stimulus time window 40-60 ms) obtained for each of the three stimulus types were separately submitted to an ANOVA, using the within subject factors 'attention' (attended or unattended) and 'presentation side' (left or right hemispace). This was also done separately for the anterior and posterior ROIs. For multisensory stimuli a significant main effect of the factor 'attention' was found in the anterior ROI ($F(1, 13) = 6.99, p < 0.02$), indicating that attended multisensory stimuli evoke larger GBRs (0.16 $\mu$V), as compared to unattended multisensory stimuli (0.11 $\mu$V). No other effects for multisensory stimuli were found over the anterior
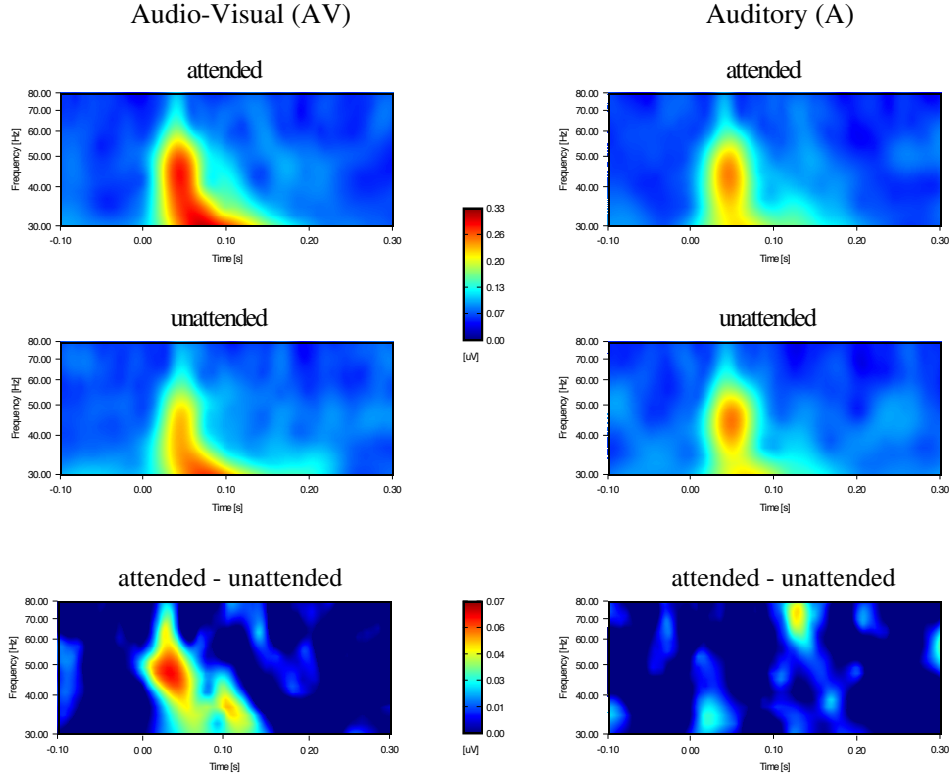
Figure 8.2: Time-frequency planes of evoked GBRs for a frontal electrode, (slightly anterior to 'Fz') for attended (upper row), unattended (middle row), and attended minus unattended (lower row) stimuli (n=14). Multisensory audiovisual stimuli are shown at the left column, unisensory auditory stimuli at the right column. An increase of evoked gamma responses was found in a frequency range of about 45 Hz, after 40-60 ms, for both stimulus types. Visual stimuli showed no increase of GBRs after stimulus onset (not plotted here). Differences between attended and unattended stimuli are shown in the lower planes. These planes indicate an early attention effect at about 45-Hz for multisensory stimuli.

region for multisensory stimuli. A similar analysis was conducted for the posterior region data, but no significant effects were found, there. Finally, unisensory auditory and unisensory visual data were submitted to the same types of analyses. At both anterior and posterior ROIs, however, these analyses did not yield any significant effects of the factors 'attention' or 'presentation side'.

Next, GBR responses to the multisensory (AV) stimuli were compared with the sum of the GBR responses to the unisensory (A+V) stimuli, using ANOVA tests that

a) Evoked 45-Hz Activity
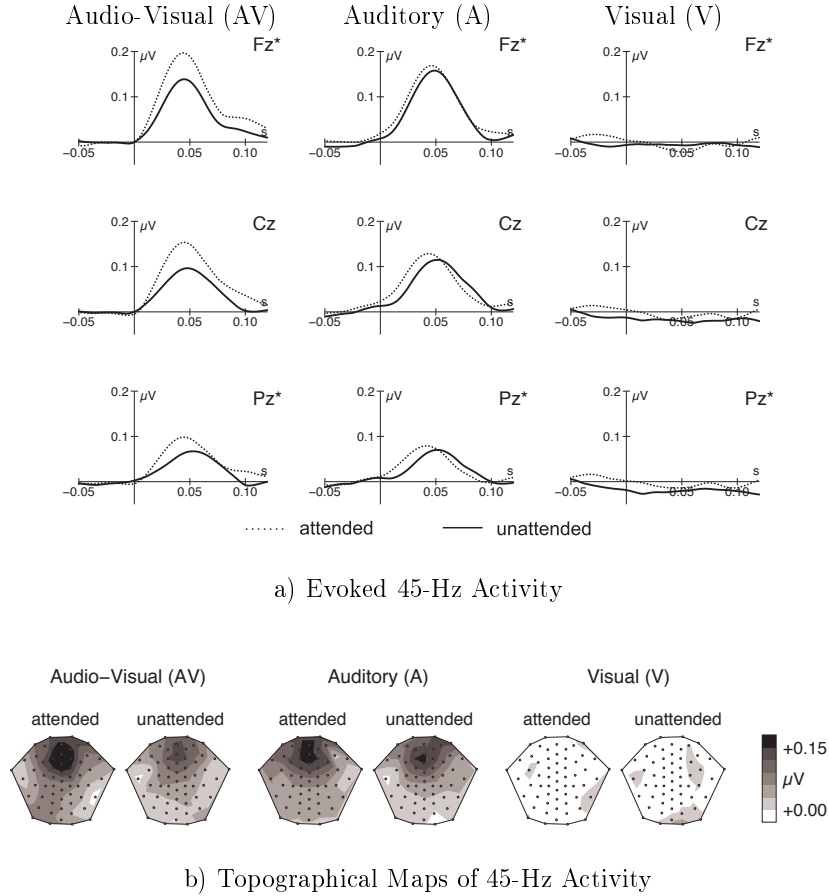


b) Topographical Maps of 45-Hz Activity

Figure 8.3: Panel a): Evoked GBRs for midline electrodes for audiovisual stimuli (left), auditory stimuli (middle) and visual stimuli (right). Panel b): Scalp topographies of GBRs for the attended and unattended condition. Notice the frontal topography of GBRs for audiovisual and auditory stimuli and the attention effect on audiovisual stimuli. (*) The electrodes are approximately located at the named electrode.

were confined to the anterior region (Fig. 8.4). These ANOVAs were run separately for the attended and unattended stimuli using the following within subjects factors 'stimulus modality': (multisensory (AV) or combined unisensory (A+V)) and 'presentation side' (left or right hemispace). When the stimuli were attended, the multisensory (AV) stimuli elicited larger GBR activity (0.16 $\mu$V) than the summated unisensory (A+V) GBR activity (0.12 $\mu$V), as indicated by a significant main effect of the factor 'stimulus modality' ($F(1, 13) = 4.71, p < 0.05$). No other effects were found in the ANOVA for
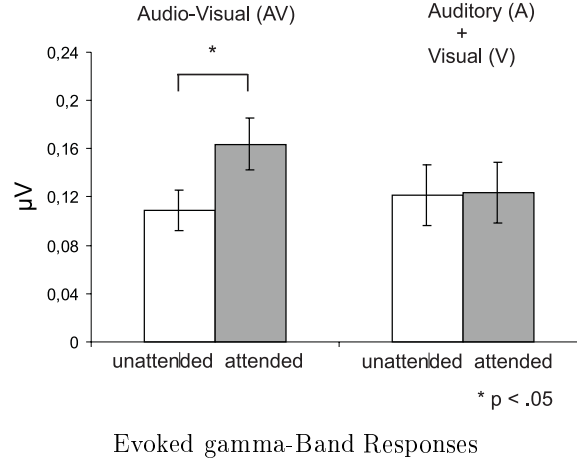
Evoked gamma-Band Responses

Figure 8.4: Mean values and standard error of evoked GBRs for audiovisual (AV) and combined auditory and visual stimuli (A+V) over medial frontal scalp areas.

attended stimuli. When unattended, however, no difference in GBR activity was found between AV and A+V stimuli, and no other effects were observed.

In addition to the evoked GBR activity, attention effects on the induced (non-phase locked) and the total (phase locked and non-phase locked) GBR activity were analyzed in both the anterior and posterior ROIs. To do so, ANOVAs on the induced and evoked GBRs were performed using the same within subject factors as reported for the evoked GBR analyses described above. Figure 8.5 shows the wavelet transformed data for the total, evoked, and induced GBR activity of multisensory (AV) stimuli at one frontal channel. For both the total and the induced GBRs activity, no attention effects were found in the ANOVAs. The absence of attention effects on induced GBR activity might be attributed to a higher noise level in induced GBRs, as compared to the noise level found in evoked GBRs.

Using further ANOVAs it was investigated how the induced or the total GBR activity changed in amplitude after stimulus onset for the multisensory stimuli. To do so, ANOVAs with the same within subject factors as for the evoked GBRs were calculated (see above). For the anterior ROI, these analyses yielded a slight (0.02 $\mu$V), but significant, increase of total GBR activity after stimulus onset, as indicated by a significant effect of the factor 'time window' $((F(1, 13) = 5.76, p < 0.03)$. No other effects were found for the total activity in the anterior ROI. In addition, no effects on the total GBR activity were found for the posterior ROI. In contrast to the slight
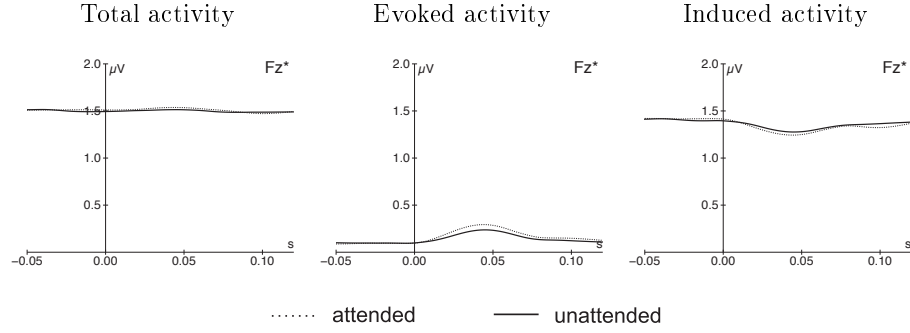
Figure 8.5: Gamma activity in response to attended (dotted line) and unattended (solid line) audiovisual stimuli. Evoked activity (middle graph) increases while induced activity decreases (right graph). Total activity did not change after stimulus onset (left graph). Data are plotted without baseline correction. (*) The electrode is approximately located at the named electrode.

increase of the total GBR activity, a much stronger decrease of induced GBR activity was found over the anterior ROI (-0.12 $\mu$V; $F(1, 13) = 34.59, p < 0.0001$). Furthermore, induced GBR also decreased over the posterior ROI ($F(1, 13) = 22.05, p < 0.0004$). No other effects over anterior and posterior ROIs were observed for the induced activity.

To summarize, for evoked, induced and total activity, an increase of evoked GBRs, a decrease of induced GBRs and a slight increase of the total GBR activity was found after the presentation of multisensory stimuli (Fig 8.5). However, the increase of evoked GBRs and the decrease of induced GBRs were about six times higher (0.12 $\mu$V) than the increase in total GBR activity (0.02 $\mu$V). This possibly indicates that a phase resetting of ongoing high-frequency EEG activity caused the observed increase in evoked GBR activity, instead of additional generators which elicited phase locked gamma activity. To further explore this issue, the degree of phase locking was examined in an additional analysis. Figure 8.6 shows the probability of uniformly distributed phases in time-frequency planes, averaged across 14 subjects, for multisensory audiovisual and unisensory auditory stimuli. A non-uniform distribution of the phases of single trials is expected in case of phase locking and therefore a significant ($p < .05$) result in the test of uniformity. Indeed, Figure 8.6 shows a significant phase locking at the same frequency (at about 45-Hz) and at the same latency (at around 40-60 ms) as the evoked GBRs. This would therefore be consistent with the view that a phase locking of oscillatory GBRs contributed to the evoked GBRs in the present study. Interestingly, Figure 8.6 indicates a more pronounced phase locking for attended than for unattended audiovisual stimuli. This finding is comparable with the effects in the evoked GBRs,

indicating that an enhanced phase locking for attended as compared to unattended audiovisual stimuli possibly contribute to the attention effects in the evoked GBRs.



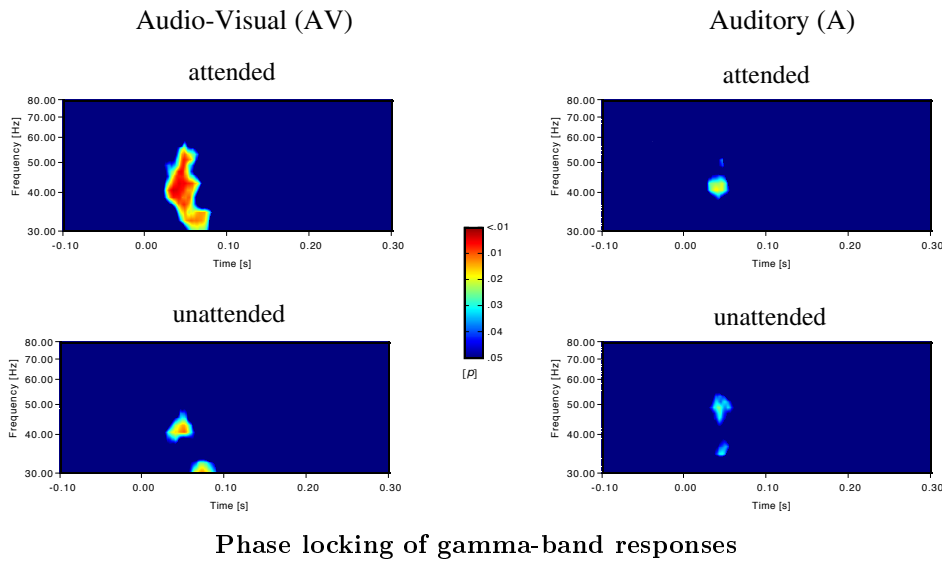**Phase locking of gamma-band responses**

Figure 8.6: Time-frequency planes at a frontal electrode (slightly frontal to Fz) for the probability of a uniform distribution of the single trial phases, averaged over 14 subjects for audiovisual (left column) and auditory stimuli (right column). A significant deviation from a uniform distribution after about 40-60 ms in a frequency range of about 40 to 50-Hz indicates a phase locking of oscillatory gamma responses after stimulus onset. Notice the differences between attended and unattended audiovisual stimuli.

### ERP responses

For a direct contrast, analysis of the ERP responses was done for the same early time interval and regions that were analyzed for the oscillatory GBRs. Figure 8.7 shows early event-related potentials for all three stimulus types (collapsed across left and right hemispaces). The ANOVAs for multisensory audiovisual, unisensory auditory, and unisensory auditory stimuli over frontal and posterior scalp regions, however, did not reveal any statistically significant effects (For longer-latency effects of attention and multisensory interactions, see companion work by Talsma and Woldorff).
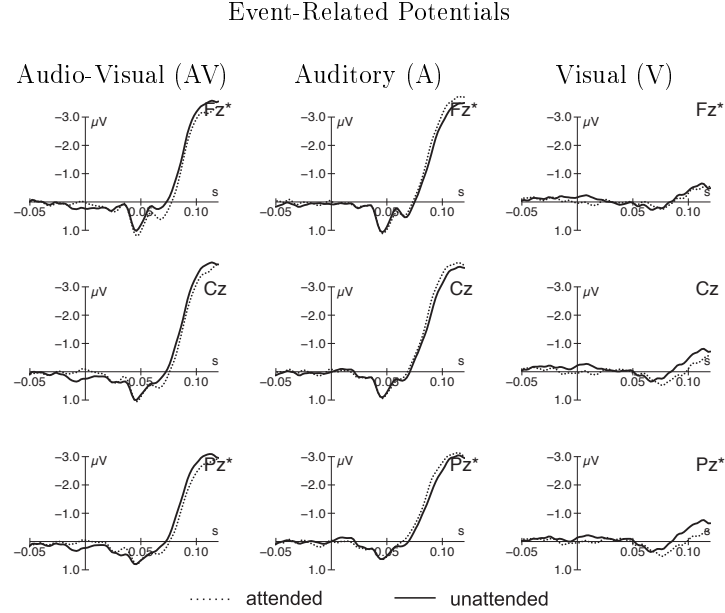
Event-Related Potentials



Figure 8.7: Early event-related potentials for midline electrodes for audioisual stimuli (left), auditory stimuli (center) and visual stimuli (right). Attended stimuli (solid line) and unattended stimuli (dotted line). No significant effects of attention were found for the early time range between 40-60 ms. (*) The electrodes are approximately located at the named electrode.

## 8.4 Discussion

**Gamma-Band Responses (GBRs)**

**GBRs to Multisensory Stimuli**

A key new finding of the present experiment is that spatial attention modulates the early-latency GBRs elicited by multisensory audiovisual stimuli. Attended multisensory (AV) stimuli evoked higher GBRs over frontal areas as compared to unattended multisensory stimuli. Furthermore, GBRs to attended AV stimuli were also stronger than GBRs to combined unisensory (A+V) stimuli. Only a few studies have addressed the role of fast oscillatory activations in multisensory processing. Sakowitz et al. (2001) reported larger GBR amplitudes for audiovisual stimuli (AV) as compared to the amplitudes of combined unisensory (A+V) stimuli. However, in that study the stimuli were passively perceived by the subjects without any explicit task to perform. In addition, in that study unisensory auditory, unisensory visual, and multisensory audiovisual

stimuli were presented separately in different blocks, which does not control for possible arousal or processing-strategy differences between blocks. On the other hand, that study does support the view that GBR activity has some relationships to multisensory integration processes.

In the present paper, all the stimuli (unisensory and multisensory) were presented in intermixed random order within the same blocks of trials, allowing us a well-controlled contrast to evaluate multisensory integration processes. Furthermore, subjects were instructed to maintain the focus of their attention on all those stimuli occurring in one hemifield, while ignoring stimuli in the other hemifield. Under this manipulation, attended multisensory stimuli (AV) elicited more GBR activity relative to combined unisensory (A+V) stimuli. No such differences were found for unattended stimuli. The GBR effects might be a reflection of an amplification mechanism that enhances the integration of attended multisensory inputs. An amplification of attended multisensory stimuli increases their signal to noise ratio and hence their discriminability from unattended stimuli (Hawkins et al., 1990). The finding that GBRs of attended and unattended stimuli only differ for multisensory and not for unisensory stimuli, suggests that GBR modulations may be particularly important for early integration of multisensory stimuli.

The effects reported in the present experiment were most pronounced over frontal scalp areas (see Figures 8.3a and 8.3b). Although this may suggest that the underlying neural generators include some in frontal brain areas, ERP/EEG activity activation from auditory cortex is also mainly picked up over the fronto-central scalp areas. The reason for this is that much of auditory cortex is localized in the obliquely horizontal Sylvian fissure, and electrophysiological activity from this area generates vertically oriented dipolar activity (leaning obliquely forward) that is generally recorded maximally over frontal and central scalp areas (Scherg and von Cramon, 1986). Pantev et al. (1991) reported two bilateral sources for early electromagnetic event-related GBRs in the supratemporal auditory cortex, providing evidence that temporal areas are involved in generating GBRs at this early latency. This finding is in line with the results of an electrocorticographic study in humans (Crone et al., 2001) and single cell recordings in monkeys (Sukov and Barth, 2001), reporting similar GBRs in regions of the auditory cortex. The topographies of the observed GBR effects reported here are thus consistent with generators in auditory cortex, although it is possible that there is additional contribution from frontal cortex.

Finally, the GBR effects on evoked responses were investigated in more detail. The magnitude of the decrease of induced GBR activity is similar to the magnitude of the increase of evoked GBRs. In contrast, the total amount of GBRs increases

only slightly after stimulus onset (about 1/6 of the amplitude change of induced and evoked activity). This finding suggests that the measured effects were possibly caused by a phase resetting of ongoing oscillatory gamma activity rather than an amplitude increase of GBRs (Kolev et al., 1998). If the strong increase of evoked GBRs were due mainly to an amplitude increase in gamma activity which occurred after each stimulus presentation, a higher increase of the total amount of GBRs would have been expected (since this activity consists of both phase locked and non-phase locked activity). For this reason, the phases of oscillatory GBRs were investigated in a separate analysis in which it was found that the phase locking of GBRs showed a similar attention modulation as the evoked GBRs. This provides evidence that selective spatial attention during multisensory processes may modulate a phase resetting of GBRs after stimulus onset in this very early time latency. However, the significant increase in the total amount of GBRs for multisensory stimuli indicates that additional generators, which are activated phase locked to the stimulus onset, may also have contributed to the present effects.

**GBRs to Auditory Stimuli**

GBRs evoked by unisensory auditory stimuli peaked at a latency of about 50 ms after stimulation, which is at approximately the same latency as auditory attention effects on GBRs reported by Tiitinen et al. (1993). In addition, the peak activation of the auditory GBRs was found near the same time range of the earliest ERP and ERF effects of unisensory auditory attention (known as the P20-50 or M20-50 effect) reported by Woldorff and colleagues (Woldorff et al., 1987, 1993). Because the GBRs in the present experiment correspond well with those reported by Tiitinen et al. (1993) and were also peaking at about the earliest time at which ERP effects of auditory attention have been observed, it is somewhat surprising that there was no attention effect on these unisensory auditory GBRs. However, this result is similar to that of Karakaş and Başar (1998) who ran a series of five different auditory experiments, in which no attention effects on early GBRs were found, leading them to conclude that such early GBR activity simply reflects automatic sensory processing activity. On the other hand, there was a robust effects of attention on the GBRs to the multisensory stimuli. This finding would thus not fit with the view of Karakaş and Başar (1998) that such activity reflects automatic sensory processing, because it suggests that early GBRs can be influenced by selective attention. As discussed earlier, GBRs to attended multisensory (AV) stimuli were higher as compared to GBRs to combined unisensory (A+V) stimuli. Because almost no visual GBR activation was found (see discussion below), the combined unisensory (A+V) gamma activity is therefore almost entirely composed of

auditory GBRs. Thus, one can argue that the attention effects on multisensory (AV) stimuli are, in fact, related to multisensory integration.

### GBRs to Visual Stimuli

In contrast to auditory and multisensory GBRs, little or no GBR activity was elicited by visual stimuli. This result differs from other studies that have consistently reported GBR activity elicited by visual stimuli (Böttger et al., 2002; Keil et al., 2001; Strüber et al., 2000). These other studies, however, presented visual stimuli at the center of the visual field, instead of the peripheral presentation that was used in the present experiment. Because stimulus properties appear to strongly influence visual GBRs (Edwards et al., 2001), it is possible that the lack of significant visual GBR activity observed here might be due to this peripheral presentation. Combined with the anteriorly distributed topography of the multisensory GBRs, the lack of visual GBRs also suggests that occipito-visual areas did not contribute much to the early multisensory attention or integration effects observed. It is interesting to note that these findings also differ from a recent study by Foxe and Simpson (2002). These authors reported that early occipital activations could influence subsequent ERP activity that started at about 80 ms over frontal scalp areas. However, the present frontal effects were notably earlier (namely beginning by around 40 ms post-stimulus) Therefore, the combination of the absence of occipital effects and the fact that the frontal effects peaked markedly earlier than 80 ms suggests that the occipital-frontal network, as reported by Foxe and Simpson (2002), is not likely driving the frontal GBR effects.

### GBRs: General Discussion

Based on human and animal studies (Pantev et al., 1991; MacDonald and Barth, 1995), as well as scalp topographies, the observed GBRs and GBR effects are probably generated in regions of the superior temporal lobe, including the auditory cortex, with perhaps additional contribution by frontal areas. The specific role of GBRs in the primary and secondary auditory cortex has been examined in several animal studies (MacDonald and Barth, 1995; Brosch et al., 2002). Furthermore, it has been suggested that the thalamus plays a crucial role in the modulation of GBRs in the auditory cortex (Barth and MacDonald, 1996; Sukov and Barth, 1998). Interestingly, Ptito et al. (2001) reported a relationships between visual processing in the thalamus and visual processing in the auditory cortex. These authors found some multisensory cells in the auditory cortex which are responsive to both visual and auditory inputs. Since the latency of the effects found in the present study (at about 50 ms) seems to be too early for an attention-modulated network between occipital and temporal brain areas, it might

be that visual-auditory thalamic connections are involved in the present attention effects. Selective attention effects at the thalamic level have recently been demonstrated (O'Connor et al., 2002; Woldorff et al., ress). Using fMRI, O'Connor et al. (2002) showed that attended stimuli evoke enhanced neural responses in the lateral geniculate nucleus (LGN) as compared to ignored stimuli and that this enhancement was directly proportional to the attentional load; LGN activations for unattended stimuli were lower when subjects performed a difficult task than when they performed an easy task. This finding indicates that selective attention can affect neuronal inhibitory and excitatory processes already at the level of the thalamus. However, since O'Connor et al. (2002) used an fMRI design in their study, no conclusions can be made about the question whether these effects occur at early or a late stages of sensory information processing. The early effects in the present study, however, may support the assumption that selective attention modulates the thalamo-cortical system at very early stages of information processing.

Although the reported GBR effects may have major contributing generators in auditory areas in the temporal lobe, it might also be that attentional control networks in frontal areas are involved in modulating the amplitude of GBRs (Brunia, 1999; LaBerge, 1995, 2001). Empirical evidence for this theory stems from a number of PET and fMRI studies that reported frontal and prefrontal activations related to multisensory processing (Gonzalo et al., 2000; Calvert et al., 2001; Lekeu et al., 2002). Similarly, Bushara et al. (2001) studied the effects of stimulus onset asynchrony on audiovisual stimulus processing using PET. In that study, subjects were required to detect audiovisual stimuli with an onset asynchrony between visual and auditory stimulus among synchronously presented audiovisual stimuli. The authors found an enhancement of activation in various cortical regions, including frontal areas, in an asynchrony detection task, as compared to a control task where all stimuli were presented synchronously and in which the color of the visual stimuli had to be discriminated. In addition, Fuster et al. (2000) have shown that the prefrontal cortex of rhesus monkeys is involved in associating visual and auditory stimuli.

**Event-related potentials**

Unlike earlier studies (Woldorff and Hillyard, 1991; Woldorff et al., 1993), the present ERP results, as well as those reported in the companion article (Talsma and Woldorff, submitted, this issue), did not show any selective attention effects on ERPs in the very early (i.e., 50 ms) latency range. A possible explanation for the absence of these early ERP effects might be that Woldorff and Hillyard (1991) and Woldorff et al. (1993) used a much higher presentation rate of successive auditory stimuli that forced

subjects to focus much stronger on one location than in the present Experiment 4. In addition, stimuli of different modalities were presented intermixed with each other in the present experiment, which forced subjects to divide their attention between visual and auditory modalities. In contrast, most studies reporting very early attention effects on ERPs stimulated only one sensory modality, and at faster rates than used here (Woldorff and Hillyard, 1991; Woldorff, 1995). As shown by these earlier studies, obtaining these particularly early ERP effects may depend critically on the stimulation rate and the very high focusing of auditory attention (Woldorff, 1995). The fact that attention affects early GBRs, but not ERPs, suggests that GBRs may be more sensitive to early attentional modulation than are ERPs.

Similarly, multisensory integration ERP effects have previously been reported to occur as early as 50 ms after stimulus onset in some studies (Giard and Peronnet, 1999; Molholm et al., 2002), whereas other studies did not report such early integration effects (Fort et al., 2002a; Teder-Sälejärvi et al., 2002). Teder-Sälejärvi et al. (2002) as well as Talsma and Woldorff (submitted) have argued that this apparent very early effect of multisensory integration might be an artifact that is introduced by the methodology used in evaluating multisensory integration in the studies that have reported it (see Talsma and Woldorff (submitted) and Teder-Sälejärvi et al. (2002) for an extensively discussion about this issue). The important point here is that there were no ERP effects of multisensory integration at the early (50 ms) latency, after correcting for this problem (by subtracting the activity from no-stim trials from the ERPs). Furthermore, no other early-latency attention effects on the ERPs were found for any of the stimuli. As noted above, however, the fact that there were attention effects of multisensory integration on the early GBRs, but not on ERPs, suggests that GBRs may be more sensitive to certain early experimental manipulations than ERPs.

The main purpose of the Experiment 4 was to analyze the influence of selective spatial attention on fast oscillatory binding processes in audiovisual integration. As a main result is was found that attention can amplify evoked oscillatory GBRs for attended audiovisual stimuli over frontal scalp areas at a very early latency (at about 50ms). This multisensory integration effect appears to be mostly due to higher phase resetting of GBRs in response to the attended as compared to the unattended audiovisual stimuli. In contrast, no such early attention modulation was found in the ERP, on which the interactions of attention and multisensory integration did not begin until around 100 ms after stimulus presentation (see Talsma and Woldorff (submitted)). Thus, it can be suggested that selective spatial attention modulates integrative binding processes of multisensory inputs, as measured by oscillatory responses in the gamma-band, at the earliest levels of cortical signal processing.

# 8.5  Summary

Integrative binding of the various sensory features of a multisensory object allows us
to perceive these separate features as a coherent whole object. Several studies have
indicated that fast oscillatory responses in the EEG gamma-band (30-80 Hz) may
reflect processes that play a crucial role in binding. So far, no study has examined
the relationship between gamma-band responses (GBRs) and attentional influences
on multisensory integrative processing. The present Experiment 4 explored the influ-
ence of multisensory (audiovisual) integration and spatial attention on GBRs in the
EEG. Streams of unisensory auditory (A), unisensory visual (V), and multisensory
(AV) stimuli were rapidly presented to the left and right hemispaces while subjects
attended to a designated side to detect occasional deviant target stimuli (where the
feature deviation could be auditory or visual). Focus of the analysis here is on trig-
gered oscillatory responses to the non-target stimuli and how these responses varied as
a function of attention and multisensory integrative processes. Evoked GBRs were ob-
served at about 50ms after stimulus presentation for both the unisensory auditory and
multisensory audiovisual stimuli. Importantly, for attended multisensory (AV) stim-
uli, higher evoked GBRs were observed as compared to unattended multisensory (AV)
stimuli and as compared to combined unisensory (A+V) stimuli over medial frontal
scalp areas. Further analysis showed that this integration effect is probably caused, at
least in part, by a stimulus-triggered phase resetting of ongoing gamma-band activity.
No corresponding attention effect was found for the unisensory stimuli. In addition,
these early latency effects (at about 50ms) were observed only in the evoked GBRs and
not in the event-related potentials. Thus, these data provide new electrophysiological
evidence for a unique relationship between selective attention in multisensory integra-
tion and early oscillatory responses in the evoked gamma-band.

# Chapter 9

# General discussion

Attentional processes have been widely associated with neuronal responses in the brain (Humphreys et al., 1999; Pashler, 1998a). Thereby, different anatomical and neurophysiological correlates of attention have been described. The present work focused on the investigation of the relationships between electrophysiological and electromagnetic brain responses and SA. In order to examine these relationships, a series of four experiments was performed (see Fig. 9.1 for a summary of the results). The specific results and hypotheses of these experiments were already discussed in the respective Chapters 5 to 8. For this reason, the present chapter will focus on the discussion of the general working hypotheses which were formulated in detail in Chapter 4. Regarding these hypotheses, the present work yielded the following results:

| | |
|---|---|
| ***Hypothesis I:*** | Enhanced ERP amplitudes were expected for attended signals. Furthermore, it is assumed that attentional top-down modulations can cause an early functional separation of activity in the auditory cortex. |
| ***Result:*** | *The experiments showed that attention causes an amplification of ERP amplitudes in most cases. In addition, the latency and source location of different ERP components were affected by selective attention.* |

| | |
|---|---|
| ***Hypothesis II:*** | Oscillatory gamma activity is positively related to selective attention. |
| ***Result:*** | *A positive relationship between selective attention and evoked gamma activity was found. Furthermore, a detailed analysis revealed that the evoked gamma activity was possibly caused by an early phase locking of oscillatory responses.* |
| ***Hypothesis III:*** | Regarding the question about the temporal order of feature binding and attention, it was expected to find evidence for the binding-first model. |
| ***Result:*** | *The present work provided evidence for the binding-first model. Feature binding processes can possibly capture visual spatial attention.* |

Amplitudes, latencies and source locations of different ERP components showed a relationship to attentional processes (Experiment 1 to 3). Thereby, enhanced ERP amplitudes as a marker of attention were found in Experiments 1 and 2. However, the results of Experiment 1 further suggest that some components, for example the P3, may decrease with enhanced demands of attentional resources. Another finding with relation to ERPs was an early functional separation of different regions in the auditory cortex which can be associated with top-down modulated attention (Experiment 3).

The relationship between oscillatory GBRs and selective attention fits well with the results of previous studies (for a recent review see Fell et al. 2003). However, the present results extended the knowledge about the positive relationship between SA and oscillatory GBRs by demonstrating that attention effects on early visual GBRs occur particularly under specific conditions, for example for centrally presented stimuli. Furthermore, the analysis of different types of gamma activity showed that attention effects on early evoked GBRs are mainly caused by a phase locking of fast oscillatory activity (Experiment 1, 2 and 4).

As a third result, a relationship between early feature binding and SA was demonstrated in Experiments 2. Visual binding can occur at very early stages of information processing. Furthermore, it is likely that these processes can capture attention, or initiate an automatic shift of visual spatial attention (Section 2.1.3). The three main results of the present work are now discussed in more detail.
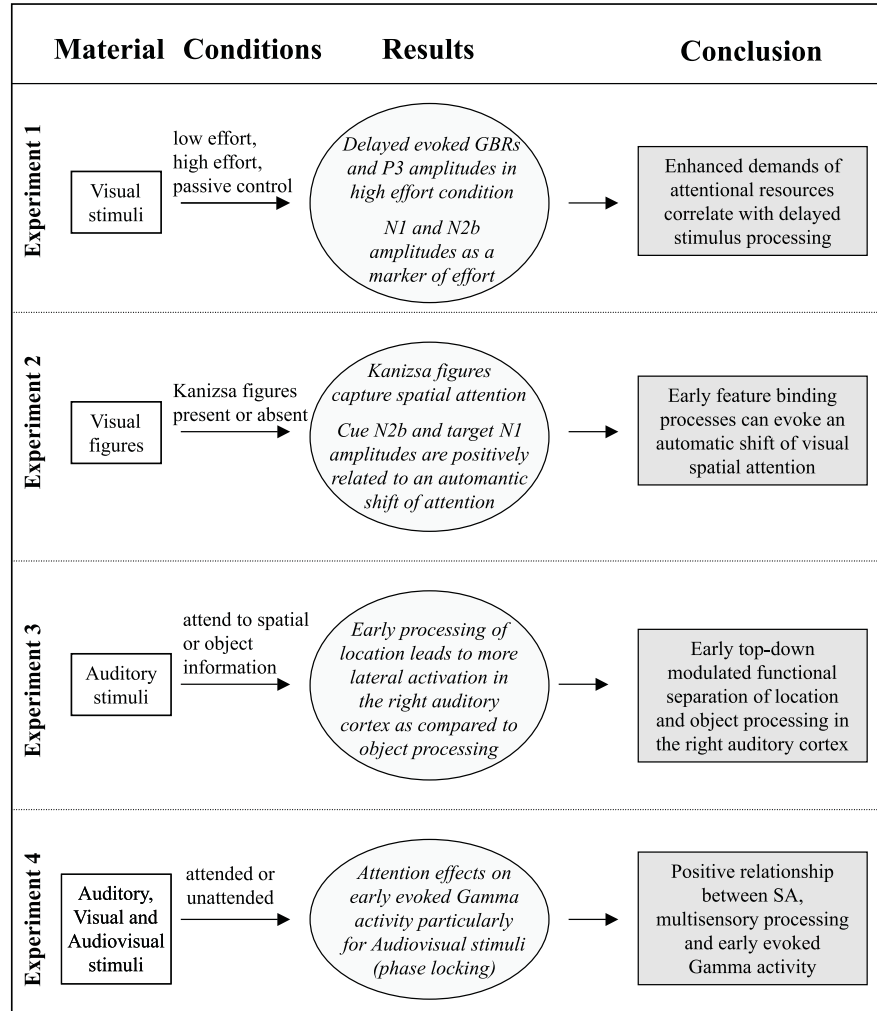
| Material | Conditions | Results | Conclusion |
|---|---|---|---|

**Experiment 1**

Visual stimuli

low effort, high effort, passive control

*Delayed evoked GBRs and P3 amplitudes in high effort condition*

*N1 and N2b amplitudes as a marker of effort*

Enhanced demands of attentional resources correlate with delayed stimulus processing

**Experiment 2**

Visual figures

Kanizsa figures present or absent

*Kanizsa figures capture spatial attention*

*Cue N2b and target N1 amplitudes are positively related to an automantic shift of attention*

Early feature binding processes can evoke an automatic shift of visual spatial attention

**Experiment 3**

Auditory stimuli

attend to spatial or object information

*Early processing of location leads to more lateral activation in the right auditory cortex as compared to object processing*

Early top-down modulated functional separation of location and object processing in the right auditory cortex

**Experiment 4**

Auditory, Visual and Audiovisual stimuli

attended or unattended

*Attention effects on early evoked Gamma activity particularly for Audiovisual stimuli (phase locking)*

Positive relationship between SA, multisensory processing and early evoked Gamma activity

Figure 9.1: Summary of the main results from the four experiments in the present work.

# 9.1 Selective attention effects on event-related potentials

The present work yielded SA effects on amplitudes, latencies and sources of different ERP components. Thereby, the most consistent correlate of SA was an amplification of ERP amplitudes. Amplification of attended signals to increase their signal-to-noise

ratio and hence their discriminability from unattended signals is an important mechanism of SA. This mechanism has also been labelled as sensory *gain control*. According to Hillyard et al. (1999), the concept of *gain control* traces back to early animal studies in the 1950s and 1960s which investigated the relationship between SA and electrical responses in sensory processing. In these studies, an increased activity for attended as compared to unattended stimuli was reported (Hernandez-Peon et al., 1956; Hernandez-Peon, 1966). This has been interpreted as a gating process which suppresses or blocks unattended inputs. The concept of *gain control* was also a central element of the first modern theories of SA which came up in the 1950s and 1960s, like for example Broadbents filter theory or Treisman's theory on perceptual selection (Section 2.1.1 and 2.1.3). Comparable with the results of animal studies, subsequent EEG studies in humans revealed a positive relationship between SA and different components in the ERP (Hillyard and Mangun, 1987; Luck, 1995; Mangun, 1995; Woldorff et al., 1997). Attended stimuli usually evoke higher ERPs as compared to unattended stimuli.

In the present work, the earliest component which showed a positive relationship to SA was the visual N1 (Experiment 1 and 2). This component peaked after about 170 ms and had an occipito-parietal scalp distribution. Experiment 1 yielded enhanced N1 amplitudes in two visual discrimination tasks as compared to a passive control task. This indicates that N1 amplitudes may reflect processes which are involved in visual discrimination (Vogel and Luck, 2000). Such discrimination processes require attention, suggesting a positive relationship between visual N1 amplitudes and SA. Attention effects on N1 amplitudes were also found for N1 amplitudes after target presentation in Experiment 2. Already in 1979, Näätänen and Michie suggested that the N1 component appears to be larger for relevant inputs (Näätänen and Michie, 1979). Furthermore, the finding that N1 amplitudes were enhanced in the two discrimination tasks as compared to the passive task, but did not differ between the hard and the easy discrimination task, may indicate that visual N1 amplitudes increase when a specific degree of attention is dedicated to a stimulus (as it was necessary to perform the discrimination tasks). The earliest component which showed a direct relationship to task difficulty and hence to the effort which is necessary to perform a task was the N2b. N2b amplitudes had a maximum over the vertex and a latency of about 260-280 ms. It has been suggested that this component might reflect an attentional filtering (Eimer, 1996), or a feature non-specific selection process (Lange et al., 1999). The present findings support these assumptions by demonstrating that N2b amplitudes are positively related to the difficulty of a discrimination task (Experiment 1) and to an automatic directing of visual spatial attention (Experiment 2). The finding that N2b and N1 amplitudes were differently related to SA indicate that these components

may reflect different mechanisms of SA. For a selective color search task, Wijers et al. (1989b) reported different attention effects on N1 and N2b amplitudes in response to the attended color. The authors suggested that occipital N1 amplitudes may reflect a feature specific attention, whereas the central N2b was assumed to be associated with processes of covert orienting of attention. The present findings fit well with this assumption. However, attention effects on the N1 and N2b components have been reported for different paradigms in specific ways (Mangun, 1995; Luck et al., 2000). For this reason, it is difficult to make general assumptions about the functional processes underlying these components. Nevertheless, the present findings indicate at least that N1 and N2b amplitudes reflect distinct mechanisms in color discrimination and visual spatial processing. These mechanisms are further associated with SA.

Another component which was related to SA was the target P3. This component has a late latency of about 300-500 ms and a maximum amplitude over parietal scalp areas. Experiment 1 of the present work yielded smaller P3 amplitudes in the hard as compared to the easy discrimination task. Furthermore, longer latencies were found in the hard task. Similar effects of task difficulty on P3 amplitudes have been reported before (Polich, 1987). It has been suggested that the reduction of P3 amplitudes in hard as compared to easy tasks might reflect a greater variability in the timing of mental operations that underlie P3 amplitudes in hard tasks (Palmer et al., 1994). Longer latencies of target P3 amplitudes in hard as compared to easy tasks might indicate a longer duration of stimulus evaluation. Assuming that the hard task requires more effort than the easy task in Experiment 1[1], the reduction and delay of P3 amplitudes may indicate that enhanced demands of attentional resources can cause a delay and a reduction of ERP components.

However, attended inputs evoke in most cases higher ERP amplitudes as compared to unattended inputs. This finding can be related to the *spotlight metaphor* of attention. According to this metaphor, attention serves as an internal eye that can shift its focus from one location to another (Fig. 1.1, p. 2). This mechanism is suggested to be particularly modulated by attentional top-down processes. Evidence for a crucial involvement of top-down mechanisms in cortical processing came also from Experiment 3. This experiment revealed an early functional separation of feature object and feature location processing in the right auditory cortex. Such an early separation of object and location processing has been described before by Ungerleider, Mishkin and colleagues for the visual modality (Mishkin et al., 1983; Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994). Thus, early anatomical separation in cortical stimulus processing seems

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[1]This assumption is based on the behavioral data of this experiment which showed longer RTs and a higher error rate in the hard as compared to the easy discrimination task.

to be correlated to top-down modulated SA. In addition, Desimone (1999) proposed
that top-down modulated processes interact with stimulus driven bottom-up mecha-
nisms. A comparable assumption is made in the integrated model of visual processing
by Bullier (Fig. 2.7, p. 15). Recent findings support the idea that recurrent connections
between early and higher visual areas form functional circuits which are affected by SA
(Tong, 2003). Such mechanisms may also explain the present findings in the context of
visual feature binding and attention which are discussed in Section 9.3.

## 9.2   Selective attention effects on gamma-band responses

Previous studies reported an enhancement of oscillatory gamma activity for attended
as compared to unattended stimuli in the visual (Gruber et al., 1999), the auditory (Ti-
itinen et al., 1993), and in the somatosensory modality (Göbbele et al., 2002). Theses
findings suggest a positive relationship between gamma activity and selective attention.
In the present work, attention effects on oscillatory GBRs were investigated in unisen-
sory visual, unisensory auditory and multisensory audiovisual stimuli. Thereby, two
main correlates of SA were found. The first correlate was an amplification of gamma
amplitudes to attended stimuli. It is likely that this amplification is caused by an early
phase locking of oscillatory activity in the gamma range (Experiment 1 and 4). The
second correlate was a delay of GBRs. The delay of GBRs corresponded with the dif-
ficulty of a discrimination task (Experiment 1). In general, attention effects on GBRs
occur earlier than on ERPs, indicating that modulation of oscillatory GBRs is a very
early correlate of attention. However, the early effects on GBRs might be related to
subsequent effects on ERPs. Evidence for this assumption came for example from the
analysis of the gamma and P3 latencies in Experiment 1. Furthermore, a close re-
lationship between oscillatory activity and ERPs has recently been demonstrated by
Karakaş et al. (2000b) and Makeig et al. (2002). Makeig et al. (2002) suggested that
ERP components might be generated, at least in broad parts, by a superposition of
phase locked oscillatory activity. By analysing the phases of single EEG epochs, Makeig
and colleagues showed that a phase locking of ongoing alpha activity may generate the
visual N1 component. This indicates that phase locking might be involved in the atten-
tion effects on GBRs and ERPs in the present work. The relationship between ERPs
and oscillatory activity has also been investigated by Başar and collagues (Başar et al.,
1999b,a, 2001a,b; Karakaş et al., 2000a). Başar et al. proposed that the analysis of
oscillatory activity in different frequencies ranges allows a better representation of cog-
nitive processes than the analysis of ERPs. The present results support this assumption

by demonstrating that attention effects on GBRs appear to occur earlier than attention effects on ERPs (Experiment 1 and 4). Also Herrmann and colleagues consistently reported earlier attention effects on oscillatory GBRs than on ERPs (Debener et al., 2003; Herrmann et al., 1999; Herrmann and Knight, 2001). Herrmann and Mecklinger (2001) found visual attention effects on GBRs at a latency of about 50-100 ms. In contrast, the earliest attention effects on ERPs a latency of about 300-500 ms. Even if the time differences for the attention effects on GBRs and ERP are shorter in Experiment 1 (60-120 ms for GBRs and 150-190 ms for ERPs), the results indicate that evoked GBRs are an earlier marker of SA than ERPs.

In general, three types of gamma activity were analyzed: phase locked (evoked), non phase locked (induced) and total (evoked+induced) activity. The analyses of the three types of activity suggested that the evoked gamma activity is possibly caused by a phase locking of oscillatory GBRs and not by an increase of gamma amplitudes. The logic behind this issue has been discussed in more detail in Section 8.4. A relationship between phase locking of oscillatory gamma activity and SA has also been reported by Yordanova, Kolev and collagues (Yordanova et al., 1997a,b; Kolev et al., 1998). This suggests that the attention effects on GBRs in the present work were probably caused by an early phase locking of gamma activity. Interestingly, no increase of induced gamma activity was found in the present work. The lack of induced GBRs is not easy to explain and until today there is no contending explanation for this finding. Thomas Gruber from the Leipzig University (personal communication) speculates that Kanizsa figures lack the associative content in order to induce gamma responses to measure them (reliably) on the scalp level. This assumption is supported by the results of Edwards et al. (2001) who showed that stimulus properties appear to influence GBRs. However, other authors who used similar stimulus material as in the present study reported an increase of induced GBRs after stimulus onset (Tallon-Baudry et al., 1996; Tallon-Baudry and Bertrand, 1999a). For this reason, it is more likely that the experimental setting in combination with the used stimulus material may explain the lack of induced GBRs. However, further studies are necessary to clarify the specific relationships between stimulus properties, experimental settings and gamma activity.

There are some remarkable findings in Experiment 4 which should be discussed in more detail here. As a main result of this experiment, enhanced GBRs for attended as compared to unattended multisensory audiovisual stimuli were found. The topography of this effect indicated that auditory cortical areas, which are located in the temporal lobe, are crucially involved in generating the gamma activity (Section 8.3). Interestingly, top-down modulated attention effects on audiovisual stimuli started already after about 40 ms. In contrast, the earliest attention effects on unisensory visual

stimuli were found for the P1 component which has a latency of about 90 ms (Talsma and Woldorff, submitted). Heinze et al. (1994) showed that the sources of the P1 component are probably located in extrastriate visual areas of the occipital lobe. For this reason, it is unlikely that occipital areas are involved in the very early attention effects on audiovisual stimuli in Experiment 4. As mention before, it is likely that the gamma activity in this experiment is generated in the auditory cortex. This raises the question where the attended visual and auditory stimuli are integrated. One possibility would be an integration via connections between the lateral geniculate nuclei (LGN) of the visual thalamus and the auditory cortex. However, there is only few evidence for such a direct connection. For this reason, it is more likely that the integration of attended audiovisual stimuli takes place at the level of thalamocortical processing, as illustrated in Fig. 9.2. The Figure shows a hypothetical model which suggests that the enhanced oscillatory gamma responses for attended audiovisual stimuli are caused by an interplay between the unspecific nucleus reticularis thalami (NRT) and the specific nuclei of the thalamus (lateral geniculate nucleus (LGN) for visual inputs and medial geniculate nucleus (MGN) for auditory inputs). Interestingly, the NRT, which has been closely related to attentional processing (Steriade et al., 1986; Weese et al., 1999), is connected with the LGN (Wang et al., 2001) and the MGN (Tennigkeit et al., 1998). In addition, a direct association between fast oscillatory responses in the acoustic thalamus and the auditory cortex has been demonstrated by Barth, Sukov, and colleagues (Barth and MacDonald, 1996; Brett and Barth, 1997; Sukov and Barth, 1998, 2001).

An important role of thalamocortical gamma activity in attentional processing has been postulated by different authors (Ribary et al., 2001; Llinás and Ribary, 2001; Steriade et al., 1990; Steriade, 2001). Also, LaBerge suggested a close relationship between fast oscillatory responses in the thalamus and SA in his *triangular circuit* model of attention (Fig. 9.3). The author proposed that the thalamus is crucially involved when a task is designed to produce sustained attention (LaBerge, 1995, 2001). In Experiment 4, the subjects had to attend to a continuous stream of unisensory auditory, unisensory visual and multisensory audiovisual stimuli. Thus, subjects had to sustain their attention during the whole experiment, which possibly required thalamocortical processing. However, it is important to point out that the EEG data from Experiment 4 suggests only indirectly that thalamocortical structures may contribute to the very early top-down attention effects on multisensory stimuli. Further studies, recording electric activity from the thalamus would be helpful to prove the hypothetical model which is illustrated in Fig. 9.2.

Another interesting result of Experiment 4 is the lack of GBRs for visual stimuli. We could show in a further study that the same visual stimuli as used in Experiment 4
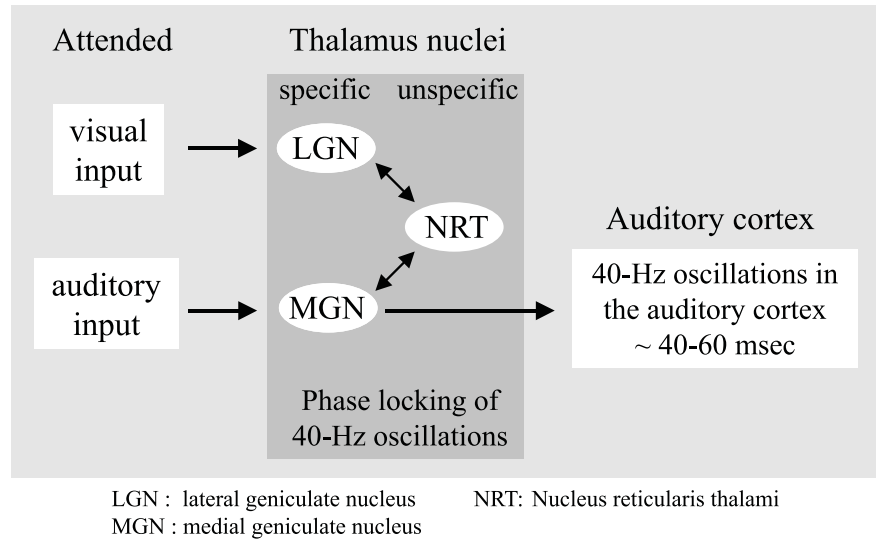
Figure 9.2: Hypothetical model of the relationship between oscillatory gamma activity in the auditory cortex and thalamocortical processing of attended audiovisual inputs (based on findings from Experiment 4). Visual and auditory inputs are processed in the specific nuclei of the thalamus at early stages of information processing (LGN and MGN, respectively). The LGN and MGN are both connected with the unspecific nucleus reticularis thalami, which was suggested to play an important role in selective attention. The model assumes that attended audiovisual inputs can cause an enhanced phase locking of oscillatory 40-Hz responses in thalamocortical processing, including the auditory cortex. Interestingly, 40-Hz oscillations in response to unattended inputs were the same for audiovisual and unisensory auditory stimuli, indicating that thalamocortical processing of multisensory stimuli can be affected by selective attention.

evoke gamma activity when they are presented centrally (Senkowski et al., 2003b). This indicates that early evoked GBRs might be particularly affected by inputs from foveal vision. This may also explain the lack of attention effects on GBRs in Experiment 2 where the cue and target stimuli were presented laterally. To summarize the results of Experiment 4, very early attention effects (at about 50 ms) were found on GBRs for audiovisual stimuli but not for unisensory stimuli. These effects were not observed in the ERPs. This suggests that attention affects very early gamma responses of multisensory but not of unisensory stimuli. Furthermore, the experiment demonstrated that the enhanced GBRs for attended as compared to unattended audiovisual stimuli are possibly related to differences in phase locking of oscillatory gamma activity. Thus, it is likely that phase locking of GBRs is a very early neuronal correlate of attention.
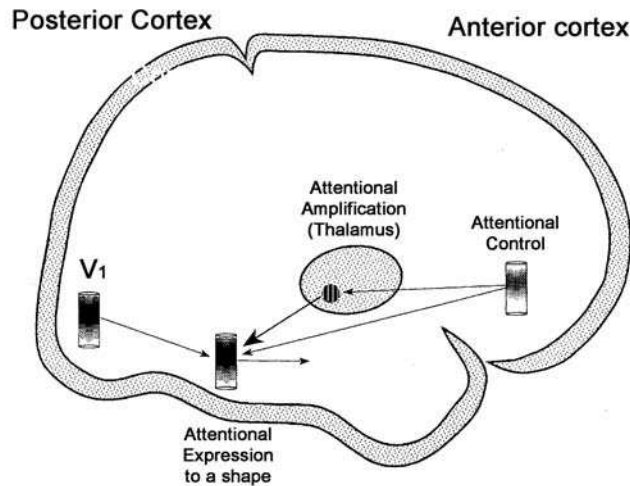
Figure 9.3: Schematic illustration of the triangular circuit theory of attention by David LaBerge. Attention is controlled in anterior brain areas which send pulses to the shape area at the posterior cortex. These two areas interact via a direct cortico-cortical pathway and an indirect pathway that involves the thalamus. It has been suggested that fast oscillatory activity plays an important role in these attentional processes. (Source: LaBerge, 2001, p. 8)

## 9.3 Selective attention and visual feature binding

Visual feature binding is necessary to integrate the different features of an object into one single coherent object. An example for a binding process was shown in Fig. 2.10 (p. 20). Feature binding processes have also been closely related to attention (Robertson, 2003). However, there are two current models regarding the temporal order of binding processes and attention. The first model assumes that binding processes operate at very early stages of information processes. It has been suggested that these processes can occur at parallel stages of information processing without top-down modulated attention (Davis and Driver, 1998). This model is called the *binding-first model*. A second model is the *attention-first model*. The *attention-first model* suggests that attention to an object is necessary in order to bind the single features of it together (Treisman and Gelade, 1980; Treisman, 1998). In the present work, the temporal order of feature binding processes and attention was investigated in an EEG experiment employing illusory Kanizsa figures among distractors as stimulus material (Experiment 2). The edges of these figures can be bound together to form one coherent object. As a main result, the experiment showed that illusory Kanizsa figures pop out of visual displays and drew the perceivers attention. This suggests that early binding processes can

capture spatial attention. Von der Heydt, Peterhans and colleagues investigated early processing of illusory contours in visual areas V1 and V2 in monkeys (von der Heydt et al., 1984; von der Heydt and Peterhans, 1989; Peterhans and von der Heydt, 1989, 1991). The authors reported that cells in the extrastriate visual cortex (area V2) respond to illusory contours, while they failed to find contour sensitive cells in the striate visual cortex (area V1). In later studies, however, Grosof et al. (1993) showed that specific cells in V1 are sensitive to illusory contours. Furthermore, Lee and Nguyen (2001) reported that neuronal responses to illusory contours begin earlier in V2 (at about 70 ms in the superficial layers) than in V1 (at about 100 ms). Such binding mechanism may amplify the signals of a stimulus. This assumption is supported by behavioral data showing that attention shifts to salient target stimuli (Nothdurft, 2002).

Interestingly, there is also evidence that higher cortical areas of the parietal lobe are involved in feature binding processes (Robertson, 2003). This indicates that attentional top-down processes may also be involved in feature binding, as suggested by the *Feature Integration Theory* (Treisman and Gelade, 1980). Friedman-Hill et al. (1995) described behavioral data from a neurological patient (R.M.) with bilateral parietal-occipital lesions. R.M. was not able to combine colors and shapes or to judge relative or absolute visual locations. The authors suggested that an inadequate spatial representation causes R.M.'s deficits. Ashbridge et al. (1999) also investigated patients with parietal lesions but failed to find evidence for an involvement of parietal areas in feature binding. These apparently inconsistent findings might be explained by recent studies from Shafritz et al. (2002). Shafritz and collagues showed that the parietal cortex is related to feature binding only under specific conditions. In their studies, parietal activity was found in a feature-matching task where the location of two simultaneously presented objects could be used to resolve scene ambiguity. In contrast, no activity was observed when the same objects were presented sequentially. Based on these observations, Shafritz et al. (2002) suggested that the parietal cortex is particularly involved in feature binding when enough spatial information is available to resolve the feature ambiguities of an object.

To summarize these results, it is likely that the temporal order of feature binding and visual attention crucially depends on the task requirements. For example, several studies supporting the *attention-first model* reported attention effects on feature binding of different dimensions of an object like color, form, and location (Friedman-Hill et al., 1995; Treisman, 1998). In contrast, evidence for the *binding-first model* came frequently from feature object binding processes within one dimension (as for example the binding of inducer disks as demonstrated in the present work). This suggests that

different types of binding might be related to spatial attention in different ways. How-
ever, the fact that both bottom-up and top-down processes have been associated with
feature binding showed that the *binding-first model* and the *attention-first model* do not
exclude each other. Furthermore, it might be that bottom-up and top-down modulated
processes interact with each other or overlap each other in time. This makes it hard
to clearly separate these two processes. However, the present work demonstrated that
feature binding processes are closely related to visual spatial attention.

## 9.4   Summary and perspectives for future research

One main topic of modern Cognitive Neurosciences is the investigation of attentional
processes in the brain. However, the cortical mechanisms underlying attentional pro-
cesses are not yet clearly understood and different models exist which try to explain
how attentional mechanisms are represented on the neuronal level (Bullier, 2001b; Des-
imone, 1999; Posner and Raichle, 1994). The goal of the present work was to examine
more general neuronal correlates of selective attention (SA) in the electroencephalo-
gram (EEG) and magnetoencephalogram (MEG). A series of four experiments, covering
different attentional paradigms, was carried out. Foci of the EEG and MEG analyses
were thereby cortical responses in the event-related potentials (ERPs) and oscillatory
gamma-band. The four experiments yielded three interesting findings.

First, attention effects on amplitudes, latencies and sources of early responses in the
ERP were found. Most ERP components showed an increase in amplitude as a correlate
of attention (Experiment 1 and 2). It has been suggested that an amplification of at-
tended stimuli enhances their discriminability from unattended inputs (Hillyard et al.,
1999). The present work further demonstrated that enhanced demands of attentional
resources can also affect a delay or even a decrease of late ERP components. This indi-
cates that amplification is not the only correlate of attentional processing in the ERP.
Another early correlate of SA was a functional separation of feature object and feature
location processing in the auditory cortex (Experiment 3). This finding is compara-
ble with previous observations in the visual modality (Ungerleider and Mishkin, 1982;
Mishkin et al., 1983), indicating the existence of functionally separated areas in sen-
sory corticies. The activation of these areas can be influenced by top-down modulated
attention.

In addition to the effects on ERPs, attention effects on evoked oscillatory gamma
activity have been found (Experiment 1, 4). Evoked gamma activity was thereby posi-
tively related to SA. Furthermore, attention affects occurred earlier on gamma activity
than on ERPs, suggesting that fast oscillatory responses are a very early correlate of

SA. In particular, gamma activity was found to occur phase locked to stimulus onset (evoked activity). More detailed analyses showed that early phase locking processes possibly caused these evoked responses and thus the attention effects on gamma activity. Experiment 4 revealed very early attention effects on audiovisual stimuli (after about 50 ms), which possibly occur in auditory cortical areas. A model which proposes an important relationship between thalamocortical processing and top-down modulated attention was formulated. The present work also revealed evidence for an association between oscillatory GBRs and ERPs (Experiment 1). Makeig et al. (2002) recently suggested that ERPs are generated, at least in parts, by a superposition of phase locked activity. In this context, further studies are necessary to clarify the precise relation between oscillatory brain responses and ERPs.

A third main finding regards the relationship between feature binding processes and SA. The order of these two processes has been discussed controversially (Treisman, 1998; Davis and Driver, 1998). The present work yielded evidence for the assumption that early binding processes can initiate an automatic shift of visual spatial attention (Experiment 2). This result suggests that early bottom-up driven processes in feature binding can lead to an automatic shift of visual spatial attention. However, there is also evidence for the assumption that top-down mechanisms affect binding (Robertson, 2003). Further research may investigate possible interactions between bottom-up and top-down modulated processes in feature binding.

To summarize, the present work revealed different electrophysiological and electromagnetic correlates of SA and discussed their practical implications. Furthermore, new evidence for a crucial involvement of gamma activity in very early attentional mechanisms was found. Thereby, phase locking of oscillatory gamma responses seems to play an important role. It can be speculated whether thalamocortical processing might be related to the presented effects. Since the MEG and EEG do not allow to make direct assumptions about these structures, further studies, maybe including single cell recordings, are necessary to investigate the hypothetical relationship between attention, gamma-band activity and thalamocortical processing. Remarkable was also an early functional separation of feature and location processing in the auditory cortex. For the visual modality, a crucial role of fast feedback connections from higher to lower order areas was suggested (Bullier, 2001b). It would be interesting to investigate whether such early feedback mechanisms also exist in the auditory modality. At least a hierarchical organisation of the auditory cortex has been demonstrated before in an fMRI experiment (Wessinger et al., 2001). In general, the present experiments do not cover the whole range of attentional paradigms. However, attention effects in language processing (Friederici et al., 2000), working memory comparisons (Berti and Schröger,

2003), reorienting of attention (Schröger and Wolff, 1998), and novelty detection (Opitz et al., 1999) revealed similar effects on electrophysiological brain responses as reported in the present work. This suggests the existence of more general correlates of attention in the brain. Future research could investigate how these correlates are related to the still open empirical questions raised from the present findings.

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# Abbreviations

| | |
|---|---|
| ANOVA | Analysis of variance |
| ANOVAs | Analyses of variances |
| CIE | Commission International d'Eclairage |
| CNV | Contingent negative variation |
| DLPFC | Dorsolateral prefrontal cortex |
| EEG | Electroencephalography |
| EOG | Electrooculogram |
| EPSP | Excitatory post-synaptic potential |
| ERFs | Event-related fields |
| ERP | Event-related potential |
| ERPs | Event-related potentials |
| FA | False alarm |
| FFT | Fast Fourier Transformation |
| Fig. | Figure |
| fMRI | functional Magnetic Resonance Imaging |
| GBRs | Gamma-band responses |
| HR | Hit rate |
| IPSP | Inhibitory post-synaptic potential |
| LAR | Left anterior region |
| LPR | Left posterior region |
| LGN | Lateral geniculate nucleus |
| MEG | Magnetoencephalography |
| MGN | Medial geniculate nucleus |
| NRT | Nucleus reticularis thalami |
| MRT | Magnetic Resonance Tomography |

RTs     Reaction times
ROI     Region of interest
ROIs    Regions of interest
PET     Positron Positron Emission Tomography
SA      Selective attention
SQUID   Superconducting quantum interference de-
        vice
VLPFC   Ventrolateral prefrontal cortex

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## Selbständigkeitserklärung

Hiermit erkläre ich, daß die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und daß die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Daniel Senkowski

Leipzig, den 5. September 2003

**Dissertationsbezogende bibliographische Daten**

Senkowski, Daniel

NEURONAL CORRELATES OF SELECTIVE ATTENTION: AN INVESTIGATION
OF ELECTROPHYSIOLOGICAL BRAIN RESPONSES IN THE EEG AND MEG

Universität Leipzig, Dissertation

166 Seiten, 331 Literaturangaben, 46 Abbildungen, 1 Tabelle

**Referat**

Für die Orientierung im Alltag braucht der Mensch die Fähigkeit, seine Aufmerk-
samkeit auf relevante Informationen zu richten und gleichzeitig weniger relevante In-
formationen zu ignorieren. Die kognitiven Prozesse, die mit der Steuerung von Auf-
merksamkeit einhergehen, werden unter dem Begriff der *selektiven Aufmerksamkeit*
zusammengefasst. Die Modelle, die sich mit den neuronalen Grundlagen der selek-
tiven Aufmerksamkeit beschäftigen, wie z.B. Theorien zur visuell räumlichen Aufmerk-
samkeit, beziehen sich überwiegend auf ein bestimmtes Paradigma und können daher
lediglich Aussagen mit begrenzter Geltung treffen. Die vorliegende Arbeit beschäftigte
sich hingegen mit paradigmenübergreifenden Mechanismen der selektiven Aufmerk-
samkeit, welche mit Hilfe von Elektroenzephalogramm (EEG) und Magnetoenzephalo-
gramm (MEG) genauer untersucht wurden. Dazu wurden vier verschiedene Experi-
mente durchgeführt, die jeweils einen spezifischen Aspekt der selektiven Aufmerksam-
keit fokussierten.

Experiment 1 beschäftigte sich mit Aufmerksamkeitseffekte in einer visuellen Dis-
kriminationsaufgabe im Zusammenhang mit dem Ressourcenansatz. Dieser Ansatz geht
davon aus, dass Aufmerksamkeit eine limitierte Ressource darstellt und dass aus diesem
Grund nicht alle auf das Wahrnehmungssystem treffenden sensorischen Informationen
aufmerksam verarbeitet werden können. In Experiment 2 wurde der zeitlichen Zusam-
menhang zwischen visuellen Merkmalsbindungsprozessen und Aufmerksamkeit in einer
Hinweisreizaufgabe untersucht. Das 'Zusammenbinden' von verschiedenen Elementen

eines Objektes zu einem einheitlichen Objekt spielt eine wichtige Rolle in der Verarbeitung visueller Informationen. Experiment 3 beschäftigte sich mit Aufmerksamkeitseffekten bei der Verarbeitung von auditorischen Reizen. Ziel dabei war es frühe funktionelle Unterschiede in der Verarbeitung von Objekt- und Rauminformationen in auditorischen Kortexarealen zu untersuchen. In Experiment 4 wurden schießlich frühe Effekten der räumlichen Aufmerksamkeit bei visuellen, auditorischen und audiovisuellen Reizen untersucht.

Die Analyse der EEG und MEG Daten mit unterschiedlichen Auswertungsmethoden zeigte, dass verschiedene paradigmenübergreifender Mechanismen der selektiven Aufmerksamkeit existieren. Ein solcher Mechanismus ist z.B. die Verstärkung von hirnelektrischen Aktivitäten für aufmerksame im Vergleich zu nicht-aufmerksam verarbeiteten Reizen. Weitere Mechanismen sind eine Verzögerung von Aktivierungen im EEG, wenn ein hoher Bedarf an Aufmerksamkeitsressourcen erforderlich ist und eine frühe funktionelle Spezialisierung von Hirnarealen im auditorischen Kortex, die von Aufmerksamkeit abhängig ist. Sehr frühe Effekte in Experiment 4 lassen darüber hinaus eine wichtige Rolle von thalamo-kortikalen Strukturen bei frühen Aufmerksamkeitsprozessen vermuten. Es sind jedoch weitere Studien nötig, um diese Frage genauer zu klären. Dennoch konnte die vorliegende Arbeit zeigen, dass sich allgemeine Mechanismen der Aufmerksamkeit in sehr unterschiedlichen Paradigmen finden lassen.

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